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 cm³, 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, Flores¹. Most of the skeletal elements for LB1 were found in a small area, approximately 500 cm^2 , 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 P₃. 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 $08^{\circ} 31' 50.4''$ south latitude $120^{\circ} 26' 36.9''$ 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 P₃ (LB2) was recovered just below a discomformity 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^{+14}_{-12} 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 P3 with relatively large occlusal surface area, with prominent protoconid and broad talonid, and either bifurcated roots or a mesiodistally compressed Tomes root. Mandibular P4 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 symphysial 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^{2,3}. 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 smallbrained 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 cm³, well below the previously accepted range for the genus Homo⁷ and equal to the minimum estimates for Australopithecus⁸. 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^{9,10} (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 Homo², results in a substantially reduced endocranial volume in comparison to Plio-Pleistocene 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 Australopithecus¹⁰. Compared with Australopithecus and early Homo² the foramen magnum is narrow (21 mm) relative to its length (28 mm), and mastoid processes are thickened mediolaterally 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^{10,11}. 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 hominins¹⁰. 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. erectus¹², 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*¹⁰ 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^{2,3}. 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^{2,3}. The infraorbital fossae are deep with large infraorbital foramina, the orbits have a particularly arched superior border and a volume of 15.5 cm³ (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. erectus¹¹. 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^{2,3}. 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^{3,14} 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_3 and M_2 , 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 M₃. 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. erectus¹⁵. While the mandibular dental arch is narrow anteriorly, and long relative to its breadth, the axis of P₃–M₃ is laterally convex rather than straight (Fig. 4).

The right P_4 is absent and the alveolus completely fused, the left P₄ was lost after death, and CT scans indicate that the maxillary right M³ was congenitally absent. The relatively small and conical alveolus for the missing left M³ suggests that it had a much smaller crown than M¹ and M². Size, spacing and angulation of the maxillary incisor alveoli, and absence of a mesial facet on the canines suggest that incisor I^2 was much smaller than I^1 , 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 P₃ 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 $M1 \ge M2 > M3$. Using the megadontial quotient as a measure of relative tooth size¹⁶, and substituting P₃ crown area for the missing



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.

P₄s, 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 P₃s have a relatively great occlusal surface area (molariform) and when unworn had a prominent protoconid and broad talonid. Both P₃s have bifurcated roots and the alveolus for the left P₄ indicates a mesiodistally compressed, broad Tomes' root. A larger, less worn, isolated left P3 from the deposit (LB2) has a more triangular occlusal outline, and a Tomes' root (Supplementary Fig. 2). Mandibular P₃s and P₄s with similar crown and root morphology have been recorded for Australopithecus and early Homo^{17,18}, and some Indonesian H. erectus mandibular premolars also have bifurcated or Tomes' roots¹⁵. Unusually, both maxillary P⁴s are rotated parallel to the tooth row, a trait that seems to be unrecorded in any other hominin. Maxillary canines and P³s have long roots and very prominent juga. The P³ juga are emphasized by the rotation of the adjacent P^4 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 wide¹⁹; 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 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_{4s} 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 canals²⁰. 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 Homo¹⁹. The neck-head junction is 31.5 mm long, with a shaftneck angle of 130°, and the femur neck is compressed anteroposteriorly (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 size²¹, 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 mm² at the midshaft and 359 mm² 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 Australopithecus²².

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^2), 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 $Homo^{21}$.

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 hominins²³. Broadly speaking, *Australopithecus* and the earliest members of the genus *Homo* are shorter than *H. erectus* and more recent hominins⁸. The maximum femur length of LB1 (280 mm) is just below the smallest recorded for *A. afarensis* (AL-288-1, 281 mm²⁴) and equal to the smallest estimate for the OH 62 *H. habilis* femur (280–404 mm)²¹. Applying stature estimation formulae developed from human pygmies²⁵ 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 mm² gives a mass of 36 kg (Supplementary Information). The brain mass for LB1, calculated from its volume²⁶, is 433.2 g; this gives an encephalization quotient $(EQ)^{27}$ 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^{28,29}. 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 data¹⁹, 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 km² 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



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.

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^{30,31}. 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 cooling³² or reduced rates of internal heat production³⁰. For African pygmies, smaller body size is the result of reduced levels of insulin-like growth factor 1 (IGF-1) throughout the growth period³³, 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^{35,36}. 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^{41,42}. 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 hominins⁴³. 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 size⁴⁴, 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 kyr⁴⁵, 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*^{21,46}, 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^{2,47}. Instead, the facial and dental proportions, post-cranial anatomy consistent with human-like obligate bipedalism⁴⁸,

and a masticatory apparatus most similar in relative size and function to modern humans⁴⁸ 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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Authors contributions P.B. reconstructed the LB1 cranium and was responsible for researching and writing this article, with M.J.M. T.S. directed many aspects of the Liang Bua excavations, including the recovery of the hominin skeleton. M.J.M. and R.P.S. are Principal Investigators and Institutional Counterparts in the ARC project, as well as Co-Directors of the Liang Bua excavations. E.W.S. and Jatmiko assisted T.S., and had prime responsibility for the work in Sector VII. R.A.D. did all of the initial faunal identifications at Liang Bua, including hominin material, and helped clean and conserve it.

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covering approximately 150 years. It was shown that even under the extreme assumption that the Sun was responsible for all the global warming prior to 1970, at the most 30% of the strong warming since then can be of solar origin.

There are 31 periods during which the 10-year averaged sunspot number consistently exceeds a level of 50. The average length of such episodes is about 30 years, the longest being 90 years (around 9000 BC). The distribution of the durations of such episodes is given in Fig. 4a. The number of high-activity periods decreases exponentially with increasing duration. The current level of high solar activity has now already lasted close to 65 years and is marked by the arrow on the figure. This implies that not only is the current state of solar activity unusually high, but also this high level of activity has lasted unusually long. Assuming the previous episodes of high activity to be typical, we can estimate the probability with which the solar activity level will remain above a sunspot number of 50 over the next decades. The result is given in Fig. 4b, which shows that there is only a probability of $8\%^{+3\%}_{-4\%}$ that the current highactivity episode will last another 50 years (and thus reach a total duration of 115 years), while the probability that it will continue until the end of the twenty-first century is below 1%.

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Archaeology and age of a new hominin from Flores in eastern Indonesia

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Excavations at Liang Bua, a large limestone cave on the island of Flores in eastern Indonesia, have yielded evidence for a population of tiny hominins, sufficiently distinct anatomically to be assigned to a new species, Homo floresiensis¹. The finds comprise the cranial and some post-cranial remains of one individual, as well as a premolar from another individual in older deposits. Here we describe their context, implications and the remaining archaeological uncertainties. Dating by radiocarbon (¹⁴C), luminescence, uranium-series and electron spin resonance (ESR) methods indicates that H. floresiensis existed from before 38,000 years ago (kyr) until at least 18 kyr. Associated deposits contain stone artefacts and animal remains, including Komodo dragon and an endemic, dwarfed species of Stegodon. H. floresiensis originated from an early dispersal of Homo erectus (including specimens referred to as Homo ergaster and Homo georgicus)1 that reached Flores, and then survived on this island refuge until relatively recently. It overlapped significantly in time with Homo sapiens in the region^{2,3}, but we do not know if or how the two species interacted.

Liang Bua is a cave formed in Miocene limestone on Flores, an island in eastern Indonesia located midway between the Asian and Australian continents (Fig. 1). The cave is situated 14 km north of Ruteng and 25 km from the north coast, overlooking the Wae Racang river valley at an altitude of 500 m above sea level $(08^{\circ} 31' 50.4'' \text{ S}, 120^{\circ} 26' 36.9'' \text{ E})$. It is 30 m wide and 25 m high at the entrance, and up to 40 m deep (Fig. 2). Formed as an underground cavern by karst dissolution, the northern end was then exposed by invasion of the Wae Racang. This river now lies 200 m distant from and 30 m below Liang Bua, but five river terraces at different elevations in the valley indicate a complex process of incision over a substantial period.

Our research at Liang Bua aims to recover evidence for the history of hominin evolution, dispersal and cultural and environmental change on Flores—an island with evidence of Early Pleistocene hominin occupation by 840 kyr^{4,5}. Work involved removing backfill from four previously excavated Sectors (I, III, IV and VII) and then continuing the excavations. We have reached a maximum depth of 11 m without encountering bedrock.

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Thus far, the most significant find at Liang Bua is a hominin skeleton in Sector VII, close to the east wall. Remains include a skull, mandible, pelvis and leg bones, some of which were still articulated when discovered (Fig. 3), with sufficient distinctive features to be designated a new hominin species, *Homo floresiensis*¹.

Sector VII, 2 m by 2 m in area, was excavated to red clay containing water-rolled boulders at 7.2 m depth (Fig. 4). The skeleton, together with animal remains and stone artefacts, was deposited on a gently sloping surface in dark-brown silty clay at 5.9 m depth, then covered by slope wash sediments. There was no stratigraphic or artefactual evidence for deliberate burial. The overlying layers of clay, silt and rockfall show that this slope was maintained until light-brown and grey ('white') tuffaceous silts settled in the lower, northern part of Sector VII. These tuffaceous silts were derived from volcanic eruptions and occur elsewhere in the cave, providing a useful stratigraphic marker horizon that is bracketed by ages of 13 and 11 calibrated kyr (Supplementary Table 1a) from associated charcoal, using acid-base wet oxidation, stepped-combustion (ABOX-SC) ¹⁴C (refs 6, 7 and Supplementary Information). From 4 m depth to the surface, deposits are horizontally laid and the same stratigraphic sequence extends across the cave floor, indicating a consistent pattern of sediment accumulation.

Radiocarbon and luminescence dating methods were used to infer the age of the hominin remains (Supplementary Table 1a, b), which, given their completeness and degree of articulation, must have been covered by fine sediments soon after death, when still partially fleshed. Three charcoal samples from the lowermost excavated deposits in Sector VII were pretreated and graphitized using the ABOX-SC method, and the ¹⁴C content of the most reliable component was measured by accelerator mass spectrometry. The two samples associated with the skeleton (ANUA-27116 and ANUA-27117) yielded statistically indistinguishable calibrated ages centred on 18 kyr (68% confidence intervals: 18.7–17.9 and 18.2–17.4 cal kyr, respectively).

Luminescence dating of sediments was used to confirm the validity of these ¹⁴C ages; in particular that 'infinitely old' charcoal had not been contaminated by radiocarbon of Holocene age, resulting in the unexpectedly young ages for a hominin skeleton with so many primitive traits. Optical dating^{8,9} of potassium-rich feldspar grains, using the infrared stimulated luminescence (IRSL) emissions, yielded ages of 14 ± 2 (LBS7-40a) and 6.8 ± 0.8 (LBS7-42a) kyr for samples collected above and alongside the skeleton, respectively. Both samples exhibited significant anomalous fading (see Supplementary Information), which will cause the measured ages to be too young, but we could not reliably extend the measured fading rates to geological timescales using available fading-correction models¹⁰. Both IRSL ages, therefore, should be viewed as minimum estimates of the time since the sediments were last exposed to sunlight.

Maximum ages for sediment deposition were obtained using the light-sensitive red thermoluminescence (TL) emissions from grains of quartz^{11,12}. The TL signal is less easily bleached than the IRSL



Figure 1 General location of Flores in eastern Indonesia, and Liang Bua in western Flores.



Figure 2 Plan of Liang Bua showing the locations of the excavated areas (Sectors) and the hominin skeleton (in Sector VII). Father Theodor Verhoeven carried out the first large-scale work at the site in 1965, and R. P. Soejono excavated ten Sectors between 1978 and 1989. Beginning in 2001, we extended the excavations in Sectors I, III, IV and VII.

signal, but does not suffer from anomalous fading. The TL ages for the two samples—38 ± 8 (LBS7-40b) and 35 ± 4 (LBS7-42b) kyr are statistically indistinguishable, supporting our contention that the body was rapidly buried soon after death. The TL and IRSL ages bracket the time of deposition of the hominin-bearing sediments to between 35 ± 4 and 14 ± 2 kyr, which is consistent with the ¹⁴C ages centred on 18 kyr.

Diagnostic evidence for *H. floresiensis* is also found at Liang Bua in deposits of greater age, showing that we are not dealing with an abnormal individual but a long-standing population. At 4.3 m depth in Sector IV, deposits beneath a stratigraphic unconformity yielded a mandibular left premolar with the same distinctive morphology as premolars in the complete hominin mandible from Sector VII. Flowstone stratigraphically overlying the unconformity returned a thermal ionization mass spectrometry (TIMS) uranium-series age of 37.7 ± 0.2 kyr (sample LB-JR-6A/13–23, Supplementary Table 1c), which provides a minimum extension of the time range for *H. floresiensis*.

In addition, a juvenile *Stegodon* molar from 4.5 m depth, just below the isolated hominin premolar, yielded a coupled ESR/ uranium-series age of 74^{+14}_{-12} kyr (sample LB-JR-8a, Supplementary Table 1e). Hominin remains excavated from between this dated level and 7.5 m depth, for which a maximum age of 95 ± 13 kyr for sediment deposition was obtained by TL dating (sample LBS4-32a, Supplementary Table 1b), are not yet species-diagnostic. They include, however, from a depth of 5.8 m, the radius of an adult with an estimated height of about 1 m (ref. 1) that we provisionally assign to *H. floresiensis* because of its size; the holotype lacks arms for direct comparison. If confirmed, this identification would extend the minimum antiquity of *H. floresiensis* to about 74 kyr.

