

Supporting Information

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SI1: Some Previous “Unique” Hominin Species

Although the Flores skeletal remains from Liang Bua Cave, Flores, have some unusual aspects, the gambit of proposing a new species to account for the characteristics of a few unusual bones is a recurrent phenomenon in paleoanthropology. Periodically the discipline is swept by one or another *idée fixe* stimulated by some specimen or sample. Usually, but not invariably, the “new hominin species” hypothesis results from a fresh discovery, but this is not invariably the case. The proposal first was made in an irregularly issued in-house bulletin for staff (1), that 14–15 Ma “Ramapithecus” was the earliest hominid (in the 1960s, hominid was the quasi-equivalent term for which hominin now is used, the shift being related to common subsequent phylogenetic placement of the great apes into the Hominidae). The proposal was based on highly fragmentary gnathic remains that had been known to paleontologists for more than a quarter of a century (2), but “rediscovered” by Elwyn Simons (3) and then promoted by him (4) and his then graduate student, David Pilbeam (5). As with “*Homo floresiensis*,” within a few years the newest “earliest human” was common textbook fare.

Such speculative phylogenetic proposals can be assessed and rejected with assurance by those who have studied the evidence in detail, as in the case of Ramapithecus (5, 6). However, time and again many paleoanthropologists and journalists fail to acquaint themselves with the primary data, instead relying upon and repeating the opinions of others. In such instances, the general acceptance of data-based refutations can take an extended period, possibly in part because the “newest new thing” has been disseminated widely through popular articles and textbooks, thereby taking hold on the professional as well as the popular imagination. Later confirmations of the early negations of these popularized concepts often are not acknowledged as such; after all, misdirections, however inevitable in science, do not redound to the credit of the field in which they occur, as recently learned in physics (7), and it sometimes seems that one “newest, new thing” simply is replaced by an alternative focus of enthusiasm, a newer newest, new thing (this is one of the few situations in which a linguistic comparative may trump a superlative).

Sometimes novel foci for evolutionary interest may represent genuine advances. Thus, the detailed descriptions and diagnoses of the finds from Hadar and Laetoli (8) attributed to *Australopithecus afarensis* appropriately shifted professional and popular attention from long ago Asia to comparatively more recent Africa, and thus coincidentally away from Ramapithecus to genuine hominids. More recently, similarly extensive coverage of additional African fossils, denominated as *Ardipithecus ramidus* (9), is serving to concentrate research into the phases of human evolution earlier than *A. afarensis* but later than the less-extensively documented earliest stem hominins, such as Orrorin (10). However, unlike *A. afarensis* and *A. ramidus*, not all novel taxonomic fabrications prove sustainable; some of them fail to hold up when examined closely and independently by others. The history of paleoanthropology demonstrates, nonetheless, that rejection of a misleading hypothesis, particularly when the hypothesis is supported by established figures and then much more widely by scientific dilettantes, may not take hold for a disturbingly long time.

During such interim periods, which can span decades, inconvenient factors and implications often are overlooked. In the case of Ramapithecus, for example, if that hypothetical taxon really had been a hominid, what were its members doing that was sufficiently different to distinguish them as a unique lineage from other dryopithecine apes found with them in the same deposits?

And where were its (also presumably hominid) descendant populations in the intervening 10 million y or so before the existence of australopithecines, which on the basis of abundant data had been established as hominids for decades? In the Ramapithecus case the correct answers proved to be “nothing” and “nowhere.” The jaws and teeth allocated to Ramapithecus were a selection of the more gracile fragments from larger samples that included more complete, more apelike specimens; so the more gracile remnants comprised not really a separate taxon on a novel adaptive plateau, and hence they did not have differentiated hominid descendants until many millennia later. However, at the time when Ramapithecus was promoted as a hominid, not only were there not any good answers to such questions, but—and this is important in the context of *H. floresiensis*—few paleoanthropologists bothered to raise them at all, and the evolutionary biologists who did paid a price in terms of access to research support and publication. The conventional academic rewards came from staying in the mainstream and generating speculative hypotheses about ramapithecine diet, behavior, and even family composition, among other aspects of postulated “adaptation” (11); that is, publications of speculative epiphenomenological analyses were favored. Drawing attention to the very sparse data was unwelcome and negatively sanctioned professionally, both openly and covertly. Eventually, the Ramapithecus episode ended in confused misdirection (12) and more or less faded from journals in any coherent form, although the “existence” of Ramapithecus as a hominid ancestor persisted in textbooks of anthropology and fields peripheral to it for about another decade.

Preceding Ramapithecus, the classic case of a mainstream *idée fixe*, backed by major figures, long accepted, and doing much harm while the illusion lasted, was Piltdown. It is easy, nearly a century after that episode, to excuse the error as coming from a time in which the total fossil record was far more sparse than it is now. Although there is some truth to that rationalization, it should not be forgotten that Piltdown itself was interpolated into a human evolutionary record that then already was nearly a century old, counting, as we well might, from the find in a Welsh cave (Goat Hole) in 1822, of remains from an anatomically modern young man whose iron oxide stained bones, accompanied by those of Pleistocene mammals, became romantically but misleadingly dubbed the “Red Lady of Paviland” (13). An excellent overview of the Piltdown diversion exists (14). In the context of the Liang Bua Cave bones, an apposite inference is that a plethora of speculative articles published over decades, based on acceptance of some hypothetical phenomenon (a new taxon requiring that all previously accepted patterns of human evolution be discarded) ultimately was worth far less than close examination of the primary specimens from the skeptical standpoint of one human biologist, Joseph Weiner (15). It did not matter that remains of more than one individual had been recovered, or that appropriately primitive stone tools (“eoliths”) and bones of Pleistocene mammals were found in association with the cranial fragments, or that among many supporters of Piltdown as setting a new pattern human evolution were some exceedingly well known anatomists and anthropologists (not only Sir Arthur Keith but also Grafton Elliot Smith and Teilhard de Chardin). Piltdown turned out to be a fraud, whereas Ramapithecus proved merely to be a case of misguided enthusiasm and suspension of disbelief, but both cases bear testimony to the ability of paleoanthropologists to create and sustain seemingly plausible delusions for years or even decades, as the primary data are

ignored or misconstrued in support of speculative discussions of epiphenomena.

Ideas have consequences, and bad ideas can have adverse consequences. Acceptance of the Piltdown bones as tangible evidence of a new species that supported the incorrect theory that the brain had led the way in human evolution blocked for decades general acceptance of small-brained australopithecines as valid ancestors, despite a growing body of evidence collected industriously by Raymond Dart, Robert Broom, and their associates. In the case of *H. floresiensis* it seems that scarce scientific resources are being expended in the unproductive search for it as well as a similarly hypothetical, dilettante-imagined “*Homo sulawesiensis*” (16).

What do these missteps share in common? The number of specimens is important. Sample size problems are compounded with other factors, including lack of confirmation by new discoveries and failure to generate predictions that can be treated as testable hypotheses. Perhaps most important, purely hypothetical hominins tend to persist as long as people focus on the epiphenomena—the permutations and penumbras of the explanations—rather than on the primary data. After all, it seems more sophisticated to conjecture about “big ideas” rather than to look at mundane evidence, particularly when that evidence is guarded from independent scrutiny. Although Piltdown was accepted as a valid phenomenon, there was far too little skepticism about what, in retrospect, seem to be some rather strange elements. Among these elements was an implement, carved from the thigh bone of late Pliocene or early Pleistocene *Elephas meridionalis*, 400-mm long, 100-mm wide, and 50-mm thick, shaped rather like the blade of a cricket bat. Where are the comparably needed skeptical assessments of what should be considered as contradictory but rationalized explications of the Flores tools?

Some doubts are raised about the Liang Bua Cave specimens, but selectively. One question that our group has faced time and again from colleagues and journalists is this: How could there have been a whole population of abnormal (or sick, or diseased, for example) individuals in Liang Bua Cave on Flores?

There are several answers to this question, which seems rooted in misunderstanding, if not a disingenuous façade. Example from a recurrent source: “. . . Jacob et al. (2006) attempted to dismiss these new fossils as pathological, pygmoid, Australomelanesian humans” (17). Statements of that sort are not isolated, but rather constitute a recurrent trope among believers in the reality of the taxon *H. floresiensis*. Another recent example is: “The unusual combination of extremely small brain size, short stature, and other unique physical traits of *H. floresiensis* have led some to argue that the skeletal remains represent a population of pathological modern humans” (18). The creation of a straw man to attack and refute the positions of others usually is a sign of weakness in the position of the fabricators. Our response is that, quite simply, we never have said or written anywhere that all of the skeletons from Liang Bua Cave are abnormal; rather, that so far the evidence indicates abnormality only in LB1. There is another more complex answer, but that is presented in the companion paper to this report (19).

SI2: Cephalic Index

The cephalic index or cranial index is the ratio of the maximum (biparietal) width of the head of an organism multiplied by 100, divided by its maximum (occipito-frontal) length, with both measurements taken in the transverse plane. The index was defined by Anders Retzius in the 19th century and first used to categorize human remains excavated in Europe. Because soft tissues are of relatively uniform thicknesses around the heads of living humans in the transverse plane of measurement, figures from past and living people are approximately comparable.

