Evolved developmental homeostasis disturbed in LB1 from Flores, Indonesia, denotes Down syndrome and not diagnostic traits of the invalid species *Homo floresiensis*

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Human skeletons from Liang Bua Cave, Flores, Indonesia, are coeval with only *Homo sapiens* populations worldwide and no other previously known hominins. We report here for the first time to our knowledge the occipitofrontal circumference of specimen LB1. This datum makes it possible to link the 430-mL endocranial volume of LB1 reported by us previously, later confirmed independently by other investigators, not only with other human skeletal samples past and present but also with a large body of clinical data routinely collected on patients with developmental disorders. Our analyses show that the brain size of LB1 is in the range predicted for an individual with Down syndrome (DS) in a normal small-bodied population from the geographic region that includes Flores. Among additional diagnostic signs of DS and other skeletal dysplasiae are abnormally short femora combined with disproportionate flat feet. Liang Bua Cave femora, known only for LB1, match interlimb proportions for DS. Predictions based on corrected LB1 femur lengths show a stature normal for other *H. sapiens* populations in the region.

asymmetry | atavism | body mass | body height

Excavations at Liang Bua Cave have produced what is termed by paleoanthropologists "the most extreme human ever discovered" (http://news.nationalgeographic.com/news/2004/10/1027_041027_homo_floresiensis.html). Its unusual features—"stature and endocranial volume approximating 1 m and 380 cm^3" (1)—first were explained by island isolation shrinking body size and then derived from a hypothetical earlier African ancestor already small in brain and body size before arrival on Flores (2). Our hypothesis (3) sees the Liang Bua Cave skeletons as normal regional *Homo sapiens*, with only LB1 manifesting anomalies in cranial size and shape (*SI Text*). Such controversies are not limited to paleoanthropology. A Festschrift volume honoring K.J.H. (4) noted "…the type of controversy in which one side simply refuses to change its mind when faced with contradicting evidence…" and "… in this modern age of mass communications a new element entered the controversy arena; the propagation of half-informed, sensational treatments by the news media." Another Festschrift volume explored the tendency for a controversy to become a paradox, "a tenet contradictory to received opinion" (5).

The Flores problem embodies multiple paradoxes: (*i*) biogeographic origins of Liang Bua hominins are explained contradictorily; (*ii*) anatomical features described as unique are only uncommon; (*iii*) LB1 resembles no single fossil hominin taxon but only scattered traits found in *Australopithecus* through various *Homo* species; (*iv*) Liang Bua cave bones are not fossilized, so references to them as fossils misrepresent their status; and (*v*) mythologizing substituted for testable hypotheses. Above all, media "propagation of half-informed, sensational treatments" (5) implies scientific consensus for what is mainly repetition of conjecture.

Geological Background for Human Evolutionary Options

Paradox and controversy are part of science; riding at sea level on a research vessel yet envisioning an ancient desert a mile below requires imagination congruent with data (6, 7). The natural world to which populations adapt on various timescales (ref. 8, p. 13) includes such cataclysmic events as the Zanclean flood refilling the Mediterranean after the Messinian salinity crisis (9), which was previously documented (10). This geological event manifested gravitational potential energy of 1.6×10^{22} J, comparable to 4% of the kinetic energy of the K-T Chicxulub meteorite impact. At 5.96–5.33 Ma, the Messinian crisis occurred just after the earliest direct evidence for human upright posture and bipedal locomotion (11). Geologic and paleoclimatic events shape hominin dispersion, variation, and evolution; many evolutionary outcomes are possible, although not all scenarios are equally probable (*SI Text*).

Origin of the Liang Bua Cave Sample: Alternative Contradictory Hypotheses

Our consistent hypothesis (3) sees LB1 as a developmentally abnormal individual member of a recent Australomelanesian *H. sapiens* population, its features reflecting multiple compatible causes (*SI Text*). In contrast to this testable hypothesis stand conjectures about a protean hominin species, with its origin hypothesis shifting against evidence static for a decade.