Concerning the behavioural context of *H. floresiensis*, associated small faunal remains include those of fish, frog, snake, tortoise, varanids, birds, rodents and bats. Many are likely to have accumulated through natural processes, but some bones are charred, which is unlikely to have occurred naturally on a bare cave floor.

The only large animals in the Pleistocene deposits are Komodo dragon and another, even larger varanid, as well as an endemic, dwarfed species of *Stegodon*. At least 17 individuals of *Stegodon* are represented in Sector IV, and at least 9 in Sector VII. The extent of

dental wear on *Stegodon* molars also indicates that most individuals were juveniles (Age Group 1 of ref. 13), with 30% (five individuals) in Sector IV being neonates. Adults are only represented by two poorly preserved post-cranial elements and a single molar-ridge fragment. Other large mammals, such as macaque monkey, deer, pig and porcupine, first appear in the overlying Holocene deposits, which lack evidence for *H. floresiensis*. These animals were almost certainly translocated to Flores by *H. sapiens*.

Peistocene deposits in Sector VII contain relatively few stone artefacts; only 32 were found in the same level as the hominin skeleton. In Sector IV, however, dense concentrations of stone artefacts occur in the same level as H. floresiensis-up to 5,500 artefacts per cubic metre. Simple flakes predominate, struck bifacially from small radial cores and mainly on volcanics and chert, but there is also a more formal component found only with evidence of Stegodon, including points, perforators, blades and microblades that were probably hafted as barbs (Fig. 5). In all excavated Sectors, this 'big game' stone artefact technology continues from the oldest cultural deposits, dated from about 95 to 74 kyr, until the disappearance of Stegodon about 12 kyr, immediately below the 'white' tuffaceous silts derived from volcanic eruptions that coincide with the extinction of this species. The juxtaposition of these distinctive stone tools with Stegodon remains suggests that hominins at the site in the Late Pleistocene were selectively hunting juvenile Stegodon.

The chronologies for Sectors IV and VII show that *H. floresiensis* was at the site from before 38 kyr until at least 18 kyr—long after the 55 to 35 kyr time of arrival of *H. sapiens* in the region^{2,3,7,14–18}. None of the hominin remains found in the Pleistocene deposits, however, could be attributed to *H. sapiens*. In the absence of such evidence, we conclude that *H. floresiensis* made the associated stone artefacts.

Stone artefacts produced by much heavier percussion also occur in older deposits at Liang Bua. At the rear of the cave, for example, river-laid conglomerates contain stone artefacts, including a massive chopper. TIMS uranium-series dating of overlying flowstones indicates that these artefacts are older than 102.4 \pm 0.6 kyr (sample LB-JR-10B/3–8, Supplementary Table 1c), but we do not know which hominin species manufactured them.

Further afield, the Soa Basin, which lies 50 km to the east of Liang



Figure 3 Plan of the hominin skeleton as found during excavation of Sector VII at Liang Bua. The relationships between skeletal elements and their proximity to the east and south baulks are shown. The right tibia and fibula were flexed beneath the corresponding femur and patella. Additional skeletal remains, such as the arms, may lie in unexcavated deposits immediately to the south.

letters to nature

Bua, has sites of Early and Middle Pleistocene age, where the remains of Komodo dragon and *Stegodon* occur in association with simple, flaked stone artefacts^{4,5}. It has been assumed that *H. erectus* made these artefacts^{19–21}. The morphological traits of *H. floresiensis* at Liang Bua are consistent with *H. erectus* as an ancestral candidate, but the potential time-depth of hominin occupation of Flores means that, at this stage, we can only speculate as to which species made the Soa Basin artefacts.

Liang Bua provides evidence for distinctive hominins descended from an ancestral *H. erectus* population that survived until at least 18 kyr, overlapping significantly in time with *H. sapiens*. We interpret *H. floresiensis* as a relict lineage that reached, and was then preserved on, a Wallacean island refuge—in the same way that Flores was a refuge for *Stegodon*, the only other large land mammal on the island during the Pleistocene. In isolation, these populations underwent protracted, endemic change; Flores was home to the smallest known species of the genera $Homo^1$ and *Stegodon*¹³.

On present evidence, the genetic and cultural isolation of Flores was only subsequently breached when *H. sapiens* appeared in eastern Asia with watercraft. How a population of tiny, smallbrained hominins then survived for tens of millennia alongside *H. sapiens* remains unclear, as there is currently no evidence for the nature of their interaction; it may have involved little or no



Figure 4 Stratigraphic section of the Sector VII excavation at Liang Bua, showing the location of the hominin skeleton. Layer key: A, coarse silt; B, silt; C–K, coarse silts; L, tuffaceous silt; M, clay; N (a–d), 'white' tuffaceous silts; O, clay and rubble; P, clay; Q, silty clay; R, sandy clay; S, clay with water-rolled volcanic boulders. The circles

enclosing the numbers 40 and 42 indicate the locations of luminescence samples LBS7-40 and LBS7-42, respectively, and the squares enclosing the numbers 5, 6 and 7 denote the locations of ¹⁴C samples ANUA-27115, ANUA-27116 and ANUA-27117, respectively.

direct contact, symbiosis, competition or predation.

The cognitive capabilities of early hominins, however, should not be underestimated, as indicated by the technology of the stone artefacts associated with *H. floresiensis* at Liang Bua. It is also significant that hominins were able to colonize Flores by the Early Pleistocene^{4,5}, whereas the required sea crossings were beyond the dispersal abilities of most other land animals, even during glacial periods of lowered sea level.

Clearly, the history of hominin occupation, evolution and cultural change on Flores, and by implication other Wallacean islands, is of much greater complexity than hitherto believed. For example, Lombok and Sumbawa are obvious stepping-stone islands for the hominin colonization of Flores from continental Asia and Java. If early hominin populations survived long-term on these islands,



Figure 5 Range of stone artefacts associated with remains of *H. floresiensis* and *Stegodon.* **a**, **b**, Macroblades. **c**, Bipolar core. **d**, Perforator. **e**, **f**, Microblades. **g**, Burin core for producing microblades. Arrows indicate position of striking platforms, where knappers detached the flakes from cores by direct percussion using hammerstones.

they would have been subject to the same insular speciation pressures evident in *H. floresiensis*. Size reduction is a predictable evolutionary trend, but other trends will reflect island-specific adaptations, demographic changes and the impacts of catastrophic events, such as volcanic eruptions. \Box

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Author contributions M.J.M., R.P.S. and R.G.R. planned and now co-ordinate the research program funded by the ARC Discovery Project grant, which includes the Liang Bua project. T.S. directed aspects of the excavations and analyses. Ages were provided by R.G.R. and K.E.W. (luminescence); C.S.M.T., M.I.B. and L.K.F. (¹⁴C); W.J.R. (ESR); and J.-x.Z. (uranium-series). R.A.D. and G.D.v.d.B. analysed the faunal remains, and M.W.M. the stone artefacts. D.R.H. supervised the stratigraphic section drawings and other aspects of the project.

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PERSPECTIVES

ANTHROPOLOGY

The Astonishing Micropygmies

Jared Diamond

B y now, every *Science* reader will have read about the discovery of skeletons representing a primitive human micropygmy population that survived until about 18,000 years ago on the Indonesian island of Flores (1, 2). These creatures were barely 3 feet tall, and had an estimated body weight of 20 kg and a brain size of 380 cm³ (smaller than that of a chimpanzee). They seem to be more similar to *Homo erectus* than to *Homo sapiens*, and are thought to

have descended from *H. erectus* independently of *sapiens*' descent from *erectus*. When I first learned of this discovery, I thought it the most astonishing in any field of science within the last decade (see page 2013 of this issue). On reflection, paraphrasing Elizabeth Barrett Browning, let me count the ways in which it is (and is not) astonishing.

In situations like this one, I've found it useful to get the perspective of a green extraterrestrial friend visiting Earth from the Andromeda Nebula. My friend remarked, "Once again, you humans are prisoners of your ingrained species-centric biases. You already know

that large mammals colonizing remote small islands tend to evolve into isolated populations of dwarfs. You have examples of insular pygmy hippos, buffalo, ground sloths, true elephants, stegodont elephants, mammoths, "Irish" elk, red deer, and even dinosaurs. So, now you have 10 examples instead of 9. What's so astonishing? Since when aren't humans subject to natural selection?"

E.T.'s response forced me to reflect. One surprise, I realized, is that we're uncertain exactly which selective pressures do select for insular dwarfs. A favorite theory is ecological release from competition, when a big species reaches an island lacking the mainland suite of smaller related species. According to this argument, the Flores micropygmy would have evolved to occupy a niche of abundant food left vacant by the lack of native apes, monkeys, and other small flightless mammals (except for rodents and a dwarfed elephant) on this island. Another favorite theory is the supposed resource poverty of islands, such that smallbodied animals will be less likely to starve than large-bodied animals. At the level of in-



Island hopping in the Late Pleistocene. The island realm from Southeast Asia to Australia and New Guinea. Solid lines denote the current configuration of land. Brown shading denotes the configuration of land in the Late Pleistocene, when the sea level was about 150 m below its present stand, and when shallow seas on continental shelves now less than 150 m deep were dry land. At that time, Bali and Java were joined to each other and to the Asian mainland, Lombok was joined to Sumbawa, and Flores was joined to Lomblen. However, reaching Flores and Lomblen from Asia still required crossing three narrow water gaps, and reaching Australia from Timor or islands to the east would have required crossing even wider gaps of water. [Adapted from (*6*)]

dividual selection, that argument won't work: Flores and other islands with dwarfed mammals have productivities per hectare at least as high as those of continents. But the argument could work at the level of group selection and could explain the regularly increasing relation between body mass of an island's or continent's top carnivore (or herbivore) and the area of the land mass (*3*). What counts is the island's total productivity rather than its productivity per hectare: An isolated population of 100 full-sized human hunter-gatherers on Flores would have been at a much higher risk of extinction than an isolated population of 700 micropygmies.

E.T.'s blasé reaction then made me think further: Flores is just one of hundreds of islands in its size range, so why weren't there micropygmies on many other islands? The catch is that, for dwarfing to evolve on an island, you need humans just barely capable of reaching the island: If they could reach it too easily, the continuing arrival of full-sized colonists would prevent evolutionary divergence. Once modern H. sapiens developed the technology to reach islands, the resulting insular populations were constantly faced with new arrivals and were no longer isolated. Hence the only examples of effectively isolated insular sapiens populations known to me are from so-called land-bridge islands (like Britain and Japan) formerly connected to adjacent continents at Pleistocene times of low sea level, and isolated around 10,000 years ago when world ice sheets melted and sea levels rose. Some recent sapiens popula-

> tions on those land-bridge islands were descended from ancestors who walked to the island during land-bridge times, lacked watercraft, and thus became completely isolated when the land bridge was severed.

> For instance, the Australian land-bridge island of Tasmania is known to have supported a human population that survived in isolation for 10,000 years after Tasmania became cut off from Australia (4). Tasmania was large enough that full-sized humans are predicted from regression equations (3) to have lived there-and modern Aboriginal Tasmanians were indeed full-

sized. However, the much smaller Australian land-bridge island of Flinders supported a human population that succumbed to isolation only after about 4000 years (5): I am unaware of skeletal remains that indicate whether these humans became reduced in size. Promising locations to search for *erectus* micropygmies are other Indonesian islands besides Flores: surely Lombok and Sumbawa, through which *erectus* colonists from the Asian mainland must have passed to reach Flores; and perhaps Sumba, Timor, Celebes, and others (see the figure). My first bet is on Celebes.

How did the ancestors of the Flores micropygmies, whoever they were, reach Flores? At Pleistocene times of low sea level, the Indonesian island chain of the Greater Sunda Islands was connected to

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the Asian mainland as far east as Java and Bali, but water gaps of 6, 19, and 3 km, respectively, separated Bali from Penida, Penida from Lombok and Sumbawa (joined in the Pleistocene), and Lombok and Sumbawa from Flores and Lomblen (also joined in the Pleistocene) (6). Across each of those water gaps, the island on the far side would have been visible to someone standing on the island on the near side. Hence the micropygmies' ancestors could have colonized the island by sailing toward it in a watercraft (perhaps a rudimentary raft, or a mere floating log), or they could have landed on the island accidentally when their watercraft was swept to sea by ocean currents. Perhaps they even swam to the island. Stegodont elephants reached Flores and Timor and Celebes, and monkeys and buffalo and squirrels also reached Celebes, all surely without making rafts; H. erectus presumably could have as well.

Why haven't remains of erectus-like humans been found in Australia and New Guinea, at the eastern end of the Indonesian island chain? Possibly, for the same reason they weren't found on Flores until 2004; perhaps these humans did reach Australia and New Guinea, but archaeologists just haven't looked hard enough for their remains. I doubt this answer; hundreds of Pleistocene human sites are now known in Australia, with no remains of humans other than those of sapiens. Instead, the answer probably has to do with geography: A modern map plus bathymetric charts show that, even at Pleistocene times of low sea level, a water gap of at least 87 km separated the easternmost Indonesian islands from either Australia or New Guinea, which would not have been visible across that wide gap (6). Such gaps were too wide not only for pre-sapiens humans, but also for stegodonts, monkeys, buffalo, and squirrels, none of which are found in Australia and New Guinea.