By dividing the continuum of ratio values into three discontinuous categories, human populations can be characterized

descriptively as dolichocephalic (long headed), mesocephalic (medium headed), or brachycephalic (short headed).

Conventional ranges for these categories are: dolichocephalic <75, mesocephalic 75.0–79.9, brachycephalic 80.0 (some sources use slightly different dividing lines for females).

Measurement of cranial length and breadth is not complex. It can be accomplished with a pair of spreading calipers on a skull or reasonably accurate cast, and in the case of LB1 approximated even in two dimensions with a ruler on widely available published photographs (figure 1 in ref. 20 and figure 1 in ref. 21).

The skull shape of LB1, compared with representative Australomelanesians, tends toward brachycephaly. The average cranial indices of Australomelanesians (22) range from 68.8 to 72.7, with LB1 at 79.0 lying ~2 SDs above the midpoint average (supplementary table 1 in ref. 20). As noted in the text of our report, this index value also was biased downward in the original publication (1). Thus, the repeated erroneous descriptive prose references to LB1 cranial proportions raise the possibility that verbal descriptions have been influenced by preconceptions, perhaps unconsciously, thereby tailoring reported results to a priori taxonomic conclusions. Quite simply, the cranial index of LB1 is borderline brachycephalic, more so than modern humans in its region and more brachycephalic than most fossils (Fig. S1).

Numerous previous craniometric analyses have been reviewed (18); these have produced contradictory results arising from numerous shortcomings of experimental design and sample composition.

SI3: Skull (Cranium Plus Mandible and Dentition)

Vault. Endocranial volume, proportions (length, breadth, and height), and shape (chiefly left-right asymmetry) all have been disputed since the earliest published reports on the LB1 skull. Just as the framing hypothesis has shifted from hypothetical island isolation and dwarfing to (comparably hypothetical) migration from an African origin at a pre-erectus level, it more recently has been conceded that the LB1 cranium is asymmetrical and exhibits proportions indicative of developmental abnormality, as noted below (18, 21).

Endocranial Volume. There have been several measurements of endocranial volume in LB1: 380 mL (20), 417 mL (23), 430 mL (24), and 426 mL (25). The extremely low value initially reported (20) remains below all others published since then by 10% or more. The only attempt to explain the endocranial volume discrepancy between the original report (20) and subsequent higher determinations was by Falk et al. (26), who noted that the “difference is attributable to how cranial holes were plugged” when Brown measured the endocranial volume with mustard seeds. However, plugging holes (a common practice before determining volume with seed filling) is unlikely to lead to a lower volume than the CT scan technique used (23) unless an excess of the material used to plug holes also somehow projected into the cranial cavity (and then such excess material were removed before the CT scan or not detected by it); such a result would indicate an improbably low level of technical skill for Brown et al. (20). Our higher determination of 430 mL [which differs by only 3% from the CT scan made by Falk et al. (26)] also was made by filling with mustard seed (24) after removing some matrix inside the vault missed by Brown’s group. A simple inference is that the low endocranial volume, stated explicitly to be “equal to the minimum estimates for *Australopithecus*” (20), resulted from an apparent technical error that biased reported cranial capacity downward toward those of earlier hominins, coincidentally heightening media attention (27). This impression has been fostered further by visual contrasts of the LB1 skull with an unusually large *Homo sapiens* skull of unspecified provenance [see figure 1 in the “Flores Hobbit-Like Human Picture Gallery” on the National Geographic

website (http://news.nationalgeographic.com/news/2004/10/photogalleries/homo_floresiensis_1/). We provide here a more appropriate regional and temporal comparison of LB1 with Liang Momer E from Flores, dated to 3,000–5,000 y ago.

Cranial and Endocranial Cast Proportions. Verbal descriptions of the LB1 skull have been subjective, and increasingly contradictory with time. Reportedly “The cranial vault is long and low” and “. . . indices of cranial shape closely follow the pattern in *H. erectus*” (20) and “align LB1 with archaic *Homo* . . . and *Homo erectus* (s.l.) in particular, such as the long, low cranial profile. . .” (28). In contrast, Falk et al. characterize the skull of LB1 as “extremely brachycephalic” (29) and according to other investigators “The LB1 vault is anteroposteriorly short relative to its breadth” (18), with similar remarks repeated twice elsewhere in the same text. Our own measurements indicate the index value of 80.1, whereas breadth and length reported by Kaifu et al. (18) yield an index value 82.0. Brachycephalic deviation from reference population norms is a feature that occurs in numerous developmentally abnormal syndromes, such as trisomy 21.

Similar remarks can be made about the several successive analyses of the LB1 endocast. One report (23) used a sample that comprised STS 5, KNM-WT 17000, 5 *Homo erectus* skulls, 10 gorillas, 18 chimpanzees, 10 normal modern humans, and 1 adult female pygmy. In that study, one principal components analysis based on length, breadth, height, and frontal breadth, grouped the LB1 endocast with *H. erectus* and separate from *H. sapiens*; a second principal components analysis that excluded *H. erectus* endocasts grouped LB1 exclusively with *H. sapiens* rather than a variety of other hominoid primates. Subsequently, LB1 was compared with 10 normal modern humans and a somewhat heterogeneous sample of 11 microcephalics (29). In this case, discriminant and canonical analyses were said to group LB1 with the normal *H. sapiens* rather than the microcephalics. A still later paper by the same set of authors reported essentially the same results (26). Within the same research group, the outcomes of various multivariate analyses appear to reflect more the sample composition and dimensions selected than the features of LB1 itself. Moreover, the overall conclusions about internal endocast dimensions, proportions, and anomalies must remain suspect as long as repeated denials of external cranial asymmetry remain uncorrected (see below). An independent study derived additional ratios from the same dataset (26, 29), augmented by much original data (30). This study showed that that several LB1 endocast ratios not computed by Falk et al. (29) fall largely outside the range of *H. erectus* and normal *H. sapiens* endocasts but within the range of microcephalic endocasts, thus supporting the suggestion (24, 31) that LB1 represents a pathological microcephalic *H. sapiens* rather than a hypothetical new species based tenuously on a single specimen.

Cranial Base Angle. Purportedly “[T]he cranial base angle (basion-sella-foramen caecum) of 130° is relatively flexed in comparison with both *Homo sapiens* (mean 137°–138° . . . and Indonesian *H. erectus* (Sambungmacan 4, 141° . . . Other small brained hominins, for instance STS5 *Australopithecus africanus*, have the primitive less-flexed condition” (20). The source for the 137–138° value (32) does not give sample sizes or measures of dispersion but much of their data derive from other studies (33, 34), showing that a sample of 99 extant humans yields a cranial base angle of 134.7° with SD = 6.09° and a range of 116–149°. Consequently, LB1 is not unique in this regard, or even unusual.

Cranial Vault Bone Thickness. Reportedly “cranial vault bone is thick and lies within the range of *H. erectus* and *H. sapiens*” (20). The deposits from which all of the Liang Bua Cave skeletons are derived span that recorded only for our own species, *H. sapiens*. Consequently there is no reason to suggest a particular affinity to

H. erectus, unless one accepts that *H. erectus* should be subsumed into our own species (35, 36), which is a matter of conceptual importance but aside from the main point of this paper.

Table S1 (20) provides data on cranial vault thicknesses for LB1 at the following sites: midfrontal, bregma, parietal eminence, lambda, asterion, and e-o-p. For comparison, measurements at these same points were provided for global pooled-sex *H. sapiens*, in which sample sizes ranged from 575 to 670, for which samples were provided the means and SDs, as well as minimum and maximum values. In all cases LB1 fell within the minimum/maximum ranges for the recent *H. sapiens* samples. Consequently, in simplest terms there is no objective basis for saying that the cranial vault bone of LB1 is thick; the verbal statement (20) is not warranted by the data provided. There is little more that can be inferred reliably, particularly given the absence of any information on the population and regional composition of the recent *H. sapiens* samples, which were very heterogeneous. Of the six cranial thickness measurements given, two (midfrontal and asterion) were above the global population sample midpoint, one (parietal eminence) was the same, and three (bregma, lambda, and e-o-p) were below, with the average of all six thicknesses falling at only about 55% of the sample maximum.

Comparison of LB1 with the global sample data are likely to be misleading directionally, because the Liang Bua Cave sample from Flores lies within the Australomelanesian population region. Australian aboriginal skulls from within that region are thicker than other populations (37) (table 8 in ref. 37 provides limited data for skull vault thickness); at vertex, Australian aboriginal skulls average 26% thicker than North American “Caucasoids” (7.33 mm vs. 5.8 mm). The skull vault of LB1 is not unusually thick objectively, and in the context of its appropriate regional population, can be characterized as thinner than average.

Foramen Magnum. Descriptions of fossil hominin skulls commonly report the antero-posterior placement and angulation of the foramen magnum, but not its length and breadth. The LB1 foramen magnum is described as narrow (21 mm) relative to its length (28 mm), but it was not stated whether this information was included to suggest that LB1 is unique, primitive, derived, normal, or abnormal (20). The foramen magnum is commonly narrowed in various developmental abnormalities, including achondroplasia and Down syndrome (38); we deal definitively with this and related points in ref. 19.

