Liang Bua *Homo floresiensis* mandibles and mandibular teeth: a contribution to the comparative morphology of a new hominin species

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ABSTRACT

In 2004, a new hominin species, *Homo floresiensis*, was described from Late Pleistocene cave deposits at Liang Bua, Flores. *H. floresiensis* was remarkable for its small body-size, endocranial volume in the chimpanzee range, limb proportions and skeletal robusticity similar to Pliocene *Australopithecus*, and a skeletal morphology with a distinctive combination of symplesiomorphic, derived, and unique traits. Critics of *H. floresiensis* as a novel species have argued that the Pleistocene skeletons from Liang Bua either fall within the range of living Australomelanesians, exhibit the attributes of growth disorders found in modern humans, or a combination of both. Here we describe the morphology of the LB1, LB2, and LB6 mandibles and mandibular teeth from Liang Bua. Morphological and metrical comparisons of the mandibles demonstrate that they share a distinctive suite of traits that place them outside both the *H. sapiens* and *H. erectus* ranges of variation. While having the derived molar size of later *Homo*, the symphyseal, corpus, ramus, and premolar morphologies share similarities with both *Australopithecus* and early *Homo*. When the mandibles are considered with the existing evidence for cranial and postcranial anatomy, limb proportions, and the functional anatomy of the wrist and shoulder, they are in many respects closer to African early *Homo* or *Australopithecus* than to later *Homo*. Taken together, this evidence suggests that the ancestors of *H. floresiensis* left Africa before the evolution of *H. erectus*, as defined by the Dmanisi and East African evidence.

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Introduction

Excavations at Liang Bua, western Flores, in August 2003 uncovered the partial skeleton of a small-bodied and small-brained hominin, large numbers of artifacts, and evidence of extinct fauna, including *Stegodon* (Brown et al., 2004; Morwood et al., 2004). Based on the combination of primitive, unique, and derived traits, the LB1 skeleton, and an isolated P_3 (LB2), the specimens were assigned to a new species, *Homo floresiensis*. While the body size and encephalization of *H. floresiensis* were unexpected (Brown et al., 2004; Falk et al., 2005b), at least in this geographic and temporal context, it was perhaps more remarkable that this hominin had reached Flores and had been regionally contemporaneous with *H. sapiens* (Lahr and Foley, 2004; O'Connell and Allen, 2004; Barker et al., 2007). When initially described, it was argued that the distinctive morphology of *H. floresiensis* was the result of an extended period of island evolution (Sondaar, 1977; Dayan and Simberloff, 1998; Lomolino, 2005), which had entailed the dwarfing, on Flores, of a population descended from a large-bodied *H. erectus* ancestor (Brown et al.,

2004). *Homo erectus* was geographically proximate on Java (Kaifu et al., 2005a,b), excavations at Mata Menge in central Flores had recovered stone tools dated to 800 ka (Morwood et al., 1998), and the body-size of the proboscids and murids at Liang Bua and Mata Menge conformed to expectations under the Island rule (Morwood et al., 1998, 1999, 2004; van den Bergh et al., 2009). However, unlike for *Stegodon*, there is currently no skeletal evidence of a larger-bodied ancestor for *H. floresiensis* on Flores. Therefore, it remains possible that the founder population arrived with brain and body dimensions similar to their late Pleistocene descendants (Brown et al., 2004). The mandibular remains have played essential roles in the interpretation of Liang Bua skeletal and archaeological remains, but many secondary analyses of these materials have presented a variety of interpretations. Consequently, the present analysis offers morphological details and comparative analyses of the mandibles and mandibular teeth, which strongly support the hypothesis that these remains represent a new species.

Background

During subsequent excavations at Liang Bua in 2004, our research team recovered more of the LB1 skeleton, the LB6