The discoverers of the Flores micropygmies conclude that they survived on Flores until at least 18,000 years ago (1, 2). To me, that is the most astonishing finding, even more astonishing than the micropygmies' existence. We know that full-sized H. sapiens reached Australia and New Guinea through Indonesia by 46,000 years ago, that most of the large mammals of Australia then promptly went extinct (probably in part exterminated by H. sapiens), and that the first arrival of behaviorally modern H. sapiens on all other islands and continents in the world was accompanied by similar waves of extinction/extermination. We also know that humans have exterminated competing humans even more assiduously than they have exterminated large nonhuman mammals. How could the micropygmies have survived the onslaught of *H. sapiens*?

One could perhaps seek a parallel in the peaceful modern coexistence of full-sized sapiens and pygmy sapiens in the Congo and Philippines, based on complementary economies, with pygmy hunter-gatherers trading forest products to full-sized sapiens farmers. But full-sized sapiens hunter-gatherers 18,000 years ago would have been much too similar economically to micropygmy hunter-gatherers to permit coexistence based on complementary economies and trade. One could also invoke the continued coexistence of chimpanzees and humans in Africa, based on chimps being economically too different from us to compete (very doubtful for micropygmies), and on chimps being too dangerous to be worth hunting (probably true for micropygmies). Then, one could point to the reported survival of the pygmy stegodont elephants on Flores until 12,000 years ago (1, 2): If stegodonts survived so long in the presence of H. sapiens, why not micropygmies as well? Finally, one might suggest that all of the recent dates for stegodonts and micropygmies on Flores are in error [despite the evidence presented in (1) and (2)], and that both stegodonts and micropygmies became extinct 46,000 years ago within a century of H. sapiens' arrival on Flores. All of these analogies and suggestions strike me as implausible: I just can't conceive of a long temporal overlap of sapiens and erectus, and I am reluctant to believe

that all of the dates in (1) and (2) are wrong. Hence I don't know what to make of the reported coexistence.

At last comes the question that all of us full-sized sapiens wanted to ask but didn't dare: Did full-sized sapiens have sex with micropygmies? The difference in body size would not have been an insuperable obstacle: Some individual modern humans have sex with children or with domestic animals no larger than the micropygmies. I suspect that the answer is the same as the answer to the question of whether we modern humans have sex with chimpanzees. We don't, because chimps are too unlike humans to appeal sexually to most of us, and because chimps are much too strong, unpredictable, and dangerous to make sex a safe proposition for any individual humans who might find them sexually attractive. Ditto for H. erectus, even when dwarfed.

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MATERIALS SCIENCE

Nucleic Acid Nanotechnology

Hao Yan

N ucleic acids are best known as the carriers of genetic information, but they are also a versatile material for designing nanometer-scale structures, because nucleic acid sequences can be designed such that the strands fold into well-defined secondary structures. In 1982, Seeman (1) first proposed using branched DNA building blocks to construct ordered arrays. In recent years, DNA has been shown to be an ideal molecule for building micrometer-scale arrays (2, 3) with nanometer-scale features. DNA can also be used to make nanometer-scale materials with moving parts, such as nanotweezers (4).

Today, two major challenges face nucleic acid–based nanotechnology: to produce complex superstructures from simple molecular building blocks, and to perform controlled mechanical movements in molecular devices. Two reports in this issue describe steps to meet these challenges. On page 2072, Liao and Seeman (5) present a DNA device that can program the synthesis of linear polymers through positional alignment of reactants. And on page 2068, Chworos *et al.* (6) use rationally designed RNA building blocks as jigsaw puzzle pieces that direct pattern formation. The two studies demonstrate that it will be feasible to build functional materials and devices from "designer" nucleic acids.

Nanotechnology researchers have sought to mimic nature's biological motors to create nanometer-scale machines that can function in an engineered environment. Liao and Seeman take an important step in this direction with a device that mimics the translational capabilities of the ribosome. The device consists of two subsections, each with two structural states. Different pairs of DNA "set strands" can be added or removed to bring the device into any one of four states. Each state allows the positional

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before the cap carbonate precipitated. This may explain the lack of a sharp Ir spike at the base of the Sturtian cap carbonate. Alternatively, during the Sturtian glacial epoch, Earth's surface may not have been fully covered with ice on which extraterrestrial material could accumulate for a long time; however, the presence of banded iron formations in and below Sturtian glacials suggests that the ocean was ice-covered at that time (3).

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The Brain of LB1, Homo floresiensis

Dean Falk,¹* Charles Hildebolt,² Kirk Smith,² M. J. Morwood,³ Thomas Sutikna,⁴ Peter Brown,³ Jatmiko,⁴ E. Wayhu Saptomo,⁴ Barry Brunsden,² Fred Prior²

The brain of *Homo floresiensis* was assessed by comparing a virtual endocast from the type specimen (LB1) with endocasts from great apes, *Homo erectus*, *Homo sapiens*, a human pygmy, a human microcephalic, specimen number Sts 5 (*Australopithecus africanus*), and specimen number WT 17000 (*Paranthropus aethiopicus*). Morphometric, allometric, and shape data indicate that LB1 is not a microcephalic or pygmy. LB1's brain/body size ratio scales like that of an australopithecine, but its endocast shape resembles that of *Homo erectus*. LB1 has derived frontal and temporal lobes and a lunate sulcus in a derived position, which are consistent with capabilities for higher cognitive processing.

The type specimen of *Homo floresiensis* (LB1, female) (1) has a brain size of \sim 400 cm³, which is similar to that of *Australopithecus afarensis* specimen AL 288-1 (Lucy) (2), who lived approximately 3.0 million years ago. Yet LB1's species was associated with big-game stone technology, remains of *Stegodon*, and charred animal bones that hint at the use of fire and cooking. Its ancestors also had to cross the sea to reach the Indonesian island of Flores (3). Could a tiny hominin with an ape-sized brain really have engaged in such advanced behaviors? Some workers reject the notion that LB1

represents a new species that was closely tied to *H. erectus* (1) and suggest instead that it was a pathological human microcephalic (4). To help address this debate, we compared threedimensional computed tomographic (3DCT) reconstructions of the internal braincase (virtual endocasts) that reproduce details of external brain morphology, including sulci, vessels, sinuses, cranial capacity, and shape (5-8), from LB1, an adult female chimpanzee, an adult female H. erectus (specimen ZKD XI), a contemporary woman, and a European microcephalic. To broaden taxonomic comparisons and supplement limited sample size, our analysis also included endocasts of the skulls of specimen Sts 5 (A. africanus), specimen KNM-WT 17000 (Paranthropus aethiopicus), 10 humans, 10 gorillas, 18 chimpanzees (9), an adult female pygmy, and five H. erectus.

Our virtual cranial capacity estimate for LB1 is 417 cm³ (10). Virtual endocasts of the microcephalic, modern woman, *H. erectus*, and chimpanzee were scaled to 417 cm³ to facili-

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Supporting Online Material

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tate shape comparisons (Fig. 1 and fig. S2). LB1's shape most resembles that of ZKD XI, which is typical of classic *H. erectus* from China and Java (Trinil) (fig. S3). Both endocasts are noticeably wider caudally than rostrally (Fig. 1A), wider ventrally than dorsally (fig. S2), and relatively long and low in lateral profile (Fig. 1B). However, LB1 lacks the de-





Fig. 1. Comparisons of virtual endocasts of LB1 (center). (A) Dorsal views. (B) Right lateral views. *Hs, H. sapiens; Pt, Pan troglodytes;* mcHs, a human microcephalic; *He, H. erectus*.

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rived occipital expansion over the cerebellum of H. erectus (Fig. 1B), and its endocast is relatively wider (more brachycephalic) (Fig. 1A and fig. S3). LB1's endocast least resembles the microcephalic's (Fig. 1 and fig. S2), which has a pointed frontal lobe, compressed occipital lobe, and flattened posterior end, with the caudalmost poles on the cerebellum. Although our sample includes only one microcephalic endocast, its shape conforms to features of its corresponding skull that typify primary microcephaly (microcephalia vera): small cranial vault relative to face, sloping forehead, and pointed vertex (11, 12). The only

criterion for secondary microcephaly is an occipitofrontal circumference below -2 SD for age and sex (11), but these data are unavailable for LB1's population. Unless a H. erectuslike endocast shape is characteristic of an unrecognized form of secondary microcephaly, we reject the hypothesis that LB1 was a pathological microcephalic (4).

Length, breadth, height, and frontal breadth measurements were collected from endocasts (Table 1 and table S1) and used to generate six ratios (Table 1). In a principal-components analysis, LB1 groups with H. erectus and is separate from H. sapiens, Sts 5 (fig. S4), and

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the pygmy, based on the first principal component (weighted heavily on relative height and the disparity between maximum breadth and frontal breadth), and is separate from H. erectus and the microcephalic in the second principal component (weighted heavily on breadth relative to length) (Fig. 2A). LB1 bears little resemblance to the pygmy (fig. S5). Typically, pygmy skulls are over 1000 cm³ (ours measures 1249 cm³) and resemble those of neighboring humans in shape (13). Unlike LB1, whose brain/body size ratio scales like that of an australopithecine, however, the ratio for pygmies is slightly larger than that found in





Fig. 2. Plots of principal components and key for basal view measurements. (A) Plots of the first three principal components resulting from the analysis of the endocast indices listed in Table 1 [excluding B-FB/H, which was highly correlated with B-FB/L (r = 0.98)]. First, second, and third principal components are aligned along the x, y, and z axes. (B) Plots of the first three principal components resulting from the analysis of basal-view endocast indices listed in table S2. (C) Key for basal view data analyzed in (B) (9). Measurements obtained from basal views were

projected onto the horizontal (basal) plane from endocasts. Landmarks: bat, most anterior point on temporal lobe from basal view; mat, most lateral point on endocast at the level of bat in basal plane; mbat, middle of the line connecting the two bats; rof, the most rostral point on the orbital surfaces of the frontal lobes; cob, caudal boundary of olfactory bulbs (cribriform plate) in the midline; rob, rostral boundary of olfactory bulbs in the midline; bcp, most posterior point on the cerebellum in basal view.

Table	1 . E	ndocast	measurements	(in mm)	of	length,	breadth,	height,	frontal	breadth,	and	resulting	indices.
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	Length	Breadth	Height	Frontal breadth	Breadth/ length	Height/ length	Frontal breadth/ length	(Breadth – frontal breadth)/ length	(Breadth – frontal breadth)/ height	Height/ breadth
Pan troglodytes $(n = 7)$	108.8	88	75.3	72.8	0.81	0.69	0.67	0.14	0.20	0.86
H. sapiens $(n = 7)$	168.0	128.0	122.0	114.0	0.76	0.73	0.68	0.08	0.11	0.95
KNM-WT 17000*	113.4	92.9	72.5	78.1	0.82	0.64	0.69	0.13	0.20	0.78
Sts 5†	119.1	93.5	86.3	85.6	0.79	0.72	0.72	0.07	0.09	0.92
ZKD III (skull E1)‡	158.6	124.5	99.7	91.4	0.78	0.63	0.58	0.21	0.33	0.80
ZKD X (skull LI)	174.6	130.4	114.9	106.7	0.75	0.66	0.61	0.14	0.21	0.88
ZKD XI (skull LII)‡	165.9	127.2	103.7	97.1	0.77	0.63	0.59	0.18	0.29	0.82
ZKD XII (skull LIII)	167.4	128	108.5	97.8	0.76	0.65	0.58	0.18	0.28	0.85
Trinil 2§	156.7	126.9	95	92.5	0.81	0.61	0.59	0.22	0.36	0.75
Microcephalic	89.1	84.4	66.3	63.7	0.95	0.74	0.71	0.23	0.31	0.79
Pygmyll	165.7	123.9	116.9	102.6	0.75	0.71	0.62	0.13	0.18	0.94
LB1	119.6	102.8	81.4	77.7	0.86	0.68	0.65	0.21	0.31	0.79
*Paranthropus aethiopicus.	†A. africai	nus. ‡H. e	rectus (forme	rly <i>Sinanthrop</i>	us, China).	§H. erectus (f	ormerly Pitheca	nthropus, Java).	Computer m	odel, virtua

endocast.

their nonpygmy neighbors, giving their heads a relatively large appearance (14). This is expected because pygmies scale allometrically along ontogenetic curves (15), leading to relatively enlarged heads and brains, as is the case for human youngsters relative to adults (16) (fig. S1). The laws governing allometric scaling of brain/body ratios are powerful and hold within other species of primates (17, 18).

For this reason, and because the morphologies of our endocast samples differ greatly, we do not believe that LB1 represents a human pygmy (19).