Other Cranial Base Features. It originally was noted of LB1 that “In common with Asian, and some African, *H. erectus* a deep fissure separates the mastoid process from the petrous crest of the tympanic. Bilaterally there is a recess between the tympanic plate and the entoglenoid pyramid. These two traits are not seen in modern humans, and show varied levels of development in Asian and African *H. erectus* and Pliocene hominins” (20). That statement is incorrect; these features commonly are found in Australian and Tasmanian crania (39–41) as well as Kow Swamp 5 and Keilor (42), a point we made several years ago (24) without any rejoinder being published since. These features obviously are not unique to LB1 in comparison with present and past members of *H. sapiens* in the geographic region of which Flores is a part, and logically cannot be a defining feature of the supposed new species.

Mandible. “The anterior portion of the corpus is rounded and bulbous and without a chin” (20). Although this absence of an external chin has been stressed repeatedly as a “primitive” feature, it is not unusual among populations in the region. This point, made years ago by Jacob et al. (24) has been denied repeatedly since, with some of these denials introducing distortions. One publication (43) provided a radiograph of an

unidentified Australomelanesian whose mandible displays a hard tissue chin, around which a supposedly nonprojecting soft tissue chin was drawn in, with the artificial enhancement made presumably because the image itself was unclear. Regardless of whatever information was meant to be conveyed by the altered image (43), the anterior region of the mandible is variably developed among Australomelanesian populations including those now living on Flores, and nonprojecting bony chins occur widely (Fig. S3).

This point has been established definitively for extant Flores *H. sapiens* now living on Flores (44). In the sample of 52 Rampasasa individuals (22 males, 30 females), 76.9% had neutral or negative chins as assessed radiographically from hard tissues (Table S2); only one male had a positive hard tissue chin that was masked by soft tissue that made it appear negative. Any attempt to demonstrate the range of variation in this phenotypic characteristic with a single example is inherently typological.

The LB6 mandible is said to confirm key features of LB1 mandibular morphology. This is not the case except in the general sense of overall size, as can be seen from figures 1–4 in ref. 43. The symphyseal region of LB6 inclines more toward the vertical as in some extant Rampasasa (44) and lacks the supposedly more “primitive” posterior, inferior, curvature of LB1 that is present in other extant Rampasasa (44). This extent of variation in the chin region even between two LB specimens parallels that documented by Hastuti, et al. (44) in the extant Flores Rampasasa population. The variants of the chin in LB1 and LB6 are observed in numerous Australomelanesian populations, past and present.

Another mandibular feature of LB1 is described thus: “The ramus is broadest inferiorly, slopes slightly posteriorly and is thickened medio-laterally, and the coronoid process is higher than the condyle” (20). The relative heights of the coronoid process and condyle have no particular phylogenetic valence that would favor allocation of the Liang Bua Cave bones to *H. erectus*, to unspecified very early *Homo* populations, or to australopithecines. Several studies (45, 46) show that relative heights of the condyle and coronoid process vary widely among extant human, Upper Paleolithic, early anatomically modern (i.e., pre-Upper Paleolithic), and Neandertal populations. These features and others favor the hypothesis that the Liang Bua Cave skeletons represent normally variable *H. sapiens* rather than some very primitive hominin population caught in a time warp.

The contrast presented by the LB6 mandible with that of LB1 (43) is even greater for the morphology of the ramus than for the symphyseal region. The taxonomic irrelevance of a coronoid process being higher than the condyle is underscored within the Liang Bua Cave sample itself, because in LB6 the coronoid process is not higher than the condyle, but rather is just about exactly the same height in the orientation shown.

Emphasis on absence of the external bony chin as a purported taxonomic uniqueness although it is not, and of the coronoid process being higher than the condyle, although this also is not a unique feature in the Liang Bua Cave skeletal sample, has served to divert attention from a different but genuinely unusual feature of the LB1 mandible (again, not shared with LB6): its strikingly tall ramus.

In discussing the possible functional significance of a tall mandibular ramus, one study (47) presented two alternative measurements of mandibular corpus height: from the inferior margin of the mandible or from the occlusal surface of the teeth to the condyle (which was the superior point measured in their study), the latter measurement removing any potentially confounding effect of mandibular corpus thickness. The results showed that in a sample of 62 extant human mandibles, the mean condylar height above the occlusal plane for both males and females is about 36 mm; that is, in their sample there was no difference attributable to sexual dimorphism. In a sample of 20 chimpanzees divided equally between males and females, the

respective measurements were 41 mm and 40 mm, for a difference in ramus height of 2.5%. Ten male and 10 female gorillas showed mean heights of 72 mm and 60 mm, respectively, the ramus in the males thus being 20% taller. In an independent study (48) mandibular ramus height in human males was reported to be about 10% greater than that in females. These limited samples of hominoid primates show the range of sexual dimorphism to be 0–20%, with males on average tending toward taller rami. We note in passing that LB1 originally was identified as female (20), an impression that has been propagated widely and uncritically. In contrast, our explicit quantitative analysis (5) showed that LB1 was a gracile male, which is reinforced by the results reported here. The ramus of LB1 is substantially taller than that of LB6 (figure 3 in ref. 20). Others have found ramus breadth to be the best predictor of sex, with males having broader rami (49). The ramus of LB1 is broader than that of LB6, again supporting our diagnosis of LB1 as male and contradicting the original impressionistic assessment (20).

Our measurements from the paper by Brown and Maeda (figure 3 in ref. 43) show the height of the mandibular ramus in LB1 to be very substantially greater than that of LB6. From the inferior surface of the mandible to the condyle, the ramus of LB1 is 40% taller than that of LB6; measuring to the coronoid tip produces a moderately higher figure for LB1 of 55%. From the occlusal surface to the occipital condyle, the ramus of LB1 is 50% taller than that of LB6; measuring to the slightly higher coronoid tip produces a 67% greater height for LB1.

Differences in ramus height between LB1 and LB6 (generally unremarked until now) are substantially greater than reported in other studies of hominins and, more widely, hominoid primates. These measurements are discrepant enough to direct attention to a situation encountered in robust australopithecines, which also have somewhat dished midfacial regions and very tall mandibular rami (50). In robust australopithecines these facial features are combined with relatively small braincases; because LB6 is a mandible without a cranium, this comparison cannot be explored except as an intriguing question, but if the australopithecine analogy holds, it implies that LB6 had a larger cranium than that known for LB1; a more extensive comparative study in that direction is beyond the scope of this paper and the existing data available to us. In the less hypothetical realm, however, several additional suggestions are possible. First, functionally, the cross-sectional mass of the masseter muscle shows a positive correlation with mandibular ramus height; we do not know what implications there might be of a relatively larger masseter in LB1. Second, developmentally the human skull achieves its adult size through a supero-inferior gradient of maturation, with the potential for bidirectional developmental influences between the lateral cranial floor and the face until about 11–12 y of age, there being a structural interface between brain and facial anatomy (51). Third, genetically, there is evidence for an association between mandibular height and the growth hormone receptor gene, as elucidated in a Japanese population (52).

One recent computationally ambitious study of mandibular measurements in the Liang Bua Cave sample (53) puzzlingly omits inclusion of LB6 entirely. Even so, results of their canonical discriminant analysis group LB1 more closely with the La Quina and Gibraltar neandertals, and also with Peninj, than with AL 288-1, and as closely with some modern humans as with Sk15. Other highly formulaic analyses of landmark data in the absence of genetic, developmental, and functional considerations (54) only reinforce the impression that the morphology of *H. floresiensis* really is just that of the individual specimen, LB1. Landmark hyperspace explorations tell us little other than that LB1 is dimensionally strange, which from the first has been evident by inspection.

Dentition. In terms of dimensions and morphology, teeth of LB1 and LB6 are not in any way unique compared with those of anatomically modern *H. sapiens*. There are some interesting details regarding wear and crown morphology alterations of LB1 teeth, but these have been described (55) and discussed (56) elsewhere.

SI4: Upper Limb Skeletal Elements

Scapula. No scapula has been described for LB1. Three major portions of this bone are known from specimen LB6/4 (57), an adult. The scapular spine appears horizontally oriented as it is in other *H. sapiens*. The scapular neck shows a slight dorsal orientation to the glenoid fossa, attributed to distortion. The ventral bar/glenoid angle is reported as 157°, also in the range of extant humans. None of the angles identified by Oxnard (58) as differentiating scapula form among primate locomotor groups distinguishes LB6/4 statistically from those of living humans, and are reported as falling within the corresponding 95% fiducial limits of modern humans. In the descriptive and comparative context provided, the scapula of LB6 accords with our hypothesis (24) that, aside from LB1, the Liang Bua Cave skeletal sample represents developmentally normal extant *H. sapiens* of small body mass and stature.

Clavicle. The clavicle is the first long bone to ossify, a process that begins in condensed mesenchyme during the fifth and sixth embryonic weeks of embryonic life from two ossification centers, one medial and the other lateral; fusion occurs during fetal development. Epiphyseal ossification occurs at both the acromial and sternal ends of the bone; the sternal end fuses with the diaphysis between 18 and 25 y of age, making this the last long bone to fuse (59). Such a developmental pattern would be expected to permit postnatal functional influences on individual development.