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mandible, and postcranial elements from 5 to 7 additional individuals (Morwood et al., 2005). The new material both confirmed and extended aspects of the original description, with the adult postcrania coming from individuals of either similar size or substantially smaller than LB1. Importantly, the discovery of most of the LB1 right arm made it clear that *H. floresiensis* had limb proportions outside the range of modern human variation (Brown et al., 2004; Morwood et al., 2005; Larson et al., 2007a), contrasting with *H. erectus* (Walker and Leakey, 1993; Lordkipanidze et al., 2007) and other species of the genus *Homo* (Reno et al., 2005). The material was strikingly similar to *A. afarensis* specimen A.L. 288-1 (Johanson et al., 1982; Jungers, 1982; Green et al., 2007; Jungers et al., 2009). Further support for a phylogenetic connection with *Australopithecus* is provided by analysis of the LB1 carpals (Larson et al., 2007b; Tocheri et al., 2007b) that lack the shared derived features of either *H. sapiens* or *H. neanderthalensis*. Instead, these bones are morphologically identical to the conditions seen in *A. afarensis* and African apes. Combined with morphological and metrical comparisons of the LB1 cranium (Brown et al., 2004; Anderson, 2007; Baab et al., 2007; Collard and Wood, 2007; Nevell et al., 2007; Baab and McNulty, 2009; Brown, in preparation-a) these studies indicate that while *H. floresiensis* has the derived and reduced molar size of later *Homo*, the combination of other skeletal traits is outside the range of variation observed in both *H. erectus* and *H. sapiens*. Moreover, the Liang Bua remains seem to share symplesiomorphies with *Australopithecus* that are absent in later *Homo*. The extent to which the observable expressions of skeletal and dental morphology in *H. floresiensis* are the results of phylogeny, convergence, homoplasy, insular dwarfing, or some combination of these factors, remains unclear. However, we believe that the existing morphological, allometric, and size-adjusted comparisons make it unlikely that *H. floresiensis* is simply a dwarfed example of *H. erectus* (Brown et al., 2004; Falk et al., 2005a; Morwood et al., 2005; Collard and Wood, 2007; Baab and McNulty, 2009).

Critical discussions of the validity of *H. floresiensis* as a novel species have focused on the possibility that LB1 was a dwarfed, microcephalic modern human, engendering a lively debate (Falk et al., 2005a, 2006, 2007; Weber et al., 2005; Holloway et al., 2006; Martin et al., 2006b; Conroy and Smith, 2007; Schauber, 2007; Taylor and van Schaik, 2007; Jungers et al., 2009). In part, the original assertion that *H. floresiensis* was an endemic island dwarfed descendant of larger-bodied *H. erectus* (Brown et al., 2004) stimulated this discussion. Subsequent discoveries enabled the exploration of limb proportions and scaling trajectories that made dwarfing an unlikely proposition (Morwood et al., 2005). *Homo floresiensis* has a body-size/brain-size relationship within the chimpanzee and early australopith range (Brown et al., 2004; Falk et al., 2005a), and surely the more pertinent questions surround issues of behavioral complexity and neural organization (Conroy and Smith, 2007), rather than possible pathology. After all, given what is known about the probability of normal brain function in the majority of extremely microcephalic humans (Dolk, 1991), they would be very unlikely candidates for the observable cultural continuity at Liang Bua. It has also been argued that a hominin with an endocranial volume in the chimpanzee and australopith range would be incapable of making the artifacts recovered from Liang Bua, and they were more likely the result of modern human behavior (Martin et al., 2006b). However, the stone tools from Mata Menge in eastern Flores (Morwood et al., 1998) and Liang Bua (Morwood et al., 2004) form part of the same "pebble-and-flake technocomplex," and are elements of a reduction sequence that extends back 840,000 years in Indonesia (Brumm et al., 2006; Moore and Brumm, 2007), and the Oldowan in eastern Africa (Moore and Brumm, 2009), well before the arrival of *H. sapiens* in the region.

Specific references to mandibular specimens LB1 and LB6 have been made to support claims that *H. floresiensis* either falls within the normal range of human variation, or has a morphology indicative of a particular developmental disorder (Jacob et al., 2006; Martin et al., 2006b; Richards, 2006; Hershkovitz et al., 2007). The original description of the LB1 holotype mandible argued that it combined features present in a variety of Plio-Pleistocene hominins. These included P_3 crown and root morphology, robusticity of the corpus, the detailed anatomy of the posterior and anterior symphyseal region, and relative tooth size. The anterior symphyseal region was described as rounded, bulbous, and without a chin, with a strongly posterior inclination of the symphyseal axis. The posterior symphyseal region, with a posteriorinferiorly inclined alveolar planum, moderate superior transverse torus, and a deep and rounded, rather than shelf like, inferior transverse torus, recalls the morphology of the Laetoli LH4 holotype of *A. afarensis* (White and Johanson, 1982). Later, when the second mandible (LB6) was described, we recognized numerous detailed similarities with LB1 in overall size, and P_3 and symphyseal morphology. As in LB1, the anterior symphysis of LB6 lacks the chin components characteristic of *H. sapiens* (mental protuberance, mental tubercles, and incurvation mandibularis) (Schwartz and Tattersall, 2000), and has similar symphyseal inclination, posterior morphology, and corpus robusticity to LB1. Additional support for these claims was provided in the associated Supplementary Online Materials (Brown et al., 2004; Morwood et al., 2005).