Significance

The population that has become known as *Homo floresiensis* has been described as "the most extreme human ever discovered." Specimen LB1 from Liang Bua Cave is unusual, but craniofacial and postcranial characteristics originally said to be diagnostic of the new species are not evident in the other more fragmentary skeletons in the sample that resemble other recent small-bodied human populations in the region (including the Andaman Islands, Palau, and Flores itself). Here we demonstrate that the facial asymmetry, small endocranial volume, brachycephaly, disproportionately short femora, flat feet, and numerous other characteristics of LB1 are highly diagnostic of Down syndrome, one of the most commonly occurring developmental disorders in humans and also documented in related hominoids such as chimpanzees and orangutans.

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The original new species hypothesis (1) stating "The most likely explanation for its existence is long-term isolation on Flores, with subsequent endemic dwarfing," was hedged with "an unknown small-bodied and small-brained hominin may have arrived on Flores from the Sunda shelf." Suggested migration of LB ancestors 2 Ma from Africa (12) arose from cranial trait cladistics, joining LB1 and *Homo habilis* as sister taxa to an unknown common ancestor (2). All early-African-diffusion-to-Flores alternatives are speculative and not based on fossil finds and embody post hoc reasoning: the new species posited to exist on Flores must have materialized there somehow, from some ancestor perhaps 8,000 km away, over an unknown route, and leaving no physical traces (13). The timing of this spread rests not on geological or paleontological evidence but instead on how skeletal, mainly cranial, traits are construed. Many LB1 features are labeled primitive, implying a species that evolved early, rather than an individual showing disturbed evolved developmental homeostasis in its actual time horizon (the last 100,000 y). No pertinent early fossil evidence is known between East Africa and Flores. There are no other hominin crania that resemble LB1 in particular or anything intermediate in characteristics between LB1 and its ostensible australopithecine or early *Homo* ancestors.

After the Liang Bua Cave find, no discoveries of hominin remains elsewhere in Eurasia or Africa provide evidence for the hypothesized new species. Recent *H. sapiens* skeletons from Palau exhibit reduced stature and other regional population features similar to those on Flores (14–16). Palau endocranial volumes scale appropriately to small body dimensions normal for these regional populations; postcrania show proportions expected for *H. sapiens* (15).

Properly reconstructed (15), the statures of LB1 and associated more fragmentary specimens are near the low end of known normal ranges for the region (3, 17), whereas LB1 endocranial volume falls several SDs below them (18). Palau crania lack the anomalies of LB1. Although the hypothetical new taxon based chiefly on the single LB1 specimen is said to overlap several hominin taxa known from the last two million years, its pattern is discordant; putatively archaic traits suggest not deep ancestry but disturbed developmental homeostasis and atavism. If LB1 establishes a new total morphological pattern, it is one that presents a marked deviation from the record of human evolution built up over nearly two centuries (19). The features first proclaimed as unique for LB1 increasingly fall within known ranges for *H. sapiens*, normal and abnormal, being neither taxonomically diagnostic nor phylogenetically congruent. Critically, LB1 iconic traits (low humeral torsion, s-shaped clavicles in dorsal view, absence of external bony chin, etc.) disappear as uniquenesses on close scrutiny, with rhetoric shifting to unusual instead of unique or as primitive features even when they are documented in extant *H. sapiens* populations. This strange situation echoes the "half-informed, sensational treatments by the news media" noted by Schlanger (4) about jounalistic attacks on Hsü's earlier work: then heterodox and now established (20).