There are numerous genetic diseases that alter clavicle morphology. Lenz–Majewski hyperostotic dwarfism causes a broad and thick clavicle, along with progressive skeletal sclerosis, severe growth retardation, and mental retardation (60). Melnick–Needles syndrome (Otopalatodigital syndrome spectrum disorders), can cause clavicular hypoplasia, curved long bones, and flared metaphyses (61, 62). Otopalatodigital syndrome type II presents with thin clavicles, microcephaly, cleft palate, and overlapping fingers (63). Maroteaux-type acromesomelic dysplasia manifests a curved clavicle with pronounced disproportionate short stature (64). This list is only a partial summary, and the clavicle remains only minimally described—or undescribed—in many other inherited disorders, including some of the more common ones, such as Down syndrome (trisomy 21). Trisomy 13 and trisomy 18 exhibit generally thin clavicles, and Turner syndrome often includes clavicles that are thin laterally (65).

An extended description and some dimensions for the right clavicle, LB1/50, has been previously published (57). It is missing the sternal end; the lateral end also has been damaged postmortem. Views include superior, inferior, anterior, and posterior. Discussions for most of these views make no claim for uniqueness. An exception is the posterior (i.e., dorsal) view: “Voisin (2006) has reported that modern humans are distinct in displaying a single inferior curve of the clavicle in posterior view. His preliminary examination of LB1/5 (based on photographs only) indicates that it retains the primitive double curvature seen in African apes and all hominins except modern humans (Voisin, pers. comm.)” (57).

Over more than half a century the clavicle has received a fair share of attention by physical anthropologists, including an early paper on techniques for its measurement (66). More recently, Voisin also has published extensively on this skeletal element (67–73). Although we do not have the text of the personal communication from Voisin to Larson et al. (57), two of us (M.H.

and R.B.E.) have examined the original specimen as well as figure 1 of Larson et al. (57). In the posterior view, both “curvatures” of the LB1 clavicle are not pronounced. This finding accords with the following statement published by Voisin (71): “Sometimes, some individuals [that is, individual extant humans] show two curvatures in dorsal view, but these curvatures are slight in regard to the condition exhibited in the great apes.”

The approach of Olivier for the quantifying the degree of curvature of the clavicle was applied to LB1, with awareness of strong methodological limitations. A significant piece of the sternal end of the clavicle is missing. This defect required that the total length be extrapolated from the preserved portion, and consequently that some points of measurement be estimated. Furthermore, the only source available for this study was the published composite figure shown in ref. 57; this approach is not as desirable as having a CT scan of the clavicle, which was unavailable to us. Three measurements were estimated for each curvature, based on the range of extrapolated total clavicle length given (57). The extrapolated length was assumed to all belong to the sternal end. This approach probably did not greatly affect measurements of the external and inferior curvatures but there is considerable uncertainty (Table S3).

For the external curvature, LB1 is within 1 SD of the mean of *H. sapiens* of 16.1, according to the reference data (71). For the internal curvature, LB1 is also within 1 SD of the mean of *H. sapiens* of 12.6 if the smallest total length is taken. The inferior curvature of LB1 is within 1 SD of the mean of *H. sapiens* of 5.1. LB1 is within 2 SD of the mean for *H. sapiens* for the superior curvature, which has a mean of 2.9.

In addition, CT scans of one human subject included in our pilot study, undertaken to provide comparative developmental evidence from patients combining short stature and skeletal anomalies, showed clavicles with some modest double curvature (subject’s superior curvature = 4.89 mm vs. human reference sample mean of 2.9 mm, SD = 1.5 mm, $n = 33$; subject’s inferior curvature = 9.45 mm vs. human reference sample mean of 5.1 mm, SD = 2.3 mm, $n = 33$). Against the background of even these limited data, use of the term “primitive” for variants that occur in some living humans, normal or developmentally abnormal, is pejorative and misleading.

Representation of the short clavicle of LB1 in *H. floresiensis* (i.e., members of the Liang Bua Cave skeletal sample) as a primitive retention, recurs in context of the statement “The recent description of comparatively short clavicles from Dmanisi (Lordkipanidze et al. 2007) supports the view that a relatively short clavicle is characteristic of early *H. erectus* and is probably the primitive condition for hominins” (1). Such a statement implies that the information contained in human clavicle size and shape is exclusively phylogenetic (because no other factors are discussed) and thus has direct taxonomic valence. The clavicle and other bones surely reflect evolutionary heritage to some extent, but there is failure to consider the possibility that the morphologies of the clavicle and other bones can contain individual developmental information as well (57). In contrast, there is strong evidence for functional influences on clavicle form and dimensions (74), with recognition that as “. . . an early-ossifying, late-fusing bone . . . [the clavicle] . . . should show clear signs of lateral loading bias, with the right side being the more heavily loaded at the population level” (74). Furthermore, based on a sample of 136 individuals including both sexes and juveniles through adults, “. . . the right clavicle tends to be more robust. In the adult males (the group in which the right clavicle is significantly thicker in both sagittal and vertical dimension at its mid-shaft), lateral curvature is significantly less in the right clavicle—which suggests that the right bone is more adapted to resist lateral buckling stresses in axial loading. The other clear correlates of length differences are asymmetrical development of the areas of attachment of the trapezoid and costoclavicular

ligaments” (74). Against this broader functional background, as well as analysis of the limited empirical evidence, the categorical statement (57) that the structure of the LB1 clavicle is distinct from extant humans by its proportions and supposedly primitive double curvature is insupportable from available data.

Humerus. Two initial points should be recalled here: first, at the time of the initial description and diagnosis of this hypothetical taxon (20), the upper limb bones had not yet been recovered, so their attributes could not have been part of its supposedly unique mosaic of features; second, as with the femora, the humerus of LB1 is the only example of this bone in the entire Liang Bua Cave skeletal sample. Thus, as for the femora, any statement about “the humerus of *Homo floresiensis*” should be read more conservatively as “the humerus of LB1.” Pertinent attributes of the LB1 humerus include its overall size (principally length), robusticity, and torsion.

Length. The LB1 right humerus is complete aside from post-mortem damage to the anterior surface of the head and greater tubercle; its length is given as 243 mm (75). This figure is repeated by Larson, et al. (57), who note that “The humerus... while short in an absolute sense, can be matched to the lower extremes of small-bodied African pygmies and Andaman Islanders (WLJ, pers. obs.)” Thus, the length of the LB1 humerus simply is not unique among extant humans.

Beyond size are bone shape considerations. “When compared with a modern human humerus scaled to the same length, the most obvious differences are the greater diameter of the LB1 shaft and the limited degree of humeral torsion (that is, rotation of the humerus head medially relative to the mediolateral axis of the distal end; Fig. 4)” (75).

Width. “All the major limb bones of LB1 have shaft and articular surface dimensions that are robust relative to length” (75). This definition of robusticity is used repeatedly in numerous subsequent papers. “In external dimensions, the humerus of LB1 is indeed robust” (23); similarly, “. . . LB1 has extremely high levels of robusticity for all limb bones. . .” (76).

“The midshaft appears rounded in cross-section with an anteroposterior diameter of 17.44 mm and a mediolateral diameter of 16.35 mm” (57). The exclusive use of external bone diameters (in isolation or in proportion to length) to represent robusticity, once standard, now is idiosyncratic and outdated. Among other investigators a broader array of robusticity measurements is used (77). The more common of these measurements involve application of beam theory, in which the cross-sectional geometry of long bone diaphyses is quantified to assess the mechanical competence of a bone (78). In this approach, calculations of biomechanical properties of cross-sections of bone diaphyses are dependent upon accurate determination of periosteal and endosteal contours of the diaphyses. Methods now available can use silicone molds and biplanar radiographs to provide accurate estimates of cross-section contours without damaging the specimen or incurring the costs and other limitations of CT (79, 80). Given the weight placed on the supposed robusticity of LB1 as a species-distinguishing factor, one would expect that the most functionally informative methods would be used.

In fact, these methods have been used, although not on LB1. Jungers previously made a case for use of such methods (81): “Employment of this methodology in the mechanical assessment of fossil long bones has been limited to date to fortuitous breaks or fragmentary specimens. . . , since postcranial remains of fossils are usually too rare to be sacrificed by sectioning.” The existence of LB1 CT data are implied by the statement of Falk, et al. (26), who wrote “. . . CT scans indicate that the cortical bone of the LB1 humerus is not especially thick, but rather is within the human range.” It is puzzling that these numerical CT scan data have not yet been published. They might be redundant, in light of the statement by Morwood et al. (75) that in the case of the LB1

humerus “. . . the mid-shaft was broken post-mortem. . .” That being the case, why were the broken ends of the shaft not photographed or measured directly and the cortical thicknesses reported? These data seem to have existed since at least 2005 in the case of the broken humeral shaft, and since at least 2009 for the CT scans. Reference to LB1 humeral “robusticity” inferred from only the most rudimentary external dimensions is more limited than necessary if the Liang Bua Cave skeletons are as important as represented. In any case, another claim of “primitiveness” or “uniqueness” lacks support.

Humeral torsion. Measurement of humeral torsion is complex for a number of reasons. The pertinent anatomical and methodological complications are reviewed informatively and independently of the controversy surrounding interpretation of the Liang Bua Cave skeletons (82, 83).