Several lines of evidence were presented to argue against a new species, with special reference to mandibular remains. For example, Jacob et al. (2006) and Richards (2006) indicated that the LB6 mandible showed traits also observed in contemporary Australomelanesians and African and Indonesian pygmies (Jacob et al., 2006; Richards, 2006). Specifically, these authors argued that the absence of a chin was not a valid trait separating *H. floresiensis* from *H. sapiens*, and suggested that 94% of living Rampasasa people on Flores have neutral or negative chins (Jacob et al., 2006). Furthermore, Martin et al. (2006a), hypothesizing that the Liang Bua skeletons represented microcephalic humans, suggested that chin development is highly variable in microcephalics, in which the mental eminence may be weak or lacking, and Hershkovitz et al. (2007) suggested that a small mandible with an underdeveloped or missing mental protuberance is a feature of Laron's Syndrome. Generally, these authors failed to provide detailed skeletal evidence in support of these claims, and several confused a receding symphyseal profile in living people with the absence of the elements of a bony chin (cf. Jacob et al., 2006; Richards, 2006). Furthermore, literature cited by these critics does not demonstrate that morphological variation in *H. floresiensis* overlaps that of modern *H. sapiens* (Keiter, 1933; Dokládal, 1958; Jacob, 1967; Marquer, 1972; Birdsell, 1993; Laron, 2004). In our view, these authors seem to be unaware of the primary literature on hominin mandibular symphyseal morphology (e.g., Weidenreich, 1936; Meredith, 1957; Murphy, 1957; Enlow, 1975; White, 1977; Hylander, 1984; Daegling, 1993; Ravosa, 1999, 2000; Rosenbloom et al., 1999; Schwartz and Tattersall, 2000). In contrast to the statements of Jacob et al. (2006) and Hershkovitz et al. (2007), small overall size has never been listed as a diagnostic species characteristic of the *H. floresiensis* mandibles (Brown et al., 2004; Morwood et al., 2005). In all, the variety of conclusions about these remains emphasizes the need for careful and meticulous description and interpretation.

Beyond arguments about pathology, interpretations of the taxonomy and evolutionary history of *H. floresiensis* broadly support its status as a distinct species, although various authors differ in the specifics of interpretation (Falk et al., 2005a; Morwood et al., 2005; Peixoto et al., 2006; Anderson, 2007; Baab et al., 2007; Larson et al., 2007a,b; Nevell et al., 2007; Tocheri et al., 2007a;

Gordon et al., 2008). To a great extent this reflects several factors, which include the unavoidable limitations in the currently published descriptions (Brown et al., 2004; Morwood et al., 2005), the unique mosaic of traits that characterizes the species, restricted time depth of the hominin fossil record on Flores, and debate over the implications of the associated cultural material. The Liang Bua Pleistocene mandibles and mandibular teeth are crucial to this deliberation: as we have previously argued, these lines of evidence indicate that LB1 was not an aberrant individual, but representative of a long-term, morphologically unique species, with a configuration of features not present in *H. sapiens* (Morwood et al., 2005).

With this in mind, the primary aim of this paper is a detailed descriptive comparison of the Liang Bua Pleistocene mandibles and mandibular teeth. We conduct comparisons with the morphological and metrical variation in large and small-bodied *H. sapiens*, *H. erectus*, and a range of African Pliocene hominins. As *H. sapiens* and *H. floresiensis* were contemporaneous, at least in the late Pleistocene (Roberts et al., 2009), we have examined the probability that they belong to the same species through multivariate comparisons of variation within a living primate genus. We selected *Pan* for this purpose because body size and levels of sexual dimorphism fall closer to the known *Homo* range than do other large hominoid primates. As the significance of small-body-size, and its influence on skeletal morphology, is central to much of the debate surrounding the status of *H. floresiensis*, both size-adjusted and unadjusted statistical comparisons are used. Unfortunately, the fragmentary nature of the hominin fossil record prevented the extension of the multivariate metrical comparison beyond *H. sapiens* and *H. floresiensis*. Given that the focus of the debate surrounding the Liang Bua Late Pleistocene mandibles is whether or not they fall within the range of variation in our species, we believe our emphasis on comparisons with *H. sapiens* is appropriate. Our analyses are based on a variety of analytical techniques, including standard statistics. We also utilize elliptic Fourier descriptors (Guy et al., 2008) to compare mandibular symphyseal shapes. These analyses offer unprecedented quantitative insights into the Liang Bua mandibular remains.