A second principal-components analysis was performed on measurements from the base of LB1's endocast and compared to similar measurements from 10 gorillas, 18 chimpanzees, 10 *H. sapiens*, KNM-WT 17000



Fig. 3. Virtual endocast of LB1 (top). Views: (A), left lateral; (B), posterior; (C), right lateral; (D), frontal. Identifications of features are shown on corresponding sketches (bottom) (damaged areas are blackened) as follows: ag, arachnoid granulations; c, frontal lobe convolutions; lb, lambdoid suture; L, lunate sulcus; mv, meningeal vessels; mmv, middle meningeal vessels; oci, inferior occipital sulcus; omv, orbital meningeal vessels; pf, foramen for parietal emissary vein; s, frontal lobe swelling; si, sigmoid sinus; Snd, Sylvian notch and depression; Syl, Sylvian fissure; t, transverse sinus.

(Paranthropus aethiopicus), and Sts 5 (9) (Fig. 2, B and C, and tables S2 and S3). The H. erectus endocasts were excluded because their bases were missing. The first and second principal-components analyses group LB1 exclusively with H. sapiens (Fig. 2B). The first principal component is most heavily weighted on 4/6 and 5/6 (Fig. 2C), which represent the relative projection of the prefrontal cortex rostral to both the anterior and posterior margins of the olfactory bulb. The second principal component is most heavily weighted on 3/6 and (6-3)/6, which represent the relative length of the frontal lobes rostral to the temporal poles and the relative length of the brain caudal to the temporal poles. As in humans, the most anterior sectors of LB1's orbital surfaces are lengthened.

The lambdoid suture is located more rostrally on the left than on the right side of the endocast (Fig. 3). Both the skull and the endocast show a left frontal and right occipital petalia (Fig. 1A) that, in humans, are statistically correlated to some degree with lefthandedness (20). After entering the middle cranial fossa, small anterior branches of the middle meningeal vessels course rostrally across the ventral surface of the right temporal lobe and across the ventrolateral surface on the left. On the right, a branch from another meningeal vessel enters the middle braincase from the orbital region and courses caudally across the temporal lobe inferior to the Svlvian fissure. Similar orbital contributions are common in apes and have been reported for certain H. erectus endocasts by some workers (21) but not others, who used a scoring system for modern humans (22). Traces of meningeal vessels are also reproduced in the right parietal region, and several arachnoid granulations appear near the vertex on the right. LB1 reproduces somewhat (artifactually) distorted transverse and sigmoid sinuses. A cast of the parietal emissary foramen appears near the medial end of the left lambdoid suture.

The right side of LB1's endocast reproduces part of the Sylvian fissure and numerous small sulci on the lateral temporal and dorsolateral frontal lobes (Fig. 3). The right orbital surface reveals three small sulci that do not extend onto the dorsal surface (the left orbital surface is damaged). In the left occipital region, LB1 reproduces an inferior occipital sulcus and a small crescent-shaped lunate sulcus medial to it and caudal to the lambdoid suture. The position of the lunate sulcus is derived and suggests cortical reorganization in the posterior parietal association cortex as compared with apes (2, 23).

LB1's orbital caps are not delimited rostrally by apelike orbitofrontal sulci that incise the borders and course toward the temporal poles on the orbital surfaces (23, 24). Instead, LB1's gyrification, orientation, and relationship of the lateral prefrontal cortex relative to the temporal poles appear derived. Following Connolly (23), we decline to identify rami that border the human pars triangularis (part of Broca's area) on the left, although the general morphology in this region would be consistent with their existence. On the left (and to a lesser extent the right), a distinct Sylvian notch separates the temporal from the frontal lobe and continues caudally as a depression. This region corresponds to a Sylvian crest within the skull of LB1 that, in humans, sometimes occurs in particularly thick skulls and is correlated with Sylvian depressions on endocasts, although the brains are, if anything, more opercularized in the corresponding area (23).

The depression for the superior sagittal sinus on LB1's frontal lobes is bordered laterally by large convolutions [which probably contained additional furrows not reproduced on the endocast (23)] that curve around the rostral tip of the endocast onto the orbital surface and meet at the foramen caecum. Dimples separate these convolutions laterally from swellings that square off the frontal lobes and give their outline a ruffled appearance in dorsal view (Fig. 1A). Although hints of such contours may be seen in chimpanzee and hominin endocasts such as in the no. 2 specimen from Sterkfontein (9), the extent of these expansions in the frontal polar region of LB1 is unusual. This part of the prefrontal cortex in humans and apes consists of Brodmann's area 10, which in humans may be involved in higher cognitive processes such as the undertaking of initiatives and the planning of future activities (25). Human frontal lobes are not larger than expected for apes of similar brain volume (26), but area 10 is both absolutely and relatively enlarged in H. sapiens as compared with apes (25). LB1's polar convolutions appear derived compared with those of H. erectus and other early hominins. Unlike the frontal lobes, human temporal lobes appear to be somewhat larger than expected for an ape brain of human size (26-28); thus, LB1's extremely wide temporal lobes (brachycephaly; fig. S3) may represent another derived feature.

Our data show that LB1's well-convoluted brain could not have been a miniaturized version of the brain of either *H. sapiens* or *H. erectus*. Nevertheless, its similarities with *H. erectus* strongly suggest a phylogenetic connection, although its australopithecine-like brain/body size ratio and morphology of the femur and pelvis (29) are not expected in a miniaturized descendant of a larger-bodied *H. erectus* (which, instead, would be expected to scale allometrically along the ontogenetic curve predicted for *H. erectus*) (fig. S1). Although it is possible that *H. floresiensis* represented an endemic island dwarf that, over time, became subject to unusual allometric constraints, an alternative hypothesis is that *H. erectus* and *H. floresiensis* may have shared a common ancestor that was an unknown small-bodied and small-brained hominin (1).

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Supporting Online Material

www.sciencemag.org/cgi/content/full/1109727/DC1 Materials and Methods

- SOM Text Figs. S1 to S5
- Tables S1 to S3 References

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Vasopressin and Oxytocin Excite Distinct Neuronal Populations in the Central Amygdala

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Vasopressin and oxytocin strongly modulate autonomic fear responses, through mechanisms that are still unclear. We describe how these neuropeptides excite distinct neuronal populations in the central amygdala, which provides the major output of the amygdaloid complex to the autonomic nervous system. We identified these two neuronal populations as part of an inhibitory network, through which vasopressin and oxytocin modulate the integration of excitatory information from the basolateral amygdala and cerebral cortex in opposite manners. Through this network, the expression and endogenous activation of vasopressin and oxytocin receptors may regulate the autonomic expression of fear.

The amygdala plays an important role in anxiety and fear behavior. Fear learning involves its lateral and basolateral parts, where the association between incoming fearful and neutral stimuli leads to potentiation of synaptic transmission. These parts project to the central amygdala (CeA), whose efferents to the hypothalamus and brainstem trigger the autonomic expression of fear (1). Selective gating of synaptic transmission through the CeA could therefore modulate the fear response (2, 3). Indeed, recent studies suggest that increased inhibition within the CeA could underlie the anxiolytic effects of benzodiaze-

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Comment on "The Brain of LB1, Homo floresiensis"

F alk *et al.* (1) presented new data on the 18,000-year-old type specimen LB1 of the dwarf hominin *Homo floresiensis* (2, 3) with regard to cranial capacity and its implications for human evolution. They revised the originally determined brain size of only 380 cm³ (2) measured with mustard seeds) to 417 cm³ [estimated by three-dimensional (3D) computed tomography] and rejected the hypothesis that LB1 was a microcephalic individual (Fig. 1). We disagree with this conclusion and have subsequently analyzed 19 microcephalic modern humans. The corresponding brain volume varies between 280 and 591 cm³, with a mean value of 404 cm³. Thus, the virtual cranial

capacity estimate for *H. floresiensis* is well within the range of variation for microcephalic brain volumes, with the newly determined capacity of LB1 being quite close to the microcephalic mean value. In addition, similarities or phenocopies between LB1 and microcephalic skulls are evident with respect to the supraorbital torus (a ridge on the frontal bone above the eye socket), the postorbital constriction, and the protrusion of incisors.

Within our collection of microcephalic specimens, we focused on an endocast with a cranial capacity of 415 cm³, which is comparable to that of the *H. floresiensis* type specimen. We calculated the same six diagnostic indices indicated for LB1 [see table 1 in (1)] and found that the values for our specimen are nearly identical to those obtained for *H. floresiensis*, which are shown in parentheses: breadth/length = 0.85 (0.86); height/length = 0.68 (0.68); frontal breadth/length = 0.64 (0.65); (breadth minus frontal breadth)/

length = 0.21 (0.21); (breadth minus frontal breadth)/height = 0.31 (0.31); and height/breadth = 0.80 (0.79)

Both skull and brain morphologies of microcephalics are extremely heterogeneous and grossly resemble the anatomy and proportions of *H. floresiensis* (Fig. 2). In microcephalic brains of similar or identical endocranial volume, we observed widely differing index measurements. For example, a 407-cm³ specimen had a frontal breadth/length index of 0.55 and a height/breadth index of 0.74, compared with values of 0.64 and 0.8, respectively, for the 415cm³ microcephalic resembling *H. floresiensis*. Even greater deviations were seen in a pair of endocasts with a volume of \sim 306 cm³, and the indices of one of them resemble those of *Paranthropus aethiopicus* (1). Furthermore, previous studies have noted that brain volume seen in primary microcephaly is comparable to that of early hominids (4, 5).

We also found great variability with regard to the overall microcephalic brain shape, with some specimens showing small frontal and temporal lobes relative to the parietooccipital region and some displaying extremely wide temporal lobes (brachyencephaly). Thus, no typical diagnostic brain shape and convolution pattern was obvious. Therefore, we agree with Thorne [cited in (6)] and others (7) in



Fig. 1. Occipital comparison of size and brain morphology between (A) a microcephalic *H. sapiens*, (B) *H. erectus*, (C) *H. neanderthalensis*, and (D) a normal *H. sapiens*. The brains of microcephalics are as a rule entirely reduced in size, with only the cerebellum sometimes being disproportionately large.

questioning the value of a single microcephalic endocast (1) as the basis to exclude a microcephalic anatomy. Moreover, simple gyrification is believed to be typical for microcephaly. However, in nine brains we observed no simplified gyral patterns, implying that this feature is not pathognomonic for microcephaly (8, 9).

The most convoluted region of the H. floresiensis brain is in the most forwardprojecting part of the frontal lobe (prefrontal cortex). This region, known as Brodmann's area 10, is expanded in modern humans and is involved in undertaking initiatives and planning future actions (10). Because this is believed to be a key component of higher cognition, it has been suggested that the Flores hominids may well have been capable of creating the stone tools that were found near them. However, compared with other brain regions, area 10 is also relatively enlarged in seven of our microcephalic brain specimens. (Five of the seven are shown in Fig. 3.) Generally, the brain function and life expectancy of individuals with microcephaly vary depending on the underlying cause of the condition (11). We know from our records that a male individual with an intracranial volume of 485 cm3 and a prominent area 10 was able to walk but could not speak even a few words or a short sentence. He showed profound mental retardation and, thus, could not plan or perform complex actions. The presence of an unusually prominent area 10 therefore does not necessarily imply advanced cognition. We also stress that brains of both adult microcephalics and healthy humans no longer occupy the entire cranial cavity (11). Therefore,

> deducing correct brain size/proportions from endocasts is widely inaccurate because brain-endocast relations have not been determined yet. Because Falk *et al.* evaluated only one microcephalic endocast (*1*), it is premature to exclude LB1 from any pathological anatomy. Analysis of other skulls from the Indonesian island of Flores will help address the correct taxonomy of the small-brained hominid.

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10 cm

Fig. 3. Exemplary frontal views of the prominent Brodmann's area 10 (with or without depression) in five microcephalic individuals. Note the degree of morphological variability in microcephalics. All of the microcephaly patients were profoundly or severely mentally retarded.

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

Weber *et al.* (1) focus on one specimen of 19 microcephalics that they analyzed and provide six indices that, indeed, are essentially identical to those of LB1 (2). Unfortunately, Weber et al. failed to provide the length, breadth, height, and frontal breadth measurements used to calculate these indices, and we are unable to derive these values from the indices, which can be reduced to three unique equations with four unknowns (i.e., the model is underspecified). One would expect this microcephalic's endocast to closely resemble that of LB1, but it remains unclear whether any of the images shown in (1) include views of this key specimen. Figure 2 in (1) supposedly provides four views of one modern microcephalic endocast, but the view in figure 2A has a pronounced frontal lobe rostrum ("beak") not seen in the view in figure 2D, and we do not believe these images represent the same individual. We also note another concern: Lateral hemispheres are traditionally oriented so that the line that connects the frontal pole (FP) with the occipital pole (OP) is horizontal, and its length represents that of the endocast (3). From the orientations of the endocast(s) in figure 2 in (1), we suspect that Weber *et al.* did not observe this convention and, further, may have measured endocast length using a nontraditional caudal landmark on the cerebellum rather than the OP on the cerebrum. Fortunately, a clear transverse and sigmoid sinus that separates the cerebrum above from the cerebellum caudally appears on their microcephalic endocast, which resembles our microcephalic in having a flattened, posteriorly placed cerebellum compared with LB1, for which the cerebellum is underneath the occipital lobes (the normal condition for Homo) (Fig. 1D).