Morwood et al. (75) noted “In LB1, humeral torsion is approximately 110°, which is the norm for *Hylobates* and quadrupedal primates such as *Macaca*, but is significantly less than in large-bodied apes, modern humans (141–178°) and other known hominins, including *Australopithecus*.” Lack of any qualification in that report created the impression that the information embodied in humeral torsion is only phylogenetic, consequently pertinent to support for the new species created the year before (20). The reported humeral torsion, being outside the range of modern humans, was held to constitute another uniqueness of *H. floresiensis*. However, this degree of torsion also is outside those of all large-bodied apes and hominins. *H. floresiensis*, as a member of the genus *Homo*, should have humeral torsion within the hominid (large apes plus humans) range, were it a healthy normal individual, so its reported value was more likely to be diagnostic of pathology than uniqueness. We responded (24) by noting that the extent of humeral torsion in any individual is developmentally labile, and that the abnormally low amount of humeral torsion in LB1 was consistent with the extremely weak muscle development indicated by its muscle insertions. Such weakness also is pertinent to the debate about LB1 humeral “robusticity” (see above). Numerous studies, some cited as references by Cowgill (82), document developmental influences on humeral torsion as a result of various pathologies (84), occupations (85), and sports, particularly those involving throwing (85; see also Whiteley et al. 86–88).

Larson (89) remarked that “since the most proximal end of the LB1/50 humerus is damaged, it is possible that the published measurement of 110° of humeral torsion is inaccurate.” The new measurements, using two slightly different indicators of humeral head position, were 119° and 121°. These measurements, not implausibly, were averaged to provide a new published estimate of 120°. Then this figure was averaged once again (not so plausibly) with the previous estimate—possibly inaccurate by her statement—to arrive at a new average of averages of 115°. This puzzling “best estimate of humeral torsion in LB1/50” was repeated in Larson et al. (57). Data in figure 4 of Larson (89) show that the 120° value is within the range of several regional populations pertinent to Flores inhabitants: Australians ($n = 4$), Melanesians ($n = 14$), Senoi ($n = 4$). Even the dubiously determined 115° figure still is higher than the average for East Central African Pygmy females ($n = 6$).

Overall, the publication history of LB1 humeral torsion—and indeed of its humerus length and robusticity as well—is one of retreat from initial stress on taxonomic uniqueness (75) to present banality of being somewhat unusual, although not among extant small-bodied humans (57, 89).

Ulna. Our comments are based on study of the specimens (by two of us, M.H. and R.B.E.) plus review of two published accounts (1, 23). Discussion is limited here because the publications cited make no particular claim for taxonomic uniqueness other than the cryptic comment in the supporting information published

online by Morwood et al. (75) with reference to the LB1 right ulna: “As LB1 is from a species with different postcranial dimensions and anatomy to *H. sapiens* it is not known how accurate this estimate is.” Such a statement confuses hypothesis with postulate in assuming a priori that *H. floresiensis* is a new species.

The material most completely described comprises LB1/51, a partial left ulna (205 mm in length, lacking proximal and distal portions), and LB1/52, a more nearly complete right ulna (190 mm with distal portion of shaft and head missing, reconstructed to ~205 mm).

Also recovered were LB6/3 and LB2/1. From the same spit [51] as LB1, LB6/3 preserves the proximal portion of a shaft with a length of 137 mm. Unfortunately it is not figured in Morwood et al. (75) or Larson et al. (57). Alignment of the preserved portions of the LB1 and LB6 ulnae might have been informative with regard to estimates of overall size (e.g., stature) because the ulnae are the only two long bones common to these two individuals, and because statements about the relative and absolute statures of various individuals from Liang Bua Cave are very problematical and contradictory; see the section on tibia in this paper (below) and also the monograph by De Klerk (90). The corresponding measurements provided in table 3 of ref. 57 for the proximal ends of the ulnae are consistently smaller in LB6/3 than in LB1/52.

Regarding the ulna specimen LB2/1, measurements provided in table 3 of ref. 57 for the proximal ends of its ulna generally, but not invariably, fall between those of LB6/3 and LB1/52. Given the much greater age of this specimen (about 74 ka in comparison, with 15.7–17.1 ka for LB6 and 17.1–18.7 ka for LB1), as well as the allusion by the authors to some unspecified pathology, further study seems warranted.

Morwood et al. (75) conclude with the statement that “Other *H. floresiensis* morphological traits, for example in the humeral torsion and ulna, are not shared with any other known hominin species. . . .” Previously in this report we found no objective support for that statement with regard to the humerus. Similarly, the ulna manifests no uniqueness at any level, against a background of individual variation that is normal for human populations, past and present.

Radius. As for the ulna, our comments here derive from the restricted study of the specimens (by M.H. and R.B.E. in February 2005) plus the published accounts (57, 75) that are overlapping.

The length estimated for the LB1 radius is 190 mm with SE = 4.208 mm.

Uniqueness in the radius is implied by the statement in the caption of supporting information figure 5 by Morwood et al. (75), in which LB1 radius length is estimated from ulna and radius lengths in extant humans: “As LB1 is from a species with different postcranial dimensions and anatomy to [sic] *H. sapiens* it is not known how accurate this estimate is.” That qualifier stands in contrast to their own statement in the text (75): “The arms of LB1 share the distinctive elongated distal segment common to tropical modern humans, including populations of small average stature, and have an estimated brachial index ((radius length × 100)/humerus length) of 78, which is close to the African human male average.” Synthesizing all this, it seems to be suggested that the ulna and radius (as well as humerus) lengths of LB1 may be those of a (dubiously diagnosed) female of a (hypothetical) different species, but they exhibit the proportions that one would expect for extant tropical male *H. sapiens*.

Although no radius appears known certainly for LB1, the penultimate entry in table 1 of ref. 75 is: “Radius (LB1?) Both epiphyses missing. 124 × 16.5 mm. (Note: from baulk collapse).”

We have not found further references to this possibility. Other pertinent radius specimens here are LB4/1, a juvenile left radius with unfused epiphyses, and adults LB6/2, and LB3. For some reason the juvenile radial fragment LB4/1 is shown in comparison

with (presumably) adult left radius LB3, but is not compared dimensionally or illustratively with any juvenile radii of known *H. sapiens*.

Adult specimen LB6/2 is a complete right radius with a highly distorted distal portion, about which Larson et al. (57) write, “which Morwood, et al. (2005) interpreted as the result of an unset, healed fracture with compensatory remodeling and callus development.” Larson, et al. (57) further comment: “A radiograph of the radius supports the interpretation of a healed fracture resulting in ulnar displacement of the distal radius (Ortner, pers. comm.; Sampson, pers. comm.).” The anatomical location of this distal radial irregularity mimics Madelung deformity, but without our being able to examine the specimen with this possibility in mind, no definite statement can be made and resemblances probably are coincidental. A healed fracture would be consistent with our overall general position that, aside from LB1, other individuals from the Liang Bua Cave site appear developmentally normal.

Although incomplete, lacking its head and distal portion, the partial radius LB3 merits discussion. It was recovered from one of the oldest sections of the Liang Bua Cave deposits, dated to about 74 ka (20) and discussed in table 1 of ref. 57. Although the shaft of this bone is rather straight and its cortical bone is noted to be thin (1.3–1.7 mm) (57), its preserved portion is 164 mm, and its estimated that total length was ~210 mm. If that reconstruction is accurate, it would place this bone within the normal modern human range. Henneberg and Thorne (31) estimated that this radius corresponds to a modern human of the stature 1.51–1.62 m tall. Larson et al. (57) comment that “. . . like LB6/2, the radial tuberosity faces more directly medially than in modern humans, judging from the position of the interosseous crest.” However, as no comparative evidence is adduced, this remains a description without demonstration of taxonomic uniqueness.

SI5: Carpal Bones

Comments on Morphology of LB1. The specimens of LB1 described so far, all from the left side, comprise a scaphoid (LB1/44), capitate (LB1/45), hamate (LB1/46), trapezoid (LB1/47), and a partial lunate.

In 2007, left LB1 carpal specimens, comprising a scaphoid (LB1/44), capitate (LB1/45), and hamate (LB1/46), were described, illustrated with multicolored cartoon-like drawings (91). Photographs of the actual specimens were not published until 2 y later (57), at which time the trapezoid (LB1/47) and partial lunate also were described and figured. After a gap of another 2 y an additional (right) capitate and two hamates from a different individual (most likely LB6) were reported in an abstract (92), followed again after a year by a full-length paper (93).

The comparative perspective initially offered (91) is misleading in a manner that is implicitly typological. That is, published figures of all three bones show several other individual specimens in addition to LB1. For the trapezoid, individual specimens comprise Qafzeh 9 and Kebara 2; for the scaphoid, Qafzeh 9, Regordou 1, and OH7; for the capitate, AL288-1w, AL333-40, and TM1526. The rest of the comparative sample comprises the extant hominoid taxa: *Pongo*, *Gorilla*, *Pan*, and *Homo* (designated Modern), each of which is represented by a single cartoon image. None of these illustrations of extant hominoid taxa are identified as particular specimens (with a collection specimen number to permit replication), and exactly how composite images might have been derived is unspecified; in some unclear way each individual cartoon seems intended to represent an entire genus or species. The impression thus created by comparison of some individuals to entire taxa—implied but not stated—is necessarily to underrepresent variation (normal and abnormal) in any of the extant taxa that might affect the morphological comparisons. However, even limited visual comparisons among the stylized abstractions in figures 1–3 of ref. 92 make it possible

to reject the implied null hypothesis of within-taxon invariance (and consequently the reliability of between-taxon differences).