LB1: From Unique Species to Common Pathology

Outré elements in the new species narrative are overlooked. One book (21) sympathetically describes the zany manner in which the decision eventually was reached to assign the Liang Bua Cave bones to a new species. First favored was "*Sundanthropus tegakensis*." Given the phylogenetic implications of taxonomy, that name signals no close relationship to any known hominin genera (*Homo, Australopithecus*, *Ardipithecus*). Subsequently grasping that "the right name for the species was important scientifically and *politically*" [our emphasis], Brown agreed to the genus designation as *Homo,* and after further debates over *floresianus, floresi, florescus, manggarii,* and even *hobbitus*, chose *floresiensis*. Separate taxonomic status was felt necessary because LB1, the only specimen with a skull, departed dramatically from human evolutionary patterns. It does, but closer scrutiny of abnormalities should have been scientifically obligatory, given that the Liang Bua Cave remains (said to span 74,000–12,000 y B.P.) overlap our own species, *H. sapiens*. Only three disorders (IGF-related postcranial growth retardation, pituitary dwarfism, and primordial microcephalic dwarfism) were noted, but they were dismissed (1). However, at least 50 syndromes express diminutive brain size and short stature, defining attributes of LB1 (3). Other telltale signs of abnormality are craniofacial asymmetry and early cranial suture closure (3, 22–26).

Originally we (3) forebore from offering a specific diagnosis of any one pathological syndrome, instead documenting the existence of a general developmental abnormality (=disturbed homeostasis), based on obvious signs. Searching for matches, we studied developmental disorders such as Laron syndrome (27), including our own primary clinical research, and other proposed syndromes (28–31).

Eventually, Down syndrome (DS) emerged from converging lines of evidence: craniofacial asymmetry, brain diminution, and limb bone disparities. Perplexingly, all of the original observations on these factors (and others) were misleadingly reported (1). Craniofacial asymmetry was unremarked, whereas our own documentation of asymmetry (3) was disparaged without quantification (24) and then temporized for several years (25, 26); endocranial volume first was reported as 380 mL, and stature as 1.06 m, both biased downward. We noted all these flaws (3, 32), illustrating and quantifying craniofacial asymmetry, reporting endocranial volume as 430 mL, and recalculating stature as substantially taller (1.20–1.38 m) (3), noting the short, dysmorphic femora that influenced stature underestimation.

Match of LB1 to DS Patient Signs

DS, occurring in about 1 of every 700 live births, is a nosological entity presenting more than 80 signs (33), markedly heterogeneous in occurrence and differing widely in expression; many are undetectable in skeletal remains. Within those limitations, the LB1 phenotype is congruent with DS being an example of disrupted evolved ontogenetic homeostatic systems (34) (*SI Text*). The result presents as atavism, with developmental characteristics of earlier ancestral stages (34) reappearing alongside some undisrupted phenotypic elements. This pattern of expression is commonplace in teratology, but naively styled by paleoanthropologists describing *H. floresiensis* as "a unique mosaic of derived (human like) and primitive morphologies" (35). Below is a discussion of some signs reported to occur in a high proportion (>10%) of DS patients.

Craniofacial Asymmetry. Normally, the face is the most symmetrical region of the skull (3, 36), with low single digit lateral deviations in percentages or millimeters marking thresholds for clinical intervention (3, 36, 37). Photogrammetric systems now used to record 3D images of facial morphology confirm results from traditional anthropometric analysis showing bilateral measurements as normally similar (38), in contrast to more marked craniofacial asymmetry in DS (39) and other disorders resulting from disrupted development.

Craniofacial asymmetry in LB1 (3) includes exaggerated, reversed frontal and occipital petalia, with marked palatal rotation. The extent of palatal rotation exceeds the normal range so markedly as to be patent in published photographs. In contrast to misleading statements (14, 25, 40), the overall craniofacial asymmetry cannot be attributed to postmortem taphonomic modification because it is reflected in asymmetric tooth wear that occurred during life. Left-right deviations from facial points (3) mirror classical evidence for fluctuating asymmetry (FA). Facial asymmetry is a sign of DS, with frequency cline of left-right differences increasing from frontal inferiorly through midface to

mandible: frontal prominence, 11.1%; lateral nasal prominences, 43.33%; medial nasal prominences, 64.29%; maxillary prominences, 95.24%; mandibular prominence, 96.67% (41). Those data led us to reexamine facial asymmetry data for LB1. Our nonstandard but repeatable measurements (3) were dictated by the statement (1) that, on the LB1 skull, most standard craniometric landmarks could not be recognized, as recently confirmed (22) but persistently ignored (25, 42). The correspondence between our measurement patterns on LB1 facial bone landmarks and those for DS soft tissue points (41) is striking, given the comparison of absolute distances in our data with published frequencies (not magnitudes) of asymmetric linear distances (Table S1).