Weber *et al.* assert that seven of their microcephalic endocasts have a relatively ex-

panded Brodmann's area 10 similar to LB1, but none of the five microcephalic endocasts in their figure 3 reproduce the two distinct, enlarged convolutions seen in the region of area 10 in LB1 (arrows, Fig. 1A). Contrary to Weber et al., normal gyral patterns are believed to be typical of true microcephalics, whereas simple gyrification typifies some kinds of secondary microcephaly (4, 5). LB1 is estimated to have been an ~30-year-old female, an age by which 78% of female microcephalics have died (6). Brain weight in microcephalics reaches its maximum in early childhood and thereafter reduces throughout adulthood, which results in the brains of elderly microcephalics fitting loosely within their crania (6). To a lesser degree, brains of normal people also shrink with advanced age, which accounts for the relatively poor reproduction of convolutions on their endocasts compared with younger individuals (3), as is typical for other anthropoids (7). For these reasons, one would not expect to obtain a highly convoluted endocast like LB1's from the braincase of a 30year-old female microcephalic.

We stress that it is important to use similar landmarks when comparing indices obtained by different workers, and we do not believe this was done by Weber et al. If one of their specimens is virtually identical to LB1 in shape as they assert, they should provide its absolute measurements, illustrate its various views (in conventional orientations) compared with LB1, and clearly delineate the separation of cerebrum from cerebellum. We have done the best we can to reply to this commentary without this information. Meanwhile, Fig. 1 suggests that Weber et al.'s microcephalic endocast(s?) resembles the one we studied, which is markedly different from that of LB1. If this is the best evidence that can be produced from

a sample of 19 microcephalics, we suggest that the authors reconsider their position on the microcephalic hypothesis regarding *Homo floresiensis*.

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Fig. 1. Endocasts, from left to right, of a microcephalic we described (2), microcephalic(s) described by Weber *et al.* (1), and LB1 (2). Views: (A) frontal; (B) posterior; (C) dorsal; (D) right lateral. Blue images are virtual endocasts (2); images are scaled to approximately the same size to facilitate shape comparison. The brainstem was used to align the lateral views. FP, frontal pole; OP, occipital pole; S, sigmoid sinus; T, transverse sinus. Stippled areas represent the cerebellum. Arrows in top row point to two distinct convolutions on the frontal lobe of LB1 that are not seen on the two microcephalics. The lateral view provided by Weber *et al.* (D, middle) appears truncated on the inferior surface of its frontal lobe, contrary to the frontal view (A, middle), which points down in the region of the olfactory bulbs. The outlines in the frontal and posterior views of our microcephalic's endocast are similar, which is also true for LB1 but not for the Weber *et al.* (see their caption for Figure 2). Arrows in the bottom row identify the superior margin of the transverse sinus. The occipital pole of the cerebrum of Weber *et al.*'s microcephalic must be rostral to the arrow (i.e., to its right), as is the case for our microcephalic on the left (2). Contrary to these microcephalics, OP in nonpathologic *Homo* (including LB1 on the right) protrudes farther back than the caudal pole of the cerebellum.

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 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 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 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 plasmamass 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 peglike, 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 highfunctioning 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 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

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 and	cestral 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	Model C Intraspecific scaling for <i>Homo sapiens</i> : combined sexes, males, females				
Homo erectus broadly defined	60	991	3.5-4.5	1.6	0.3, 0.007, <0.001				
Ngandong Homo erectus	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				

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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



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 halfskull 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.

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

Dean Falk,^{1*} Charles Hildebolt,² Kirk Smith,² M. J. Morwood,³ Thomas Sutikna,⁴ Jatmiko,⁴ E. Wayhu Saptomo,⁴ Barry Brunsden,² Fred Prior²

Martin *et al.* claim that they have two endocasts from microcephalics that appear similar to that of LB1, *Homo floresiensis*. However, the line drawings they present as evidence lack details about the transverse sinuses, cerebellum, and cerebral poles. Comparative measurements, actual photographs, and sketches that identify key features are needed to draw meaningful conclusions about Martin *et al.*'s assertions.

artin *et al.*'s (1) efforts to show that LB1's cranial capacity cannot be attributed to intraspecific dwarfing in *Homo erectus* suggest that Falk *et al.* (2) claimed otherwise. However, Falk *et al.* documented that LB1's cranial capacity is too small to be attributed to normal dwarfing of *H. erectus* and further showed that its relative brain size is consistent with those of apes/australopithecines (Fig. 1). It would therefore be surprising if LB1's relative brain size scaled like a dwarfed elephant, for example, leading us to question the aptness of table 1 and figure 1 presented by Martin *et al.*

As noted in (2), the virtual endocast of the microcephalic in question was prepared from a skull cast reposited in the American Museum of Natural History (AMNH), and Falk *et al.* scaled the virtual endocasts of all comparative specimens to match LB1's volume (417 cm³) to facilitate shape comparisons. We have since reanalyzed the CT data and determined a capacity of 276 cm³ for the microcephalic (*3*). Although the AMNH was unable to provide a recorded age for the microcephalic, its anomalous teeth suggested to us that that it might be a juvenile, and we are happy to learn that it is, in fact, from a 10-year-old male.

Contrary to Martin *et al.*, we did not assume that there is only one type of primary microcephaly, as detailed in the text of our supporting online material (2). Martin *et al.* claim that there are more than 400 genetic syndromes associated with primary microcephaly that "typically have autosomal recessive inheritance." This conflicts with our reading of the literature. Rather than being associated with primary microcephaly, small head size "defined as an occipitofrontal circumference that is at or below –2 standard deviations (SD) at birth...constitutes a feature found in more than 400 genetic syndromes" (4), and these 400 syndromes are not portrayed as generally uniform nor of known genetic inheritance (4). Our more restrictive definition of microcephaly (2) is therefore warranted, especially in discussions pertaining to LB1, because adult primary microcephalics typically have a brain volume of about 400 cm³ (4).

Martin *et al.* further argue that because LB1 was an adult, comparison with microcephalics should focus on high-functioning types (which can survive to adulthood) and that Jakob



Fig. 1. Cranial capacity in cubic centimeters as a percentage of body weight in grams (RBS, relative brain size) plotted against body weight (kg) for humans and apes (10). Indices (i) describe apelike RBS (i = 1) and RBS that are twice (i = 2) and three times (i = 3) those expected for apes of equivalent body weights. Congo pygmies are placed on the human curve at their mean body weights of 42 kg and 48 kg for 319 women and 405 men, respectively (11). The curve for *H. erectus* is hypothetical because it is based on data showing that i = 2 from only one available skeleton (KNM-WT 15000). Estimated juvenile and adult weights for WT 15000 are 48 kg and 68 kg, respectively (12). LB1's cranial capacities are 880 and 909 cm³, respectively (12). LB1's cranial capacity of 417 cm³ places it on or near the ape curve at its minimum, mean, and maximum body weight estimates (16 to 36 kg, mean 26 kg) (9), which is consistent with data from australopithecines. Figure and legend from figure S1 in (2).

Moegele's early death renders comparison inappropriate. On the contrary, "early death" in low-functioning microcephalics is defined as "death that typically occurs within the first several years of life" [table 1 in (4)]. Because Jakob Moegele lived to be 10, one cannot rule out that he may have been a high-functioning primary microcephalic. Martin et al. were indeed fortunate to locate a 32-year-old female microcephalic, because by that age 78% of female microcephalics are estimated to have died (5). Because of brain shrinkage, one would also not expect to obtain a highly convoluted endocast (like LB1's) from such a specimen (5, 6), and we gather from the lack of detail on Martin et al.'s line drawings that neither of their microcephalics reproduced endocasts that are highly convoluted. As illustrated in (6), Jakob Moegele's virtual endocast is shaped remarkably like that of endocasts from other microcephalics, rather than like that from LB1 as claimed (7), and we are glad to have a microcephalic specimen of its size and age in the sample of microcephalics that we are currently investigating.

The weight of Martin *et al.*'s comment is their assertion that they have identified one hemicast and one complete endocast from microcephalics that appear similar to LB1's. However, the line drawings they provide lack crucial details about the transverse sinuses and

frontal and occipital poles [figure 2 in (I)]. Although the authors provide a line drawing for LB1's skull, no image is provided for its endocast. A line drawing is provided for an endocast of a microcephalic from the Field Museum, but not for its skull, which, as described (and illustrated in actual photographs) in the reference cited by Martin et al., "is longheaded and narrow, with a lowly vault, the face narrow, with apelike protrusion of the jaws" (8). This skull differs starkly from LB1's, which is extremely brachycephalic (2, 9). Providing drawings of one hemicast and one endocast from microcephalics and asserting that they look like the virtual endocast from LB1 without illustrating the latter is therefore inadequate.

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Comparative measurements along with actual photographs of the microcephalic hemicast and endocast should be compared with published images of LB1's endocast in frontal, occipital, lateral, and dorsal views (2) and accompanied by corresponding sketches that identify key features, such as the transverse sinuses and cerebellum, similar to Falk *et al.* (2, 6). Without this evidence, the assertions of Martin *et al.* remain unsubstantiated and difficult to address in further detail.

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SCIENCE SCOPE

PALEOANTHROPOLOGY

Tools Link Indonesian 'Hobbits' to Earlier *Homo* Ancestor

The battle of the hobbits is heating up. Two weeks ago, skeptics argued that fossils found on the island of Flores in Indonesia were simply diseased modern humans (www. sciencemag.org/cgi/content/full/312/5776/999b) rather than a dwarf species evolved from an early *Homo* ancestor, as its discoverers had claimed. Now the discovery team fires back. In this week's issue of *Nature*, they argue that stone tools associated with *Homo floresiensis* resemble newly discovered tools from a much more ancient nearby site, suggesting cultural continuity over hundreds of thousands of years.

The tool data "establish an independent source of evidence linking late Pleistocene *Homo floresiensis* with an early Pleistocene progenitor," says Russell Ciochon of the University of Iowa in Iowa City. But some caution that the tools are so simple that inferences of cultural continuity may not be warranted, and a few skeptics question the dates.

The ancient tools come from Mata Menge, 50 kilometers from the Liang Bua cave on Flores where *H. floresiensis* bones and tools were found by an Indonesian-Australian team including Michael Morwood of the University of New England (UNE) in Armidale, Australia. Researchers had previously uncovered stone tools at Mata Menge and dated the artifact-bearing layers to between 800,000 and 880,000 years ago using fission-track dating on volcanic tuffs.

In 2004 and 2005, Fachroel Aziz of the Geological Research and Development Centre in Bandung re-excavated Mata Menge and invited Australian colleagues including Morwood and first author Adam Brumm of Australian National University in Canberra. They found a bonanza of artifacts: 507 small, well-shaped pieces made from volcanic cobbles, with a few chert pieces.

The team then compared the Mata Menge tools to the much younger artifacts from the Liang Bua cave, dated from 95,000 to 12,000 years ago—and found a match in both the types of artifacts and the methods used to create them. At both sites, hominids produced elongated flakes by rotating cores and striking downward; they also created "perforators," pointed tools with retouched edges. "All of the techniques at Mata Menge are also at Liang Bua," says co-author Mark Moore of UNE. "These are quite common approaches to reducing stone."

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MARK MOORE/UNIVERSITY

CREDIT

They are also simple approaches. That's in contrast to the team's original publication, which described a few Liang Bua tools as much more sophisticated. That led some researchers to claim that the tools must have been made by modern humans, not a hominid with a brain the size of a grapefruit. But Moore now says that although some elongated flakes resemble "blades" used by modern humans, that may simply be coincidence. Richard Potts of the Smithsonian Institution in Washington, D.C., agrees: "Yes, [the Liang Bua hominids] are making what people have called 'blades,' but that doesn't imply that you have to have a certain number of neurons," he says. Morwood is more emphatic: "Some of our critics have claimed that these Liang Bua artifacts are so



Toolmaking tradition? Tools from an ancient site on Flores (*top row*), including a "perforator" (*left column*), resemble those found near hobbit bones (*bottom*).

sophisticated that they must have been made by modern humans. The [new] evidence shows that the basis of that argument is just plain wrong."

Morwood adds that the team now considers the hobbits' most likely ancestor to be a small early *Homo* species, smaller than the classic *H. erectus* found in nearby Java but perhaps similar to fossils found in Africa and Dmanisi, Georgia.

However, Kathy Schick and Nicholas Toth, knapping experts at Indiana University, Bloomington, caution that the technology is so simple that different kinds of hominids might converge upon it. And James Phillips of the University of Illinois, Chicago, a co-author of the critique published in *Science*, thinks that the tools may be out of sequence.

Morwood points out that many hominid species were first greeted with skepticism. The type specimen of *H. erectus*—uncovered in 1891 on Java—was described at the time as a "microcephalic idiot, of an unusually elongated type," in a review in *Nature*. **–ELIZABETH CULOTTA**

New Archaeology Fund

A new grants program for young archaeologists in Indonesia and East Timor has made its first awards, notwithstanding the current devastation and turmoil in the archipelago. A three-person team from Makassar, Indonesia, and an archaeologist from Yogyakarta, the ancient city near the recent quake's epicenter, will each receive \$3800 for prehistory research from the Anthony F. Granucci Fund. The fund is endowed from the estate of the late lawyer, who had a passion for Indonesian culture.

"Most students [in the region] are forced to work on government-sponsored projects designed by someone else," says archaeologist John Miksic of the National University of Singapore. He says the grants "should lead to a lot more innovative research topics and strategies" by encouraging students to pursue their own ideas.

-RICHARD STONE

A Climate of Change?