Trapezoid (figure 1 in ref. 91). In figure 1 of ref. 91, in palmar view (top row) Qafzeh 9 (Upper Paleolithic *Homo*) resembles Kebara 2 (a Neanderthal) more than it resembles the Modern morphotype; note the extent to which this visual comparison is influenced by the nonarticular surface (pink). In proximal view (middle row), Qafzeh 9 resembles the Modern morphotype in outline, but not in articular surface for the capitata (green). In ulnar view (bottom) Qafzeh 9 resembles generic Modern less than it does Kebara 2 (a Neanderthal). Among generic ape taxon morphotypes, in all three views (palmar, proximal, ulnar), *Pan* resembles *Pongo* strikingly more than either does *Gorilla*. These patterns of similarity and difference are explicable in functional terms [indeed, the authors do so to some extent on page S7 of their supporting information (91)], but the inescapable critical inference is that these visual comparisons of overall shape and articular patterns simply are not reliable as indicators of phylogenetic relationship, and it is the nature of the phylogenetic relationship that is the intended focus of that paper. Against this background, any inference about the phyletic position of the individual LB1 specimen is indeterminate at best and subjectively determined a priori at worst. The proximal view (middle row) in particular emphasizes this point. Although on first glance LB1 superficially shares an outline more similar to the ape genus morphotypes, that impression is dominated by its horizontal dimension in figure 1 of ref. 91; if anything, this is beyond the pongid range in its elongation, which obscures the contradiction posed by the articular surfaces, particularly for the capitata (green), which far more resembles the Modern morphotype.

Scaphoid (figure 2 in ref. 91). In figure 2 of ref. 91, in contrast to the trapezoid, with *Pongo* largely eliminated from most comparisons because of its unfused os centrale, other differences in the cartoon images are more minor. In radial and ulnar views, LB1 shows comparable extents of resemblance to the Modern human and *Pan* morphotypes. The distal views are marginally more informative, although unclear in the inferences that can be drawn from them. In outline shape of the bone, LB1 resembles Regourdou (a Neanderthal) more than any of the others, and its trapezium-trapezoid articulation (light blue) is closer to OH7 (*Homo habilis*), with neither resembling the *Pan* morphotype, which in this regard is more like the *Gorilla* morphotype. Again, these patterns of similarity and difference are conflicting, more enigmatic than enlightening.

The trial study described in *Materials and Methods* produced for the first subject we studied a dorsal view of a right scaphoid that was a nearly perfect (mirror image) match with comparable dorsal view of that shown for *H. floresiensis* (i.e., LB1; compare our Fig. S4 with figure 7 in ref. 57, both scaphoids being boomerang-shaped in outline rather than resembling a rounded triangle shown for their typical human).

Of course far more extensive studies could be pursued, but there are major cost/benefit ratios that must be considered. Carpal bone variants are extensive, and the causes of these variations remain incompletely understood. It is highly probable that scaling factors and developmental anomalies will influence heavily the range of carpal variants that will result from further study.

Capitate (figure 3 in ref. 91). As a general observation applying to all views of this bone shown in figure 3 of ref. 91, there is a contrast between articular facet orientations (broadly similar across all images) and overall bone shape (more disparate). Particularly in palmar view, the capitate of the *Pongo* morphotype is sharply waisted, whereas that of the Modern human morphotype is broadly rectangular. Among the early hominin

specimens, AL288-1w (*A. afarensis*), which is *Pan*-like, contrasts sharply with TM1526 (*A. africanus*), which appears hyper-Modern in many respects. AL333-40 is intermediate between the other two australopithecines, vitiating formal taxonomic assignments. Although LB1 can be said to resemble the *Pan* morphotype here in palmar view, in fact there is more apparent visual difference between AL288-1 and TM1526 than there is between LB1 and the *Homo* morphotype. Similarly, radial views are not particularly distinguishing, although there is more of an overall pattern contrast between all ape genus morphotypes as a group with the group comprising all australopithecines and the Modern morphotype, particularly with regard to second metacarpal articulation; in this regard, LB1 groups far more conformably with all of the hominins. In distal view all of the specimens and morphotypes are complexly disparate. If the Modern morphotype is representative—which cannot reliably be assumed because its single image represents a sample from or composite of at least 20 specimens—then it manifests the greatest deviation from the overall patterns of shape and articulations. Most notably, the Modern human morphotype as represented here is matched very closely by LB1 in all respects save the portion of the third metacarpal articular facet that extends just below (figure 3 in ref. 91) the articulation for the second metacarpal.

Comments on Multivariate Plots of LB1 Carpal Bones. The multivariate plots convey a similarly confusing impression, with the same caveat with regard to multidimensional shape complexity and near-impossibility of making any simple inference from them about the phylogenetic position of the LB1 specimen.

Trapezoid (figure 1 in ref. 91). For specimens from known taxa, the plot of CAN2 vs. CAN1 appears to show a clear separation of hominins from nonhominins, with LB1 sorting into the latter. On closer examination, the placement of LB1 is located centrally within the fringes of all of these nonhominin groups, about equidistant from the marginal scattering of *Pan*, *Pongo*, *Gorilla*, and *Papio*. Incidentally, the inclusion of *Papio* in the comparative sample is puzzling, because to our knowledge, no investigator with the exception of Gert van den Berg (94), a member of the group that advocates the recognition of *H. floresiensis* as a separate species, has postulated a quadrupedal locomotor pattern for LB1; that this (94) astonishingly heterodox (and thoroughly implausible) view has gone unremarked is another example of the suspension of disbelief about nearly anything said concerning LB1 as long as the taxonomic validity of *H. floresiensis* remains unquestioned. Nonetheless, this otherwise inexplicable expansion of the comparative sample provides the basis for an unexpectedly telling point: LB1 is morphologically plesiomorphic with regard not only to hominoids, but with regard to catarrhine primates more broadly. Because abnormal development very commonly produces atavistic phenotypes, this is an important observation with which we deal elsewhere (19). The plot of CAN3 vs. CAN2 shows an even more extreme placement of LB1 beyond the fringe of all groups represented in this study.

Scaphoid (figure 2 in ref. 91). For various reasons *Pongo* (unfused os centrale) and *Papio* (unspecified) are not included in the comparative sample for this bone. Based on what evidence is depicted, LB1 falls among *Pan* specimens; however, because *Pan* specimens present such a wide scatter, LB1 is more separated from many *Pan* than it is from numerous Modern humans. Similarly, LB1 is more distant from OH7 than it is from some Modern human specimens.

Capitate (figure 3 in ref. 91). There is broad separation along CAN1 of *Gorilla* and Modern human specimens, with *Pan* and *Pongo* specimens scattered between them. All three australopithecines, regardless of taxon, fall more or less between these two groups,

with AL288-1w and AL333-40 closer to Modern humans and TM1526 within *Pan* and *Pongo* (which overlap extensively, raising questions about the meaning of these data in terms of wrist function as well as any inferred phylogenies). Against this background, LB1 falls within both *Pan* and *Pongo*. Broadly similar observations and inferences about patterning of distributions apply to the plot of CAN3 vs. CAN1. All these carpal bones vary quite complexly in their 3D shapes and articulations; therefore, it is not surprising that the canonical plots below them are at marked variance with the misleading impression created by the monomorphic cartoon images.

Summarizing their findings, Larson et al. (57) commented that these LB1 carpals lack the suite of derived features that characterize modern human and Neandertal carpals, and instead show a symplesiomorphic pattern that also characterizes carpals belonging to African apes, *Homo habilis* (OH 7), *Australopithecus africanus* (TM 1526), and *Australopithecus afarensis* (A.L. 288-1, A.L. 333-40). In contrast, we find the overall morphological pattern presented by the LB1 carpals to be far less clear, with the new species supporters' phylogenetic inferences contradicted by their own evidence. In that context, the papers by Tocheri et al. (91) and Larson et al. (57) represent advocacy positions more than hypothesis tests. As supported by our own observations above, the results of the analyses by Tocheri et al. (91) and Larson et al. (57), although extensive, do not make a clear or decisive case, especially with respect to the broadly phylogenetic or narrowly taxonomic inferences that have been drawn. However, even the limited comparisons that are possible provide strong evidence for rejecting the hypothesis that LB1 is especially similar to, and hence derived in some direct and special way—that is, separately from the ancestry of other *H. sapiens*—from Plio-Pleistocene hominin ancestors.

On the basis of their results, if anything LB1 appears to most closely resemble *Pongo*. In plots of the canonical variables (91) in figures 1 (trapezoid) and 3 (capitate) of ref. 91, LB1 plots most solidly into the point distributions of *Pongo* specimens; figure 2 of ref. 91 is an exception, but only because it includes no *Pongo* specimens. If similarity of carpal bones is intended to be the basis for inferring phylogenetic relationship, and if LB1 is posited to be a normal representative of some hominoid taxon separate from *H. sapiens*, then the results presented (91) indicate *Pongo* as its closest congener. This appears to be such a counter-intuitive result that Tocheri et al. (91) and Larson et al. (57) have not mentioned it. We concur that it is not a likely inference, but this realization points decisively in another direction. When any particular investigation produces results that are at such variance with multiple additional lines of evidence, inference from the specific methodology itself should be called into question.