Materials and methods

Samples

We examined a geographically and temporally robust adult modern human skeletal sample ($n = 2063$) for comparisons with *H. floresiensis* and other Plio-Pleistocene hominins (Brown et al., 2004; Morwood et al., 2005). Our aim, given the constraints of museum collections, was to place the Liang Bua mandibles in the context of variation within our species. The *H. sapiens* sample was weighted towards the Australia-Melanesian (southeast Australia, Papua New Guinea, and New Britain, $n = 378$) and East Asian regions (China Gwandong and Hubei provinces, Edo Period Japan, and modern Japanese, $n = 339$) (Brown, 2000; Brown and Maeda, 2004), but also included recent sub-Saharan Africans (Nigeria, $n = 78$) and western Europeans (Spitalfields, Poundbury, and Terry collections, $n = 341$). Small-bodied modern humans were represented by African Pygmies ($n = 5$) and Andaman Islanders ($n = 15$). The early part of the Australian sample, Kow Swamp, Coobool Creek, and Lake Mungo (Brown, 1987, 1989) ($n = 57$), and Minatogawa (Suzuki, 1982; Brown, 2000) overlapped *H. floresiensis* in time (Brown, 1989). The early Holocene was represented by a large Chinese Neolithic series (Brown, 2000) ($n = 235$), a Japanese middle-late Jomon sample ($n = 137$), and the Mesolithic series from Sarai Nahar Rai and Mahadaha, northeast India (Kennedy, 1984) ($n = 19$). Most of the modern human mandible data were collected by PB, but more recently by both PB and TM working together. Data

on any Plio-Pleistocene hominins not examined by the authors was obtained from the literature, substantiated by casts, or obtained directly from researchers who had examined the original specimens.

We have previously argued that symphyseal shapes in LB1 and LB6 fall outside the range of variation in *H. sapiens*, and instead bear similarities to early australopiths (Brown et al., 2004; Morwood et al., 2005). However, Jacob et al. (2006) disputed the similarity of LB1 with LB6, and also claimed that symphyseal shape in these mandibles is within the range of living *H. sapiens* from the same geographic region. Recently, Guy et al. (2008) demonstrated that elliptic Fourier descriptors (EFD) were a powerful tool for distinguishing two-dimensional shapes, including hominin midsagittal symphyseal outlines. They found that variation in symphyseal shape had taxonomic significance, and the outlines of *H. sapiens* were distinct from those in australopiths and living, large-bodied apes. We used EFDs to test whether or not symphyseal shape in LB1 and LB6 fell within the range of Melanesian *H. sapiens* ($n = 12$), *A. afarensis* ($n = 20$), *H. erectus sensu lato* ($n = 12$), and a broad sample of Pleistocene *Homo* ($n = 14$). The *H. erectus* sample contained KNM-WT 15000, KNM-ER 730, OH 22, Dmanisi D211 and D2600, Ternifine 1, 2, and 3, Sangiran 1, 5, and 6, and Zhoukoudian ZHH1. We are aware that there is continued debate over whether some of these mandibles should be allocated to *H. ergaster* or *H. habilis* in east Africa (Groves and Mazak, 1975; Rightmire, 1990; Collard and Wood, 2007), *H. ergaster*, *H. georgicus*, or *H. habilis* at Dmanisi (Rosas and De Castro, 1998; Gabounia et al., 2002; Rightmire et al., 2008) or *Meganthropus* at Sangiran (Weidenreich, 1945; Kaifu et al., 2005b; Tyler, 2006).