Although they aren't likely to pass any legislation this year related to climate change, U.S. lawmakers seem to be warming to the issue. Senator James Inhofe (R-OK), despite viewing controls as a "hoax" based on the "supposed threat of global warming," last week convened a closed meeting that included oil and gas business leaders and environmentalists to promote "a better understanding of the technologies that drive emission reductions." Inhofe chairs the Environment and Public Works Committee. The same day, the Senate Foreign Relations Committee called on the government to reengage in the United Nations Framework Convention on Climate Change process with an eye toward "minimiz[ing] the cost."

Supporters of climate change measures also noted three other developments last week. The Government Accountability Office, the watchdog for Congress, reported that federal voluntary carbon-cutting programs touted by the Bush Administration account for less than one-half of U.S. emissions, and that there are few administrative controls to track company participation. A poll found that 70% of a national sample of hunters and sport fishers believe that warming poses a "serious threat" to humans. "There's a shift going on in ... the political dialogue," says David Doniger of the Natural Resources Defense Council. He and other activists also hope for a boost from An Inconvenient Truth, a documentary on former vice president Al Gore's antiwarming crusade.

-ELI KINTISCH

Pygmoid Australomelanesian *Homo sapiens* skeletal remains from Liang Bua, Flores: Population affinities and pathological abnormalities

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Contributed by K. Hsü, July 7, 2006

Liang Bua 1 (LB1) exhibits marked craniofacial and postcranial asymmetries and other indicators of abnormal growth and development. Anomalies aside, 140 cranial features place LB1 within modern human ranges of variation, resembling Australomelanesian populations. Mandibular and dental features of LB1 and LB6/1 either show no substantial deviation from modern *Homo sapiens* or share features (receding chins and rotated premolars) with Rampasasa pygmies now living near Liang Bua Cave. We propose that LB1 is drawn from an earlier pygmy *H. sapiens* population but individually shows signs of a developmental abnormality, including microcephaly. Additional mandibular and postcranial remains from the site share small body size but not microcephaly.

Indonesia | microcephaly | skeletal pathology | asymmetry | dentition

n 2004, skeletal material from the Indonesian island of Flores was described (1) as the holotype of a new hominin taxon, Homo floresiensis. It comprised one fairly complete adult skeleton, Liang Bua 1 (LB1), plus an isolated lower left third premolar (P₃) (LB2). Estimated from LB1 were notably low values for stature (1.06 m) and endocranial volume (380 ml), the latter trait all the more remarkable for its association with advanced microblade tools (2). This single individual's traits came to characterize broadly a new species. Other skeletal and dental traits reported as unusual were used to define a taxon that "... combines a mosaic of primitive, unique and derived features not recorded for any other hominin" (1). Additional skeletal remains described 1 year later (3) included not a single fragment of braincase, but it was incorrectly maintained that there are multiple individuals sharing LB1's traits (3). The second mandible (LB6/1) shows no traits that are unknown among modern Australomelanesians, and only some limb bones resembled LB1. There is no support for exceedingly small brain size, the focal characteristic of the postulated new species.

H. floresiensis is maintained to be distinct from the two human taxa recognized in the surrounding region, *Homo erectus* and *Homo sapiens*, interpreted by some as temporal subdivisions of one widely dispersed evolutionary species (4–6). *H. erectus* previously was held to have reached the island \approx 840,000 years ago (840 ka), on the basis of Middle Pleistocene stone tools found on Flores (7, 8), remaining totally isolated while giving rise to *H. floresiensis*. Genetic isolation from other hominin populations is a necessary postulate, because prolonged isolation is needed to attain the requisite level of taxonomic distinctiveness (9).

This scenario was disseminated widely and endorsed (10) without critical examination of contradictions inherent in the data. It raises a number of questions. If brain sizes smaller than average for chimpanzees were normal for the new species, how were these hominins able to manufacture stone microblades postulated to have been hafted as compound tools (2), previously known to have been crafted only by humans with brain sizes three times larger? How could such tools, convergent in detail with those made by *H. sapiens* elsewhere but similar only in broad commonalities to earlier tools on Flores (11), not raise the question of contact between populations? How likely was it that Flores was reached by hominins only once during >800 ka?

Most importantly, premature elaboration of speculative evolutionary scenarios diverted attention from detailed study of the morphological characteristics of the specimens themselves. All but lost was any realization that the species diagnosis that had attracted so much attention centered on a single, distinctly odd, individual. Although LB1 exhibits a very small skull and numerous anomalies, other skeletons that also exhibited serious abnormalities (12) were not used to establish new species, a point implicit in our initial publication on LB1 (13), which cited 10 examples of microcephalic skeletons from the Upper Pleistocene and Holocene (14, 15, ‡‡). Other Liang Bua Cave bones described later merely (3) confirm general body size and unremarkable anatomical similarities.

The notion of a new, long-enduring species of humans raises problems concerning the supposed isolation of a taxon of large mammals. Assuming Flores was colonized by a founding cohort of a few *H. erectus* individuals who reached the island by crossing a water barrier only once, descendants would have comprised a highly inbred isolate, with the adaptive constraints implied by that consequently narrow gene pool. Confounding this problem is the question of whether the land area of a single island, Flores, was sufficient to support a hunter–gatherer population for some 40,000 generations. Furthermore, if this population had been isolated genetically up until the very recent past, how can identical anatomical features shared by members of the putative new taxon and subsequent *H. sapiens* be explained? Alternatively, if contact and interbreeding did occur, how could separate species status for *H. floresiensis* be justified?

Because of these questions raised by published descriptions of the holotype specimen, the initial diagnosis was challenged with an alternative hypothesis that LB1 exhibited abnormal morphological signs indicative of microcephaly (13, 17). These signs occurred in an individual sampled from a *H. sapiens* group that was small in

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Abbreviations: Liang Bua 1, LB1; ka, thousand years ago; $\mathsf{P}_3,$ lower third premolar; $\mathsf{P}_4,$ lower fourth premolar.

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stature,^{§§} as still common on Flores today. Several of the publications (18-20) supporting microcephaly subsequent to our own (13) have been contested (21, 22).

From the beginning, the "H. floresiensis discovery" was treated as a matter of hominin taxonomy and phylogeny. Curiously, however, comparisons of LB1 were made mostly with H. sapiens from other geographic areas of the world, principally Europe. Yet it would have been more appropriate for a supposedly novel human species from the Australomelanesian region to have been compared with other human populations, present as well as past, from that region. Therefore, in contrast to erecting a new species (1, 21, 22), we consider the alternative hypothesis that LB1 was an Australomelanesian H. sapiens who manifested microcephaly, which commonly is accompanied by other developmental abnormalities. This hypothesis is testable by comparing the Liang Bua remains with extant Australomelanesian H. sapiens populations to assess whether its complex of normal characters conforms to regional patterns, while also documenting cranial and other skeletal features of LB1 that are developmentally abnormal.

Following the initial reports in 2004 (1, 2), the Indonesian chief investigator (R.P.S.) of the original research team asked T.J. to restudy the bones, who in turn invited several of the other authors (E.I., R.B.E., M.H., and A.T.) to join him. We present results of our examination of the original skeletal material, plus previously unreported data from an appropriate living reference population, beginning with an alternate interpretation of Flores' paleogeography.

Evidence Against a New Species

Demography, Continuity, and Isolation. For nearly 4 decades, archeological evidence suggested early human presence on Flores, with stone tools reportedly associated with bones of Stegodon estimated to have lived \approx 750 ka (23). Additional debated findings extend this date to \approx 840 ka (8, 24). If correct, these reports place humans on Flores by the latter half of the Quaternary. To support the hypothesis that H. floresiensis evolved in extended isolation there, it is necessary to prove that island was reached once and only once, as contended (2), yet in numbers large enough to embody genetic diversity sufficient to establish a new mammalian species (25) within a relatively short period, then maintain a viable population for some 40,000 human generations in a restricted land area. Such restrictions are not supported by the data for elephant colonization of Flores, because stegodons reached the island at least twice during repeated Pleistocene sea-level oscillations (26). Given this evidence, the premise that humans must have been limited to a single colonization event (2) is unjustifiable.

Global cooling leading to Northern Hemisphere continental glaciation started at the beginning of the Pleistocene, 2 million years ago. Oxygen-isotope studies of deep sea cores indicate more extreme variations, starting with large ice volumes 600-900 ka (27, 28). That time range encompassed lower sea levels, reducing odds against early hominins crossing narrowed seaways beyond Java. Later glaciations also were intense, with >30 glacial and interglacial stages during the last 700 ka. Continental glaciation reached its maximum extent during Isotope Stage 2 of 18 ka, just before the deglaciation leading to the present high-sea-level strand (Isotope Stage 1).

During the glacial stages, water gaps between islands were reduced by lowering global sea-level due to increase of polar ice-volumes documented by isotope studies. At glacial maxima, Bali was contiguous with Java, and a transient unitary land mass connected Sumbawa through Komodo and Rinca to Flores, leaving water gaps of just several kilometers on either side of Lombok (29). Assuming that the earliest hominins reached Flores during the first intense glacial stage \approx 750 ka, there could have been numerous hominin arrivals during later glacial stages with low sea levels, before the final higher sea levels at the beginning of the Holocene (10 ka) again might have constrained contacts. These environmental perturbations replicate on a more limited scale events that occurred elsewhere when various geological phenomena transformed the Mediterranean Sea into a desert and back to a massive body of water (30), with consequent effects on mammalian faunas.

Although today the 14,200-km² island of Flores has a population of >3.5 million people, this small land mass, even if entirely suitable for human habitation, would have been capable of supporting far fewer humans at a hunting–gathering subsistence level. Conventional figures of 1 person per 25–2.5 km² would yield one-generation total census population sizes (*N*) of 570 to 5,700 people and much lower effective population (*N_e*) sizes (31). These figures are below minima estimated (5,816–7,316 adults) for survival of vertebrate populations over 40 generations (32), which is 0.001 of the term posited for human isolation on Flores (2). An alternative approach (33) using home ranges rather than *N* or *N_e* (34, 35) yields similar results.

Reduction in size on Flores is unsurprising in an ecosystem characterized by a humid climate, hilly topography, and abundant undergrowth of vegetation. Maintenance of body temperature alone can be a sufficient selective factor for small body size in such surroundings. Selection need only be sufficient to overcome limited levels of gene flow expected on an island separated by stretches of water constituting just filter barriers. Many of the surrounding regions (Peninsular Malaysia, the Andaman Islands, Sumatra, Java, Sulawesi, Papua, and Northern Australia) include populations relatively short in stature (e.g., ref. 36). Diminutive body size does not in itself constitute convincing evidence for either isolation or speciation, because size fluctuations occur repeatedly in mammalian, including human, lineages. In living African pygmies, for example, spatial and genetic isolation manifestly is incomplete (37).

On Flores, there were two separate *Stegodon* invasions, minimal distances from islands occupied by other human populations, a low probability that colonization by an original founder group provided sufficient genetic diversity for adaptation over tens of thousands of generations, and insufficient resources available for sustaining in isolation an adequate effective population size of hunter–gatherers. These are strong arguments against the evolution *in situ* of a new hominin species.

Neurocranium and Face. Considerable damage was done during excavation to the LB1 neurocranium, face, and mandible. Later, when the specimen was disassembled and reconstructed, the skull surface was heavily varnished (1), obscuring some details. However, despite these problems, many anatomical features are clear.

Aside from abnormalities discussed below, not one of the 94 descriptive features of the LB1 cranium or the 46 features observed on both mandibles (see Table 1, which is published as supporting information on the PNAS web site) lie outside the range for modern humans (38–41) from the region. The form of the superciliary area, nasal floor, subnasal region, orbits, and occipital superstructures of LB1 all are encountered routinely among Australomelanesians. Other neurocranial features, excluding small size, asymmetry, and damage (see Supporting Text, which is published as supporting information on the PNAS web site), also lie within the range of Australomelanesians. Purportedly (1), the LB1 cranium displays two skeletal features "not seen in modern humans." In one, "a deep fissure separates the mastoid process from the petrous crest of the tympanic" bone. The other is "a recess between the tympanic plate and the entoglenoid pyramid" on the medial part of the mandibular fossa (1). Australian and Tasmanian crania commonly display both of these features (39–41). The latter trait also is present in two Pleistocene Australians, Kow Swamp 5, and, in a reduced form, Keilor (42).

^{§§}Eckhardt, R. B., Kuperavage, A., Sommer, H. J., Jr., & Galik, K. (2005) Poster presented at the International Society of Biomechanics XXth Congress/American Society of Biomechanics 29th Annual Meeting, Cleveland, OH, August 2, 2005.



Fig. 1. Absence of external chin is common in Australomelanesian populations. Here we show Rampasasa individual No. 26, who lacks a chin. Our work on the Rampasasa population determined that 93.4% of the sample have neutral (flat) or negative chins. Absence of a chin cannot be a valid taxonomic character for the Liang Bua mandibles. (Photograph is by E.I.)

Absence of a true chin has been listed as a distinguishing feature (1, 3), but our observations on the Rampasasa population determined that 93.4% of these people have neutral (flat) or negative chins (Fig. 1). It is not valid to contend that chin absence is a taxonomic character in separating the LB hominins from *H. sapiens*. Finally, mandibular size is not a valid criterion. For example, of five partial mandibles from Klasies River Mouth (KRM), three clearly are smaller than LB1 and LB6/1 (43). One KRM mandible is $\approx 66\%$ of the size of LB6/1, yet virtually all researchers regard the KRM sample as *H. sapiens*. Overall, the Liang Bua sample is characterized by many features that, rather than being unique, are widespread human structural polymorphisms.