Comments on Morphology and Multivariate Plots of LB6. Orr et al. (93) add more information on carpal bones but no greater clarification of the overall problem. This more recent paper presents description and analysis of carpals attributed to at least one other individual from Liang Bua Cave represented by a right capitate (LB20) that is said to be smaller than LB1-45 and two hamates (LB21 and LB22), with LB20, LB21, and LB22 possibly all representing the same individual, which may be LB6.

In terms of the results presented, several observations are possible. At the simplest level, in figure 2 of ref. 93 the LB1-45 and LB20 capitates do not look “just like” each other, and that remark applies even more obviously to figure 3 in ref. 93, which shows the LB1-46 vs. LB21 and LB22 hamates. Furthermore, the value of these comparisons is vitiated strongly by the absence of illustrations of variation among extant humans, developmentally abnormal and normal, particularly small-bodied individuals. Much of the needed frame of reference simply is nonexistent in this paper.

Regarding the canonical variates for the capitate metrics, CAN1 vs. CAN2 places LB1 and LB20 into the area of overlap among gorillas, chimpanzees, and orangutans; CAN3 vs. CAN1 is similar, with placement if anything more clearly among orangutans. Canonical variates for the hamate metrics, CAN2 vs. CAN1 place LB1 and LB22 in an area of overlap among normal extant humans, neandertals, and orangutans, particularly orangutans; CAN3 vs. CAN1 places LB21 and LB22 most clearly among gorillas. Regarding the many other metrics, ratios, and comparisons made it would be possible to offer numerous detailed responses, but the main one is that no clear pattern of similarity emerges, although with the numerous assertions of plesiomorphy, the absence of any discussion of atavism in the context of developmental abnormality is telling. The close similarities of LB1 to *Pongo* in particular, and to the other nonhuman primates studied here in general, should at least have led to some consideration of the potential presence of atavistic features widely recognized by orthopedic surgeons as emblematic of a broad spectrum of developmental abnormalities. As with Tocheri et al. (91), there is some *pro forma* gesture in the direction of considering developmental abnormalities as influences on the carpal morphology of LB1, but their analysis in this regard is tangential at best because it included only two developmentally abnormal modern human specimens (a pituitary giant and a pituitary dwarf, neither of which is at all pertinent to the Liang Bua Cave problem; it almost seems that for purposes of these authors seeming to have considered developmental abnormality, any abnormality will do). However, there are hundreds of developmental syndromes that are known to produce the most commented-upon features of the Liang Bua Cave skeletons, unusually short stature and extremely low endocranial volume (while ignoring its manifest asymmetry and disproportion). Even if carpal bones for all or many of these syndromes were not available for morphometric analysis, that is not a justification for ignoring the extensive orthopedic literature. The case for the LB1 carpals possibly representing atavisms remains intriguing and worthy of further investigation. So does the possibility that in the case of the carpal bones we are not dealing with abnormality, but instead with a situation in which the features described are influenced heavily by scaling factors in small-bodied humans. Also seemingly unconsidered are influences of regional human variation. Lost among the trees of geometric morphometrics is the possibility that important aspects of developmental forest layout are being overlooked. There is much data here, but one strains to see its persuasiveness.

In their introduction, Orr et al. (93) assert: “. . . two main debates have emerged in relation to *H. floresiensis* [sic]. The first involves whether these remains represent a hominin species distinct from modern *H. sapiens* or modern humans with atypical morphology due to disease, pathology, or disorder; the second acknowledges *H. floresiensis* [sic] as a valid taxon, but addresses whether or not this taxon evolved from *Homo erectus sensu stricto* (i.e. Asian *H. erectus* – the only other fossil hominin currently known from Indonesia and the specific evolutionary processes involved. . .).”

Taking the second debated point first, in the context of the overall problem we find it puzzling that the results of the extensive carpal bone analyses have caused the advocates of *H. floresiensis* to abandon the (also flawed) explanatory hypothesis of island isolation without establishing a credible basis for derivation of that hypothetical taxon from any clear Plio-Pleistocene antecedent. The papers by Tocheri et al. (91), Larson et al. (57), and Orr et al. (93) fall far short of accomplishing this, instead showing only diffuse similarity to various hominoid primates, hominin, and nonhominin (particularly orangutans).

On the first point of whether LB1 represents a valid new species or an abnormal individual, we are skeptical about results of the carpal analyses and will remain so until there is much more

comparative context in the form of data on carpal morphology in developmentally abnormal and normal small-bodied humans. It should not be overlooked that the original postulate that LB1 was a new species was not based at all on carpal morphology. Symmetrically, our hypothesis that LB1 was developmentally abnormal was based on developmental signs (chiefly asymmetry and disproportion in many—but not all—cranial and postcranial features) completely without reference to carpal morphology and metrics. For LB1 to be accepted as developmentally disrupted it is not essential that every feature of its skeletal morphology must be abnormal, and thus morphologically distinct from developmentally normal members of the same population. To assume that this must be the case as implied (4) is to reinforce the impression, clear from other evidence as well, that the authors do not have very much experience in the study of syndromes involving disrupted developmental pathways. Investigators familiar with the extensive literature on human developmental genetics know that there are families with both multiple affected and multiple unaffected individuals, with the added complexity that some individuals who are chromosomally abnormal (as in Down syndrome) can present as phenotypically normal in many skeletal features. In such cases, deciding whether some shared characteristics (as in details of carpal morphology) among individuals (such as LB1 and LB6) are normal or abnormal is beyond the scope of the data presented so far for the Liang Bua Cave skeletons.

Given that the most heavily emphasized features (small brain and body size) of *H. floresiensis* are more compatible with developmental abnormality than phylogenetic novelty, and that as shown elsewhere in this paper, all of the original subsidiary “uniquenesses” (low humeral torsion, for example) simply are not unique, special pleading of a totally new sort would be necessary to establish the hypothetical new species *H. floresiensis* solely on the residual basis of carpal morphology. No other hominin species ever has been defined on the basis of carpal morphology alone, and *H. floresiensis* is not supportable on that basis either.

SI6: Lower Limb Skeletal Elements

Ossa Coxae. Aside from the degree of iliac flaring, Jungers et al. (17) make a detailed case for correspondence of LB1 with modern humans: “Total pelvic height. . . is at least 165 mm; this is indeed a small bony pelvis but it can easily be matched in skeletal samples of African pygmies. . . and in Andaman Islanders. . . . The breadth to length ratio of the ilium of LB1/7 is 1.17, and this shape index also falls well within the range of small-bodied humans. . . . The ratio of ischial length to iliac length is 0.52 in LB1/7, and this proportionality is also well within the range seen in African pygmies and other groups. . . .” Other characteristics fit with these details: “The anatomy of the acetabulum is decidedly human-like” (17). We concur with this detailed, if inadvertent, support for our long-continued position that the LB1 skeleton is that of a small anatomically modern human.

The degree of iliac flaring is pertinent to discussions of the LB1 individual. We agree that the body proportions and other aspects of skeletal anatomy make diagnosis of Majewski osteodysplastic primordial dwarfism type II (MOPD II) questionable, and that Rauch et al. (95) “. . . simply ignored these observations in their facile speculation that LB1 suffered from MOPD II” (17).

The LB1 specimen is developmentally abnormal, but not all specific diagnoses are equally well-founded, and our group had considered and rejected MOPD II as an explanation years ago. Jungers et al. (17) critique other diagnoses proposed for LB1 as well, but their own inference seems to be that because a few disorders can be ruled out, therefore LB1 must be a normal representative of a new hominin species. A full assessment of the very large number of syndromes that combine a strikingly small brain with very short stature and documented cranial and post cranial skeletal asymmetry is beyond the scope of this paper, but

the iliac flaring seen in LB1 is consistent with several developmental anomalies, particularly Down syndrome. There is no evidence that any of the supporters of LB1 as the type specimen of a new human species have carried out in necessary detail the appropriate differential diagnoses.

In one sense, of course, the pelvis of LB1 is unique. That is, it is the sole example from the Liang Bua Cave skeletal sample that we have for this portion of the body. However, in such a case, being the only one of its kind does not support taxonomic distinctiveness, especially against the fact that other descriptive details provided correspond pervasively to small-bodied members of various *H. sapiens* populations.

Femora and Patella. The only femora that have been recovered from Liang Bua Cave to date both belong to LB1, so again any discussions of the femora, or limb proportions incorporating the femur as one element of the hypothetical taxon *H. floresiensis*, are those of just this one individual. As we have noted, in describing LB1, Brown et al. (20) inexplicably published the left femur (LB1/9) incorrectly as right (LB1/8), which error they still were rationalizing three years later in a trade book (96), despite our research group having brought this point to their attention early in 2005.