LB1 Absolute and Relative Brain Volume in the Context of DS. Microcephaly is defined as an occipitofrontal circumference (OFC) of at least −2 or −3 SDs below population norms for age and sex (43). Of many possible causes for LB1's microcephaly, few were systematically investigated. Here we consider DS as a diagnosis for the reasons already stated.

Cognitive limitations are variably present in 99.8% of all DS patients; reduced endocranial volumes highly diagnostic of DS patients vary widely and are not consistent with other signs (44, 45). The average of 1,296 ± 149.1-mL cranial capacity for combined-sex modern humans (2) places the LB1 430-mL cranial capacity about 5.8 SDs below that population mean. In clinical practice, brain volume is rarely determined, but OFC is collected routinely on living patients; diagnosis of DS in LB1 requires OFC, published here for the first time. In 2005, our team (3) collected craniometric data, including the OFC, while Liang Bua Cave skeletal material was held at the Laboratory of Paleoanthropology, Gadjah Mada University. Measurement with a tape passing just above the supraorbital prominences was 385 mm. We asked Ralph Holloway and Ian Tattersal independently to measure OFC on the LB1 casts in their possession. Their values, using the same standard procedure, were 382 and 385 mm, respectively. The casts themselves may differ slightly from each other and from the original specimen, but all three determinations cluster tightly; the most likely OFC of the dry LB1 skull is 385 mm.

Regression equations are used to reconstruct OFC from the volume of the cranial cavity. Because equations for Australomelanesians inhabiting Indonesia were unavailable, we used craniometric data for adult Australomelanesians in Australia: $n = 73$, both sexes combined, with OFC directly measured plus cranial capacity determined by linseed filling (46). Linear regression using these data produces the following equation: OFC (mm) = 0.1649 CC + 311.0 ± 13.2 mm, where CC is the cranial volume in milliliters. Applying this equation to the LB1 CC of 430 mL yields an OFC of 382 mm.

Even more appropriate comparisons for the LB1 OFC are the Rampasasa people living today near the Liang Bua cave and small human skeletons recovered in Palau (14, 15). The head circumference of the Rampasasa people reconstructed by the above regression from their cranial capacity of 1,270 mL (3) is 476 mm, with a 95% CI of 450–522 mm. For this range, the SD of 20.5 mm (46) produces z-scores of –3.17 to –6.68 SDs for the LB1 OFC of 385 mm. Cranial capacities of Palau skeletons are not precisely known but are estimated as ≤1,000 mL (14). Using our regression equations and a range of OFCs for 950 and 1,000 CC with 95% CIs around each estimate produces an OFC from 441 to 502 mm. Against this range, the LB1 OFC lies somewhere between –2.73 and –5.71 SDs.

For comparisons with living patients, the dry skull OFC must be translated into OFC′ to include soft tissues of living individuals. The average forehead soft tissue thickness of 4.5 mm (47) is likely to be of similar magnitude around the braincase. To convert the dry skull OFC to that of a living person (OFC′), a simple equation based on the circumference of a circle was used: $OFC' = OFC + 4.5(2\pi)$. For LB1, the OFC′, including the soft tissue, is 413 mm (i.e., $385 + 4.5 \times 2\pi$).

A study of growth hormone deficiency in DS (48) included 20 patients (13 boys and 7 girls; age range, 15 mo to 13.9 y). More than one-third of those patients had OFC values between −3.29 and −6.60 SD. These overlap with those for Rampasasa people (−3.17 to −6.68 SD) and Palau skulls (14) (−2.73 to −5.71 SD). Because there is no basis for any objective assessment of LB1 other than its evident multidimensional idiosyncrasy—however explained—the main point is that its estimated brain size can be matched from the available biomedical literature on DS. One patient with a *DYRK1A* locus mutation (which strongly influences development of microcephaly) at 4 y of age had an OFC circumference of −6 SD (49), with brain sizes of DS patients lagging those of normal children with advancing age (50). Extensive cytogenetic diversity underlying DS phenotypic variation reemphasizes that this is a disorder of disrupted evolutionary homeostasis of development.