An unarguable feature of LB1 is its small brain coupled with a short stature. Compared with our Rampasasa sample, with average cranial capacities of 1,198 ml (n = 41) for females, 1,354 ml (n = 35) for males, and 1,270 ml for the combined sex sample, LB1's cranial capacity directly measured using seed displacement was 430 ml. This volume is slightly higher than other published estimates, but we removed from the endocranial surface some breccia that had lowered earlier estimates. Comparatively, LB1 falls 5.5 SD below the combined sex Rampasasa mean, whereas our estimate for stature^{§§} falls 3.3 SD below Rampasasa average stature of 1.46 m. A similar ratio characterizes some families of microcephalics. For example, Burton (44) found individuals in three successive generations with head circumferences some 6 SD below normal population means and statures 3–5 SD below average in this lineage.

Microcephaly is clinically heterogeneous, with numerous syndromes in which very small brain size is but one sign. Causes of microcephaly range from defects at known genetic loci to numerous chromosomal and environmental disturbances that can affect prenatal or postnatal development. Review of 184 syndromes in which microcephaly is one sign (45) shows body size reduction commonly is another: 57 are identified explicitly as exhibiting short stature. Associated signs include facial asymmetry and dental anomalies, as well as trunk/limb disproportions, overtubulated bones, and signs of paresis in the postcranial skeleton (45). Another indication of abnormality is the advanced suture closure in LB1. As described originally (1) and confirmed by us, "[w]ith the exception of the squamous suture, most of the cranial vault sutures are difficult to lcoate and this problem persists in computed (CT) scans." We found a portion of the right lambdoidal suture preserved ectocranially, but this level of suture closure and obliteration is atypical for any species of Homo, Australopithecus, and most nonhuman primates. Age cannot be a factor because all sutures should be open in the LB1 young adult. It may in fact have led to the neurocranial deformities discussed below. As reviewed below, we find evidence for all these signs in LB1, but we do not attempt diagnosis of a specific developmental syndrome from its skeletal remains. Rather, we simply test whether LB1 represents the developmentally normal holotype required for a new species (46) or an abnormal member of our own.

After allowance for left orbital region damage, asymmetry affects frontal breadth, position and contour of the lower orbital border, angle of inferior nasal margins, location of the (broken, off-center) nasal spine, and expression of the canine juga. Asymmetry also extends to other areas on the cranium. Detectable in the original figure 1 in ref. 1 but not mentioned, and more clearly here (see Fig. 7, which is published as supporting information on the PNAS web site), the palate midline is rotated $4-5^{\circ}$ from the midsagittal plane, so that a line extending the midpalatine suture does not bisect the foramen magnum. In addition, right parietal and left occipital bones are flattened compared with their more rounded antimeres. The nuchal torus is markedly asymmetrical, and the antimeric mastoid regions differ greatly. This pervasive asymmetry suggests growth anomalies producing a vault and face with substantial lateral contrasts.

Patterns of asymmetry in the human skull are well documented (47-49), with typically greater neurocranial asymmetries than in the face, where asymmetries are slight overall (50, 51). For mandibular dimensions (52), the largest mean asymmetry was 0.77 mm. For the nasal region (53), the largest mean difference was 0.4 mm, with most differences <0.1 mm. The same study reported left/right orbital height variation from 0.20 to 0.39 mm and breadths from 0.00 to 0.38 mm. These differences represent small (typically <1%), fluctuating asymmetries. Reanalysis of these data (49) supported the earlier statement that "(t)he face is the most symmetrical region of the skull" (48). Similar results were obtained with radiographic and stereophotogrammetric methods (49, 54, 55). Studies of facial asymmetry are medically important and have diagnostic applications, with low single-digit lateral deviations in percentages or millimeters marking thresholds for clinical intervention (56, 57).

We quantified craniofacial asymmetry for LB1 to the extent possible by dividing digital photographs of the cranium into right and left halves along the midsagittal plane by using Photoshop (Adobe, San Jose, CA), then making composite images by mirroring the left and right sides (Fig. 2). On a digital image of the face, we also measured left and right deviations from the midline. Six of seven measures were larger on the right, by amounts ranging up to nearly 40% (distance from mental foramen to midline). The only measurement larger on the left was the 6% for distance from the orbit lateral rim to midline (see *Supporting Text*). Gauged by anthropometric (47–53, 58) and clinical (49, 54–57) standards, LB1 asymmetry exceeds clinical norms where determinable, providing evidence for rejecting any contention that the LB1 cranium is developmentally normal.

Dentition. Various aspects of the teeth are argued as taxonomically distinctive for LB1 and LB6/1 (1, 3). These traits include P₃ teeth with enlarged occlusal surfaces, P₃ and P₄ teeth with Tomes roots (indented or bifurcated), and rotated upper fourth premolars (P⁴ teeth). Others, such as M1 \approx M2 or canines with "long roots," do not differ from common conditions in *H. sapiens* and establish no taxonomic novelty. Except for the anomalous P₃ teeth (see below), mandibular bucco-lingual breadths closely replicate modern *H. sapiens* (figure 5 in ref. 1), and data for the maxillary dentition do not differ from this assessment. Tooth size is not discordant with *H. sapiens*, as documented in the original reports (1, 3).

LB1 has enlarged, block-like P_3 teeth. These traits occur worldwide in *H. sapiens* (59–64), with examples similar to LB1 and LB6/1 common bilaterally. Variants similar to LB1, designated (63) as tooth shape deviations, also common bilaterally, are found in



Fig. 2. LB1 in three different views to illustrate facial asymmetry. (*Left*) The actual specimen. (*Center*) The right side doubled at the midline and mirrored. (*Right*) The left side doubled and mirrored. Differences in left- and right-side facial architectures are apparent and illustrate growth abnormalities of LB1. (Original photograph in *Left* is by E.I.; original photographs in *Center* and *Right* are by D.W.F.)

worldwide samples including Amerinds (59), Japanese (60), New Guineans (61), and at $\approx 3\%$ in a mixed Euro-African-Native American sample (62). Overall (64), "lower premolars present wide variation [in *H. sapiens* and] there is no such thing as a premolar that is typical of its group."

Tomes roots also are frequent in *H. sapiens* populations (65–67) and are part of the standard Arizona State University dental recording system (66, 67). Tomes roots in P₃ teeth reach frequencies as high as 37% in non-Khoisan sub-Saharan Africans (68) and 15–25% in Sunda-Pacific populations (69). Lower frequencies ($\approx 4\%$) are found in P₄ teeth (70). Thus, Tomes roots on LB1 in either P₃ or P₄ are completely within expectations for *H. sapiens* populations from the region.

It was argued (1) that the P^4 teeth of LB1 are "unusually, ... rotated parallel [sic] to the tooth row, a trait that seems to be unrecorded in any other hominin." However, dental rotation is common in modern *H. sapiens*, typically indicating developmental abnormality, crowding, or agenesis (71). No other maxillae are known from the Liang Bua Cave sample, but it is highly unlikely that any species of Homo normatively would have bilaterally rotated upper premolars because this anomaly clearly would interfere with occlusion. In the Rampasasa sample, 13 of 50 individuals (26%) show premolar crown rotation ranging from slight to 90°. None show bilateral rotation of maxillary premolars, but a 32-year-old female has a left P³ rotated perpendicular to the tooth row, and a 25-vear-old female has a right P4 rotated almost 90° (Fig. 3). Although more work needs to be done on the etiology of dental rotations, living pygmy groups from Flores exhibit tooth rotation more commonly than other extant human populations.

Other dental traits linking LB1 to modern pygmies from the Liang Bua region include a tendency for the longitudinal fissure to shift away from the buccolingual axis on lower molars, tremata (spaces between teeth), rhomboid outlines of upper molars reflecting hypocone reduction, squared lower molar outlines related to hypoconulid loss, and large buccolingual P_3 diameters. Overall, the dentition of LB1 exhibits modern human traits, with bilateral rotation of the upper fourth premolars and tooth shape deviations in lower premolars, both of which seem to occur at elevated frequencies in the Rampasasa.

Postcrania. Throughout the postcranial skeleton is evidence that contradicts any notion that LB1 is normal (see also *Supporting Text*). For example, the right humerus shaft of LB1 (Fig. 4) appears thick in relation to its length and epiphyseal dimensions, but the superficial appearance of robusticity is contradicted by very weakly marked muscle attachment sites. The deltoid tuberosity is poorly developed, and below it the shaft does not narrow to the usual extent. The humeral torsion angle of 110° is reported as falling

outside the 141° to 178° hominin range but corresponding to norms in *Hylobates* and *Macaca*, implying that the extent of humeral torsion reflects only phylogenetic information (3). However, torsion of the humerus is in part ontogenetic (72) and a response to the dynamic forces exerted by shoulder rotators on the growing bone. Because the lateral rotators insert within the proximal epiphysis whereas most of the medial rotators act distally on the shaft, forces working in opposite directions during development normally add 32° of secondary torsion (73, 74) characteristic of hominins. In contrast, the abnormally low amount of humeral torsion in LB1 is consistent with the extremely weak muscle development indicated by muscle insertions.

The right ulna is missing its most distal portion. The midshaft sagittal diameter is 12 mm, the same value estimated for the partial ulna recovered from the SAS (shell and sand) member in cave 1A at Klasies River Mouth (75), with both specimens being larger in this dimension than a small San reference sample (mean 11.1 mm, n = 8) and an Australian reference sample (mean 11.6 mm, n = 4).

The holotype statement (1) describes and illustrates a "right" complete femur, but this bone is a left femur. Largely complete but for a missing lateral condyle, it has a prominent lesser trochanter with lipping in its anterior portion. The true right femur is truncated postmortem proximally by loss of the greater trochanter, most of the neck, and the entire head. Proximally, the intertrochanteric crests on the femora are highly asymmetrical (larger on right), with sizes and positions of lesser trochanters differing substantially between sides (Fig. 5). On the right, the spiral line, adductor insertions, and lateral gluteal lines converge toward the midshaft,



Fig. 3. Partial to 90° premolar rotation is common in the Rampasasa pygmy sample from Flores. (*Left*) Rampasasa 041 is a 32-year-old female showing an upper left third premolar with 90° rotation, so that the buccal aspect is in the mesial position (arrow). All other teeth in both jaws are positioned normally. (*Right*) Rampasasa 033 is a 25-year-old female with a lower right fourth premolar rotated nearly 90°, with the usual buccal aspect oriented distally here (arrow). The tooth also has an anomalous shape, resembling an upper premolar. (Original photographs are by E.I.)



Fig. 4. Anterior aspect of the humerus. Note near absence of deltoid tuberosity as well as minimal difference in subdeltoid and supradaltoid width of the shaft. These indicators of extremely weak muscle development are consistent developmentally with an abnormally low degree of humeral torsion.

where they run parallel for only \approx 30 mm before dividing again into borders of the popliteal surface. These lines are barely visible, even in the middle of the shaft, unlike a normally robust and prominent *linea aspera*. The arrangement of muscle attachments is similar on the shaft of the left femur, but lines are not visible distally. Such atypical features imply severe muscle hypotonia (paresis) during life, associated with complications of abnormal growth.

Right and left patellae are completely preserved, and like the femora show asymmetry, with the left patella $\approx 10\%$ longer su-



Fig. 5. LB1 femora. (*A*) Lateral views of both femora, showing antimeric contrasts in diameters as well as sizes and orientations of lesser trochanters. Note thin cortex in the small postmortem break on shaft of left femur. (*B*) Posterior aspect of both femora. Note shortness of linea aspera and large size of popliteal areas.



Fig. 6. CT scans of LB1 leg bones (vertical scales are subdivided into 10-mm units). (*Top*) Longitudinal scan of the left femur (up, anterior). (*Middle*) Midshaft cross-section of left (*Left*) and right (*Right*) femora (in all cross-sections, down is anterior). Note differences in cross-sectional outlines and internal structures, indicative of same evident left-right asymmetry also seen in Fig. 5. (*Bottom Left*) Cross-section of left tibia at level of tibial tuberosity. (*Right*) cross-section of left tibia at midshaft. Note that cortical bone (completely radio-opaque area) in all sections is only ~2 mm thick, abnormal for an adult primate of either sex, and body length >1 m.

peroinferiorly. The right tibia is complete, except for the medial malleolus and the area immediately proximal, whereas the left tibia lacks both proximal epiphysis and medial malleolus. Tibial shafts are oval in cross-section rather than approximately triangular (see *Supporting Text*), an unusual feature suggesting compromise between the need to support and move body mass and generally weak muscle development.

