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

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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

In 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 (P_3) (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 ≈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; P_3, lower third premolar; 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 ≈750 ka (23). Additional debated findings extend this date to ≈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 ≈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-km^2 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 km^2 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.


[redacted]

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 ≈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° 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 P_3 teeth with enlarged occlusal surfaces, P_3 and P_4 teeth with Tomes roots (indented or bifurcated), and rotated upper fourth premolars (P^4 teeth). Others, such as M1≈M2 or canines with "long roots," do not differ from common conditions in *H. sapiens* and establish no taxonomic novelty. Except for the anomalous P_3 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 ≈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 P_3 teeth reach frequencies as high as 37% in non-Khoisan sub-Saharan Africans (68) and 15–25% in Sunda-Pacific populations (69). Lower frequencies (≈4%) are found in P_4 teeth (70). Thus, Tomes roots on LB1 in either P_3 or P_4 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 P^3 rotated perpendicular to the tooth row, and a 25-year-old female has a right P_4 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,

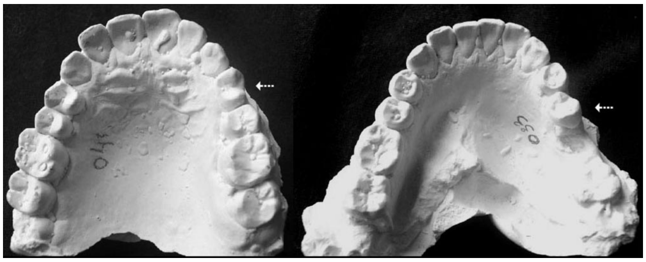

Fig. 3. Partial to 90° premolar rotation is common in the Rampasasa pygmy sample from Flores. (*Left*) Rampasasa 041 is a 32-year-old female showing an upper left third premolar with 90° rotation, so that the buccal aspect is in the mesial position (arrow). All other teeth in both jaws are positioned 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 ≈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 ≈10% longer superoinferiorly. 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.

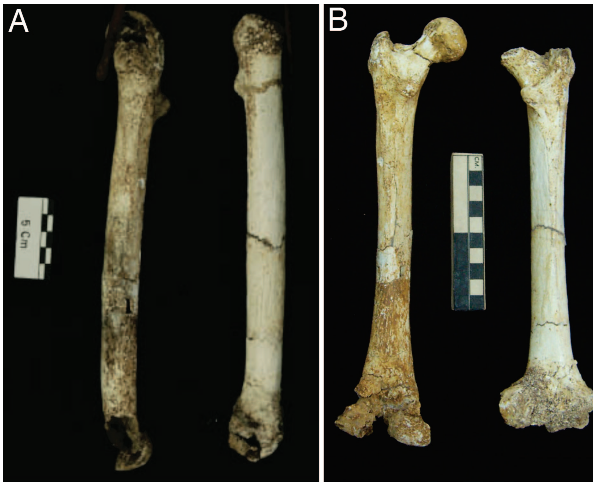

Fig. 5. LB1 femora. (*A*) Lateral views of both femora, showing antimeric contrasts in diameters as well as sizes and orientations of lesser trochanters. Note thin cortex in the small postmortem break on shaft of left femur. (*B*) Posterior aspect of both femora. Note shortness of linea aspera and large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

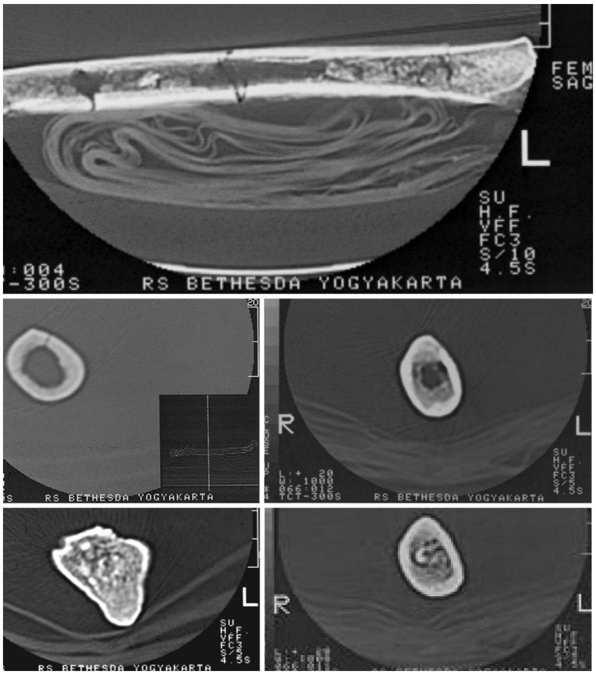

Fig. 6. CT scans of LB1 leg bones (vertical scales are subdivided into 10-mm units). (*Top*) Longitudinal scan of the left femur (up, anterior). (*Middle*) Midshaft cross-section of left (*Left*) and right (*Right*) femora (in all cross-sections, down is anterior). Note differences in cross-sectional 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.

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 (≈2 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 (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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