LB1 Limb Lengths and Proportions Mirror DS and Skew Stature Estimates. Long bone lengths and ratios are pertinent to testing the DS hypothesis for LB1; if this hypothesis cannot be rejected, there are important implications for stature estimates not only for this individual but also for inferences made about the population from which LB1 was sampled. If the femora of LB1 are abnormally short but wrongly taken as representative, the stature of what is represented as the *H. floresiensis* taxon is underestimated.

Among the many supposedly unique features of *H. floresiensis* exemplified only by LB1 are its feet, known from relatively complete left and partial right foot skeletons. "LB1's foot is exceptionally long relative to the femur and tibia, proportions never before documented in hominins. . ." (51). However, stated later in the same paper, "The relatively high foot-to-femur ratio, not unlike the high humerofemoral index, is driven primarily by an exceptionally short hindlimb." Among the many Flores paradoxes, this one (are the feet long or the femora short?) can be resolved by comparing LB1 with normal and developmentally abnormal members of extant human populations and by matching proportions of its foot with other skeletal elements of the Liang Bua Cave sample.

The reconstructed fleshy foot length of LB1 at 196 mm (51) is not absolutely or relatively unique in extant *H. sapiens*. In a study of 1,905 US Air Force women (52), the average foot length was 240.7 mm, with an SD of 11.3 mm. The foot of LB1 is 4.0 SDs below this large sample of mainly European ancestry. The shortest foot length in the sample was 210 mm ($n = 8$), so the foot of LB1 was just 14 mm (1.24 SD) shorter than this. In this same sample, the average stature was 1,621.1 mm, with an SD of 60 mm. The regression equation was as follows: stature = 3.682 (foot length) + 734.83 mm. Stature predicted for LB1 from this equation is 1,456.5 mm against an observed sample minimum of 1,452.5 ($n = 2$); LB1 extrapolates to 4 mm taller than the shortest of the Air Force women. However, similar result for stature reconstructed from the femur could not be obtained because of the unusually short LB1 femur length.

More regionally appropriate comparisons are possible. In 132 Indonesian females (53), mean foot length was 230 mm, with an SD of 26.0; the LB1 foot is just 1.3 SDs below this mean. The 50th percentile of stature for these Indonesian women is 1,500 mm. Using the ratio scaling method (54) and constant body ratio benchmarks (55), estimated stature for LB1 is ~1,380.5 mm, which is inexact (due to mathematical and demographic limitations) but far from the reiterated 1,060 mm. In these comparisons, irrespective of stature predictions, the LB1 foot appears moderately short in absolute terms, as expected in DS and not "exceptionally long" (51).

Further anthropometric data on rural Javanese women also include stature and foot length (56). Reliable ages are lacking, and no means are given. The midpoint of minimum and maximum foot lengths, 138 and 245 mm, respectively, is 191.5 mm, probably biased downward due to possible inclusion of immature subjects. The regression equation is $y = 0.139x + 2.318$, with stature = x and foot length = y. Substituting the LB1 fleshy foot length (196 mm) gives a predicted stature of 1,243.31 mm. Probably due to inclusion of some immature subjects, this stature is lower than predicted for LB1 from the previous results (53) but still well above the stature reiterated for LB1 and thus *H. floresiensis* (1). From these comparisons, an LB1 stature of 1,060 mm is shorter than would be predicted from feet of comparable length in extant human populations, even ones drawn from the same geographic region. The driver of this deviation from the general human pattern chiefly is the very short femur length of LB1. Using LB1 femur length = 280 mm and tibia length = 235 mm (1), the stature predicted from femur length is 45 mm shorter than that based on tibia length alone (57) (Table S2); the short femur of LB1 reduces the estimated stature. Irrespective of method (Table S3), when the upper limb bones of LB1 are used, the estimated stature is taller, which is similar to the lower limb, where regressions using the tibia yield greater statures than those using the femur. Various regression equations, most cogently those derived from Asian and Australomelanesian populations, show the stature of LB1 to be consistently taller than that originally reported (1). Estimates derived from the upper limb again are higher than those from the lower limb, and those based on femur length alone are among the lowest.