Repeated statements that the long bones are "robust" reflect the observation that they are large in diameter and circumference proportionate to their length, but also imply that they are massive and strongly developed (see also Supporting Text). Ratios of shaft circumference to LB1 maximum long bone lengths do seem unusually large. For the left femur it is 38.4%, whereas in our modern Indonesian reference skeleton and the LB78 femur excavated in upper layers of Liang Bua, the values are 26.6%. Similarly, the ratio for the right humerus is 30.9%, against the normal adult Indonesian reference specimen's 24.8%. The ratio for the LB1 tibia is 29%. However, CT scans of diaphyses show thin ($\approx 2 \text{ mm}$) cortical bone and very large marrow cavities (Fig. 6), providing further evidence that shafts of long bones of LB1 are abnormal (16). Inflated circumferences, combined with very thin cortical bone showing very weak muscle markings, indicate not robusticity, but long bone overtubulation indicative of disordered growth.

Additional postcrania (3) generally are consistent with inferences that the Liang Bua Cave population was small-bodied. However, the most recently described material does introduce some additional conundrums. For example, the LB8 tibia, with an estimated length of 216 mm, is used to reconstruct a stature of 1.09 m, greater than that of LB1 at 1.06 m, although LB1 tibia length is 235 mm. Importantly, none of the newly described postcranial bones (3) nor LB6/1 indicate anything about the neurocranial dimensions of individuals from which they were sampled.

Discussion

Our reexamination of the original skeletal material shows that there is insufficient morphological or metric evidence for a new hominin species on Flores, where evolution over millennia in total isolation is unproved, unlikely, and at variance with Stegodon migrations and glacial geology. The skeletal material excavated from the Liang Bua Cave represents individuals sharing small body size, although unlikely as diminutive as proposed, plus some dental and other traits previously documented. Such commonalities are expected on grounds of shared environment and relationship in a local group, as are variations due to age, sex, microevolutionary trends, and other intraspecific factors. Against this background, rather than exhibiting "a mosaic of primitive, unique and derived features not recorded for any other hominin" (1), the LB1 individual exhibits a combination of characters that are not primitive but instead regional, not unique but found in other modern human populations, particularly some still living on Flores, and not derived but strikingly disordered developmentally.

Materials and Methods

Standard osteometric instruments were used for skeletal measurements, and a whole-body scanner (Toshiba, Tokyo, Japan) at the Bethesda Hospital in Yogyakarta (Indonesia) was used for CT scans. During our study of the bones at the Laboratory of Bioanthropology and Palaeoanthropology at Gadjah Mada University

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(Yogyakarta, Indonesia), direct comparisons of their size and morphology were made with an adult male Indonesian reference skeleton (in vivo stature ≈ 1.55 m), supplemented with published data on skeletal variation, particularly human skeletons excavated earlier on Flores (38) and in Australomelanesians (39–41). In April, 2005, a team led by T.J. studied Rampasasa pygmies in Waemulu village, ≈ 1 km from Liang Bua Cave.

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allowed Cao and Zhu to claim "the first written account of a complete proof of the Poincaré conjecture and the geometrization conjecture of Thurston."

In June, Bruce Kleiner and John Lott of the University of Michigan, Ann Arbor, released a manuscript that had evolved publicly online since Perelman's visit. Its gradually increasing detail helped cement the community's acceptance of Perelman's work. "They were the main people who carried the torch forward over the last 3 years," says Michael Anderson of Stony Brook University. Finally, last month, John Morgan of Columbia University and Gang Tian of MIT completed a manuscript that will be published as a book. Their work, like Kleiner and Lott's, sticks closely to Perelman's outline.

Perelman's exegetes have played a crucial role in making his work accessible to other researchers, says James Carlson, president of CMI. "Like a program written in open-source code, many eyes will be looking at it," he says. "Instead of having to work out the arguments by themselves, mathematicians will be left with the much easier task of verifying that the worked-out details are correct."

The wait begins

According to CMI's rules, the \$1 million for each Millennium Prize can be presented 2 years after the proof is published in a refereed journal. Even though Perelman's own papers have never been formally published, Carlson confirms that the clock is now ticking toward awarding the first prize. "Close to 2 years from now, we will form a committee to study the issue," Carlson says.

Shing-Tung Yau of Harvard University thinks that Hamilton deserves a share. "For 20 years, he worked on this problem alone, with some help from me. The part he proved is absolutely nontrivial, and it was devised purposely to solve this problem," says Yau. At present, however, Yau's seems to be a minority view. "Perelman broke through the barriers," says Robert Greene of the University of California, Los Angeles. "If Perelman's papers didn't exist, I think we would still be stuck. It's the unsticking that counts."

Some mathematicians who know him, however, think Perelman would simply decline the Millennium Prize as well. "When I talked with him at Stony Brook [in 2003], I had the impression that he's not interested in it at all," Anderson says. If Perelman refuses the award, Carlson says, CMI may consider other uses for the \$1 million, such as contributing it to Russian mathematics or to the International Mathematics Olympiad, which Perelman won with a perfect score in 1982. **-DANA MACKENZIE** Dana Mackenzie is a writer in Santa Cruz, California.

PALEOANTHROPOLOGY

Skeptics Seek to Slay the 'Hobbit,' Calling Flores Skeleton a Modern Human

Strange new hominid or just another modern human? That's still an open question for the "hobbit" bones unearthed in Liang Bua cave on the Indonesian island of Flores. Their discoverers described them 2 years ago as a new species, *Homo floresiensis*, but critics have



Hobbit critic. Teuku Jacob and Etty Indriati argue that the tiny Flores skull (different skull pictured here) is that of a diseased modern human.

insisted from the start that the leading specimen, a 1-meter-tall, 18,000-year-old skeleton with a brain the size of a grapefruit, was that of a diseased *Homo sapiens*.

This week, the skeptics laid out their most detailed case yet in the *Proceedings of the National Academy of Sciences (PNAS)*. The paper argues that living people have some of the traits claimed to be unique to *H. floresiensis*, and that the lone skull is simply deformed. "This is not a new species," says co-author Robert Eckhardt of Pennsylvania State University in State College. "This is a developmentally abnormal individual."

But the hobbit's discoverers and others who have also studied the original specimens are unimpressed. "Complete nonsense," snaps Peter Brown of the University of New England in Armidale, Australia, who did the original anatomical analyses. The paper "cherry-picked features and ignored counterevidence," adds Susan Larson of Stony Brook University in New York, who has linked the hobbit shoulder to an ancient human species, *H. erectus* (*Science*, 19 May, p. 983). "Nothing they say has caused me to question my assessment." The new paper is the first full-length critique in a high-profile journal, and researchers on both sides have long awaited the data in it. The authors include Teuku Jacob of Gadjah Mada University in Yogyakarta, who in a contentious incident borrowed the Flores

> bones for study in November 2004 (*Science*, 25 March 2005, p. 1848). In 2005, Jacob and others, including Gadjah Mada colleague Etty Indriati, also studied 76 modern Rampasasa pygmies living only a few kilometers from Liang Bua cave.

The team uses several lines of evidence to challenge the hobbit's novelty. One new argument is that a hominid could not have evolved in isolation on Flores because fossils show that elephants reached the island twice, and so humans probably also arrived more than once; lack of isolation would have prevented the evolution of a new dwarf species, they say.

The team further argues that

the skull, part of the specimen labeled LB1, is so asymmetrical that it must have suffered from a developmental deformity. Mirror imaging the left side of LB1's skull and putting those halves together creates a distinctly different face than two right halves put together in the same way.

The paper also reports new data showing that some Rampasasa pygmies lack chins and have odd premolar teeth, features identified as distinctive in *H. floresiensis*. The original work on the Liang Bua bones "largely looked for 'otherness'—finding reasons to believe that this population is entirely different from anything that has been seen before," says Indriati. "That simply isn't true." The Rampasasa results are "relevant and revealing," agrees Robert D. Martin of the Field Museum in Chicago, Illinois, who has argued in print that LB1 suffered from microcephaly, a genetic disorder marked by a puny brain.

But other experts are fiercely critical of the *PNAS* paper. "My first reaction was, 'How did this get published? Was there any peer review?'" says brain evolution expert Ralph Holloway of Columbia University. (Eckhardt reports that there were five external reviewers, chosen by the team in accordance with *PNAS* guidelines.) Holloway adds that he thinks the brain of LB1 shows "possible pathologies" but not for the reasons cited by Jacob and his co-authors.

Others are ready to rebut each point in the paper. The first elephant colonization was too early to have any bearing on the hobbit debate, says Russell Ciochon of the University of Iowa in Iowa City. And the paper's focus on skull distortion is misplaced, adds Brown, because it happened after death, when the specimen was buried deeply in the cave.

As for the treatment of chins, which relies on a photo of a living Rampasasa, it is "superficial indeed," because one must look at a jaw without its covering of flesh to see whether a chin is present, says Colin Groves of Australian National University in Canberra. (Groves and colleagues compare the hobbit to microcephalics and modern humans, including those from Asia, and conclude in a paper in press in the *Journal of Human Evolution* that it is indeed a new species.) Other details, such as claimed signs of pathology in LB1's leg bones, constitute "a flimsy house of cards," says Bill Jungers of Stony Brook University, who studied the bones last year in Jakarta.

Given these flatly contradictory statements, it's likely to take some time for the field to settle on a coherent view of ancient hobbits. "We have a ways to go before the controversy is resolved," says Indriati. The battle of the shire is far from over.

-ELIZABETH CULOTTA

ARCHAEOLOGY After 2 Millennia on Ice, a Nomad Resurfaces

BERLIN—Decked in a magnificent fur mantle and gilded wooden headdress, a nomad probably a fierce warrior—was buried more than 2200 years ago in the icy highlands of Mongolia. This week, a team of archaeologists, led by Hermann Parzinger, director of the German Archaeological Institute in Berlin, announced that they had found his partially mummified remains. The finding will reveal more about the culture and conditions that preserved the body. It is urgent work, observers say, because a warmer environment could destroy specimens like this.

In 2004, the 30-member team from Germany, Russia, and Mongolia surveyed

more than a dozen stone-covered burial mounds in northwestern Mongolia. Last year, they returned to the 2600-meter-high plateau in the Altai region, a remote mountain range that borders Russia, China, and Mongolia, with electromagnetic sensors, temperature probes, and other instruments to look for ice layers that might indicate intact burials.

Parzinger has made spectacular finds before. In 2001, he pulled

nearly 20 kilograms of artfully worked jewelry out of a similar grave mound in the Russian republic of Tuva. Archaeologists say the Altai plateaus are the burial grounds of the Pazyryk, members of a larger Scythian culture that occupied Central Asia as early as the 9th century B.C.E. and struck fear into the hearts of the ancient Greeks and Persians.

Scythians used a distinctive type of embalming, says Esther Jacobson-Tepfer, an

archaeologist and art historian at the University of Oregon, Eugene. "They removed the innards and filled the body with sweetsmelling grasses." High-status individuals were dressed, surrounded by goods, and buried under earth and stone mounds, or kurgans.

Shortly after burial, water sometimes seeped through the stones and froze, forming ice lenses insulated by the stone mounds above and permafrost underneath. The body found this summer was surrounded by slain horses and dressed in felt boots. Fantastical animal tattoos were visible on the man's skin. "Instead of archaeology, the material culture is so well preserved it's almost a kind



Well preserved. A Scythian buried with fur, felt boots, and horses.

of ethnography," Parzinger says.

Parzinger's success comes as the Altai's permafrost is melting fast. "The warming up of the general climate is a danger for these kurgans," Parzinger says. As rising temperatures threaten to bring the mummies out of deep freeze, the Scythian royalty may face decay and disintegration for the first time in millennia. **–ANDREW CURRY** Andrew Curry is a writer in Berlin.

SCIENCE SCOPE

Controls Sought ...

AIDS researchers have known for years that a small percentage of people infected with HIV do not show symptoms of the disease, but they have yet to understand why. Now immunologist Bruce Walker of Massachusetts General Hospital in Boston has identified about 100 so-called elite controllers in the Boston area and says that dozens of investigators want to join an international consortium he's organizing to uncover genetic or immunological clues to this group's good health.

Elite controllers—thought to number about 3000 in the United States—by definition show no immune damage and have unusually low levels of the AIDS virus in their blood 1 year after being infected, despite taking no anti-HIV drugs. Walker says a consortium could perform haplotype mapping of the controllers, comparing their genes with those of uninfected people. One key difference encoded within the controllers' DNA, for example, may be high levels of so-called PD-1 receptors; these immune cell surface proteins, Walker's lab reported online 20 August in *Nature*, appear to play a key role in controlling HIV replication.

The proposed effort, for which Walker has received \$2.5 million from the Mark and Lisa Schwartz Foundation to launch, "could provide important insights into what's important to intervene with prevention strategies," says virologist Douglas Richman of the University of California, San Diego, who has joined the consortium. –JON COHEN

... Controls Eased

The U.S. Department of Defense (DOD) has abandoned a controversial proposal that would have required universities to keep a watchful eye on foreign nationals involved in defense research. DOD proposed the rules 13 months ago to prevent the transfer of sensitive technologies to countries seen as security threats. Under the proposal, universities not only had to supplement the normal export licenses for the researchers with new "unique badging requirements" but also with "segregated work areas" for foreigners (*Science*, 22 July 2005, p. 544). Academic lobbyists said that a tougher regime would scare off needed foreign expertise and that existing rules were sufficient.

Now the Pentagon has removed the badging and separate work area requirements, bringing its rules in line with those at the Commerce and State departments. "We're pleased," says Toby Smith of the Association of American Universities of the plan, for which comments will be accepted until 13 October. –YUDHIJIT BHATTACHARJEE