Jungers et al. (17) belatedly acknowledged our correction about the reversal of femur antimeres, but ignore the caution that the “uniqueness” of LB1 inheres in there being no other Liang Bua Cave individuals whose bones duplicate the detailed anatomy of these parts that have been represented as supportive of a unique species. In this way they have influenced heavily the various epiphenomenological aspects of discussions about the hypothetical taxon. The femora of *H. floresiensis* are the femora of LB1 alone. Statements such as “It is noteworthy that these bones bear very little resemblance to modern human femora excavated from more recent archeological sites on Flores” (17) can be interpreted alternatively as meaning that the LB1 femora are either phylogenetically unique, or that they are abnormal modern human femora. The balance of evidence now favors the latter hypothesis even more strongly than it did initially, and carries with it the consequence that, for various reasons, the stature of LB1 is substantially underestimated (24).

Overall, the treatment of the femora of LB1 oddly combines fulsome description with scant dimensional data. There are several references to chips and cracks, for example (17): “The diaphysis of LB1/9 was fractured but repaired just below midshaft, and a large anterior bone fragment was glued back into place.” However, no measurements are given for the cortical and trabecular bone thicknesses exposed as a result. Other important data are alluded to but not given (17): “. . . CT-based measures of left-right asymmetry in cortical area at femoral midshaft are also well within the ranges seen in modern humans of both sexes.” Verbal generalizations without dimensions are unexpected.

We have documented (24) by CT scans that the cortical bone thicknesses of the femora are low, and their shaft diameters are large in relation to total length, producing an appearance of shafts of tubular shape enclosing unusually wide marrow cavities. Even if we accept without any data that “the thickness of . . . cortices is well within the ranges seen in healthy modern humans” (17), the fact that this supposedly “normal” cortical thickness occurs in bones that are “robust” in their external dimensions indicates abnormal shape of shafts: relatively straight, wide, tubular bones with wide marrow cavities. In terms of mechanics, widening of tubular elements increases their strength to withstand axial pressures without much effect on their cross-sectional strength. In the case of a human body, this means that wide tubular bones are able to support upper body weight while not being much stimulated by actions of muscles providing transverse force vectors. This shape presents a conundrum in the context of very low estimates of LB1 body mass.

The mention that in LB1 the dimensions and "...morphology can be readily matched in the large sample of human patellae from the Indian subcontinent..." (17) reinforces our point about lack of specific uniqueness of the individual in many respects despite the anomalies and disproportions already documented.

Tibia. In their description, Jungers et al. (17) reconstruct the length of the LB1/13 tibia to be 235–240 mm and comment that "...this is shorter than the tibia of any modern human of which we are aware, including African pygmies and Andaman Islanders." It is noted that Brown et al. (20) remarked on the "...slight curvature in the long axis of LB1/13." Jungers et al. (17) concur that the curvature of this bone is "...very slight indeed...especially when viewed together with an articulated fibula." In the case of LB1/13, cortical bone thicknesses are given from locations where there were natural breaks, a salient contrast with the absence of these data for the femora, as noted above.

Another adult tibia, LB8/1 is also described. In this description cortical thickness dimensions are alluded to but not given (17): "It was possible to examine cortical bone thickness near the mid-shaft when the separate pieces were cleaned prior to being reglued; the cortical bone of LB8/1 is relatively thick (i.e. the cortical index is in the high normal range)." This statement implies the possibility that there is a discrepancy in bone thickness between the two individuals, with LB1 having thinner cortical bone, consistent with our hypothesis that the latter individual is developmentally abnormal. However, in the absence of the actual cortical thickness measurements for LB8/1 this must remain a surmise, one which data that are available but unpublished might have dispelled. Views other than anterior for the tibiae also might have been informative.

Overall, the tibiae of the specimens described document relatively short stature, but no morphological uniquenesses. They fall within the ranges known for extant *H. sapiens*.

Fibula. Jungers et al. (17) describe the right fibula LB1/14 and left fibula LB1/53 as being relatively straight and overall "...quite human-like in overall morphology." Again, there is no uniqueness that would warrant invention of a new hominin species.

Foot. Jungers et al. (17) devote more than six pages to describing various bones of the foot. There are relatively frequent references to one or another "primitive" feature, but as a rule these statements lack systematic comparative context. Here is one example (17): "There is an asymmetrically (proximomedially) placed calcaneal process or 'beak' on both cuboids. Although the expression of this process is variable in modern humans, it

usually is regarded as the hallmark of a derived, bipedal calcaneocuboid joint that locks or close-packs in inversion late in stance phase, thereby providing a stable longitudinal lateral column." Referential data are lacking and the comparisons made create an aura of oddity rather than convincing genuine uniquenesses. Thus, "Metatarsal I is a robust bone as in humans, and articular and shaft dimensions are large relative to length... It is clearly an adducted, non-grasping hallux... it appears to be quite broad and relatively flat mediolaterally in distal and dorsal views; in this respect, it is more derived in the direction of modern humans than is *Paranthropus*, *A. afarensis*, and apparently early *Homo* from Dmanisi..." (17). This presentation does not say that the bone is different from the range of variation that might be documented in extant humans (with no real comparative data provided for these), but through the references to taxa known from genuine fossils, one is left with the impression that, perhaps, there might be something taxonomically distinctive here from extant humans. There isn't.

Jungers et al. (97) discuss the LB1 foot separately. The authors state that "LB1's foot is exceptionally long relative to the femur and tibia, proportions never before documented in hominins..." However, stated later in the same paper is that "the relatively high foot-to-femur ratio, not unlike the high humerofemoral index, is driven primarily by an exceptionally short hindlimb." It is possible to resolve this contradiction 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. We deal with the pertinent detailed comparisons of measurements and proportions at length in another paper (19), and here will note only that the LB1 foot is not unusually long, but rather the femur is short, and that these statements are not transitive once other limb elements are taken into account. Aside from that, the LB1 foot exhibits the maladaptive "uniquenesses" of lacking arches that produce what is known, in simple terms, as a flat foot, and also has osteophytes that are indicative of high stress. We do concur with the authors in their conclusion that "The foot of *H. floresiensis* [sic] was not well-designed for either high-speed or efficient endurance running" (17). However, in contrast we conclude that flat feet and osteophytes are indicators of functional abnormality (and, in the case of flat feet, functional abnormality that accompanies abnormally short femora in developmental abnormalities such as Down syndrome), not taxonomic distinctiveness.

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Fig. S1. LB1 skull in dorsal view showing brachycephalic proportions, in contrast to verbal descriptions of its proportions being long and low or resembling *Homo erectus*.



Fig. S2. LB1 skull (*Left*) compared with Liang Momei E skull (*Right*). Photograph of Liang Momei E skull taken at Naturalis Biodiversity Center (Leiden, The Netherlands).



Fig. S3. Mandible of Australian Aboriginal woman buried at Roonka Flat on the Murray River in South Australia. The site is dated at the Holocene (10,000–200 y B.P.).

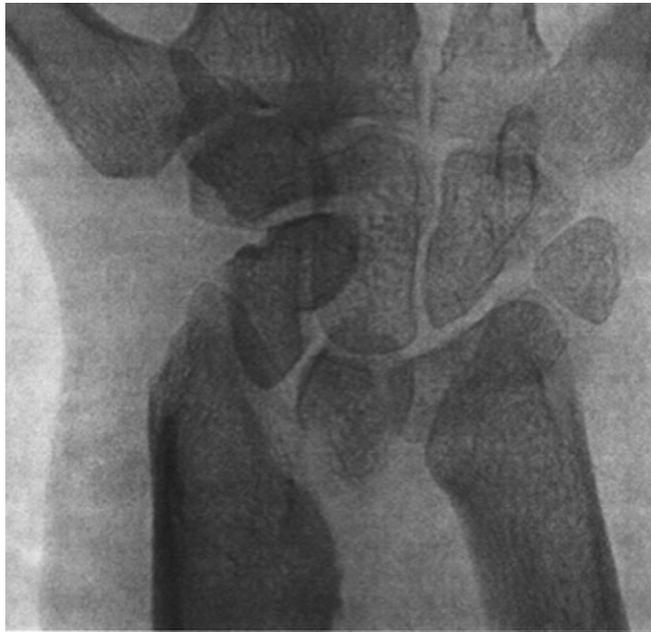


Fig. S4. Radiograph of *Homo sapiens* scaphoid variant resembling LB1.

Table S2. Concordance between soft and hard tissue chins in the Rampasasa population (data from ref. 44)

Match	Male <i>n</i>	Male (%)	Female <i>n</i>	Female (%)	Total <i>n</i>	Total (%)
Positive-positive	2	9.1	2	6.7	4	7.7
Positive-negative	1	4.6	0	0.0	1	1.7
Positive-neutral	2	9.1	0	0.0	2	3.9
Negative-positive	0	0.0	0	0.0	0	0.0
Negative-negative	3	13.6	4	13.3	7	13.5
Negative-neutral	3	13.6	8	26.7	11	21.2
Neutral-positive	1	4.6	7	23.3	8	15.4
Neutral-negative	1	4.6	1	3.3	2	3.9
Neutral-neutral	9	40.9	8	26.7	17	32.7
Total	22	100.0	30	100.0	52	100.0

Table S3. Measurements of LB1 clavicle curvature in dorsal view

Size	External	Internal	Inferior	Superior
Smallest	14.6	11.5	3.6	5.6
Medium	14.6	17.9	3.6	5.2
Largest	14.6	19.2	3.6	5.4