This pattern matches the finding from anthropometric data for DS patients, in whom the syndrome results in greater shortening of the lower limb than the upper limb. The z-scores of DS patients 6–18 y of age (58) are as follows: stature, −2.36; upper limb length, −2.24; lower limb length, −2.82; sitting height, −1.30.

The proportion of the upper limb length shortening to lower limb shortening is 1.24 (2.82/2.24), and LB1 stature calculated using Australomelanesian data from upper limb elements to lower limb elements is 1.20 (Table S3). The length of the trunk is affected by DS less than the length of limbs, so limb bone lengths are not appropriate for the estimation of the expected population stature norms from DS individuals unless substantial correction is made. The true (developmentally normal) stature of LB1 can be calculated by correcting the stature estimated from a given limb bone by proportions of limb lengths and stature in DS patients: upper limb, 2.36/2.24 = 1.05; lower limb, 2.36/2.82 = 0.84.

The stature for LB1 estimated from lower limb data should be 1.26 m and not 1.06 m (1); for the upper limb, using the same

Table 1. Skeletal signs of DS and their presence in LB1 and accompanying skeletal fragments of other individuals

Signs	Presence in LB1	Presence in other LB specimens	Sources/comments
Small brain	Yes	Unknown	Own measurements CC = 430 mL, OFC = 385 mm (cranial) 413 mm (fleshed)
Brachycephaly	Yes	Unknown	Cranial index from (22) = 82.0; ours = 80.1. Brown et al. (1) overestimated maximum cranial length, obtaining cranial index = 79.0
Atlanto-occipital abnormality	Yes	Unknown	(22)
Facial asymmetry	Yes	Unremarkable in LB6 mandible	First documented (3): Confirmed (64): Basis: characteristic increase of fluctuating asymmetry from frontal to mental eminences (41)
Small/missing skull sinuses	Yes	Unknown	CT scans in refs. 1, 22, and 65 (especially figure 9 showing no clear sphenoid sinus, although Brown says there is sediment in the sinus, figures 1 and 2 show reduced frontal sinus), deep (concave) infraorbital areas of maxillae, no trace of frontal sinuses in the area of excavation damage (see numerous photos and CT scans)
Microgenia (Micrognathia)	Yes	Yes LB6/1, but see notes	(40)
Taurodontism	Yes	Equivocal	(31, 66, 67)
Short stature	Yes	Yes	Individuals from Liang Bua Cave all are relatively small but stature based on LB1 is underestimated All may be within a range normal for the local small-bodied population (3)
Short femora	Yes	Unknown	Foot to femur ratio: foot/thigh = 0.61 DS compared with 0.58 in unaffected
Flat feet	Yes	Unknown	(51)
Flaring ilia	Yes	Unknown	(1)
Short digits	Yes	Unknown	Foot length near lower bound of modern human range, hand bones small (68)
Periodontitis, low caries prevalence	Yes	No	(40, 67)
Plagiocephaly	Yes	Unknown	Neither positional nor primary developmental defect; possibly resulting from atlanto-occipital subluxation (22) or premature suture obliteration
Hypothyroidism	Yes	Equivocal	(30, 31, 69–71)
Anomalous wrists	Unclear	Unclear	(35, 72, 73)
Small cerebellum	Yes	Unknown	(74)

Signs are noted as follows: bold, typical; no bold, less common.

appropriate ratio yields a recalculated stature of 1.22 m. This stature is −3.3 SD (of 60 mm) below the Rampasasa people's mean stature of 1.46 m and matches statures estimated after correction for DS limb proportions. The congruence of estimated statures after the correction is made for DS effects on limb length further supports the diagnosis of DS in LB1.

A study focused primarily on gait analysis (59) provided anthropometric data from 12 adults (age, 35–62 y) with DS. These data (six males and six females) were compared with US Civilian American and European Surface Anthropometry Resource data on ∼1,100 male and ∼1,200 female Americans 18–65 y of age (*SI Text* and Tables S4 and S5). Combining the data (60, 61), the LB1 ratio of bony foot/femur = 191/280 = 0.68 (closer to DS than to controls). Similarly, by a simple proportion, given an LB1 femur length of 280 mm, the corrected stature should be 280/0.233 = 1,200 mm, approximating our previous determinations.

Overall, if we are trying to envision the average size of the normal individuals in a population from which developmentally impaired LB1 is sampled, their stature would be at a minimum of ∼200–400 mm taller than originally estimated for LB1 (1), or about 1,260–1,460 mm. About half of that difference is due to correction for the abnormally short DS limb lengths (particularly femur), and the remainder is due to more regionally appropriate regression formulae. In the Imperial measuring units chosen by one journalist (61), rather than being "barely 3 feet tall," the inferred stature for LB1 should be more than 4 feet tall (about a quarter to nearly half a meter greater stature). In today's world, particularly in the geographic region that includes Flores, such short-statured people are far from uncommon, and no one of such a stature could reasonably be labeled as unique (15).

Estimated Statures of Other Liang Bua Cave Skeletons in Regional Context. Radii include deformed radius LB6/2 (35); a partial radius (from sector IV spot 58R LB3) dated to 74 ka, with an estimated length 210 mm; and a distally defective juvenile incomplete radius LB4/1 from sector XI. These three cannot be reliably used for stature reconstruction. The only other postcranial bone for which measurements were given is the LB8 tibia. Its length of 216 mm was used to reconstruct a stature of 1,090 mm (62). However, using the Asian regional regression equations (57, 63), respective stature reconstructions would be 1,185.3 and 1,330.74 mm. The average of these two determinations is 1,258.02 mm, which is within the general range of corrected stature determinations for LB1 using all postcranial elements other than the femur. As we long have maintained (3), there is no reliable evidence that Liang Bua Cave sampled an abnormal population. The data are consistent with the LB1 individual being abnormal (*SI Text*). An independent study of small-bodied populations (15) notes that "while *H. floresiensis* [sic] are small-bodied, they are not the smallest recorded specimens with almost all measurements falling within the range of the modern comparative sample used in the present study (that included the Palauan specimens)" and "*H. floresiensis* [sic] may be small-bodied, and specifically within the body size range of extant insular populations, as hypothesized previously (3). The proposed stature of 106 cm [Morwood et al. 2004 (1, 62)] is most likely incorrect and should be re-evaluated. . .."

Summary of DS Signs Matching LB1. The summary is presented in Table 1. No observable signs of LB1 contradict signs typical for, or common in, DS. A detailed discussion of the signs listed in Table 1 is provided in *SI Text*.

Discussion

The Liang Bua Cave skeletal remains demonstrate the existence on Flores, Indonesia, of a small-bodied Australomelanesian population that conforms with its regional and temporal provenance. Against this background, the abundant pathological signs that mark cranial and postcranial morphology of the LB1 individual establish a very high probability of that specimen manifesting DS. Regardless of any specific diagnosis, DS or other, for its array of morphologies to be considered typical for a new species, the taxon's defining feature would have to be an abnormality. Because teratological individuals are barred as type specimens by the International Code of Zoological Nomenclature (75), documentation of serious anomalies in LB1 leaves *Homo floresiensis* as a *nomen nudum.*

Materials and Methods

The endocranial volume of LB1 was determined by filling the cranial cavity with mustard seed. Occipitofrontal circumferences of LB1 and members of the extant Rampasasa population were determined with a tape measure. Corresponding measurements were retrieved from the clinical and paleoanthropological literature. Statistical procedures used for population comparisons are described in the text where appropriate.

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