The conventional approach to the paleospecies identification is to assume that variation in the past was similar to that which exists today, particularly for closely related taxa with similar body size and sexual dimorphism (Martin and Andrews, 1993; Teaford et al., 1993). Variation within a contemporary species may then provide insights into taxonomic schemes, helping test the adequacy of the morphological and metrical characters used in classification. Issues of sample size and preservation make this difficult to test in fossil primates, and we realize that the uniformitarian assumptions are problematic, especially when bottlenecks and range expansions impact genetic variation (Flagstad et al., 2003; Mitrovski et al., 2007). As statistically adequate samples of well preserved, contemporaneous, and geographically proximate hominin mandibles, apart from *H. sapiens*, do not currently exist, we first tested the ability of our measurements to distinguish between the species and subspecies of a living primate genus (Supplementary Online Materials). We therefore chose the genus *Pan* because large, wild caught samples with detailed provenance data are available. Moreover, the genetic, skeletal, and behavioral differences between species and subspecies of *Pan* are well documented (Shea et al., 1993; Morin et al., 1994; Wrangham et al., 1994; Braga, 1995; Uchida, 1996; Gagneux et al., 1999; Kaessmann et al., 1999; Gonder, 2000; Stone et al., 2002; Taylor and Groves, 2003; Eriksson et al., 2004; Won and Hey, 2005). Levels of sexual dimorphism are comparable to *H. sapiens* (Taylor, 2006) and body size overlaps estimates for *H. floresiensis* and some other Plio-Pleistocene hominins (McHenry and Coffing, 2000; Brown et al., 2004).

Measurements

Mandibular and dental measurements were restricted to those that could be recorded in the LB1 and LB6 *H. floresiensis* mandibles, and had previously been recorded for our *H. sapiens* and *Pan* samples. For multivariate comparisons, we recorded nine linear dimensions (Table 1). We do not believe that they cover all aspects of variation in our mandible sample, but they are adequate in terms

Table 1
Mandibular dimensions used in multivariate comparisons of the *Pan* and *Homo* samples, and the two dimensions used for size adjustment.

Measurement	Measurement definition (number and author)
1. Symphyseal height	141 (Wood, 1991)
2. Symphyseal thickness	142 (symphyseal breadth) (Wood, 1991)
3. Corpus height at M_2	154 (Wood, 1991)
4. Corpus thickness at M_2	155 (corpus breadth) (Wood, 1991)
5. External arch breadth at M_2	Most superior point on the alveolar margin of the lateral corpus at the midpoint between the mesial and distal roots.
6. Bigonial breadth	66 (Martin and Saller, 1957)
7. Minimum ramus breadth	Minimum breadth of ascending ramus.
8. P_3 mesiodistal length	193 (Wood, 1991)
9. M_1 buccolingual breadth	286 (Wood, 1991)
10. Basicranial length (size adjustment)	5 (Martin and Saller, 1957)
11. Max. femoral vertical head diameter (size adjustment)	18 (Martin and Saller, 1957)

of the different developmental regions of the mandible and the statistical procedures employed. For the descriptive statistics, buccolingual (BL) and mesiodistal (MD) crown dimensions for I_1–M_3 were recorded. In the *H. sapiens* and *H. floresiensis* samples, the P_3–M_3 measurements were corrected for crown loss through interproximal wear (Wood, 1991). Previously published MD measurements for LB1, the LB2 isolated P_3, and LB6 are uncorrected (Brown et al., 2004; Morwood et al., 2005). Maximum femoral head diameter, maximum femur length, maximum humerus length, basicranial length (basion–nasion), and endocranial volume were used as controls for body size, and exploration of mandibular scaling relationships and evidence of behavioral adaptations. Mandibular symphysis and corpus cross-sections were produced from scanned silicone impressions and CT scans that were compared with the external dimensions of the original bone. The open source DICOM viewer OsiriX 3.3 was used to examine CT slices, and the public domain software ImageJ 1.4, produced by the National Institute of Health, was used to measure cross-section areas from TIFF images of silicone molds.

Statistical procedures

A variety of statistical and graphical methods were employed to examine differences in mandibular size and shape. These procedures were first applied to the chimpanzee sample in order to establish whether or not a limited number of mandibular and dental dimensions could distinguish between species (*Pan troglodytes* and *Pan paniscus*) as well as between subspecies (*Pan troglodytes troglodytes* and *Pan troglodytes schweinfurthii*). These methods were then applied to the modern human, *H. floresiensis*, and hominin samples where data sets were large enough for analysis. In the human sample, missing data, most often due to postmortem damage or the affects of acute tooth wear on dental and corpus dimensions, substantially reduced the number of mandibles available for multivariate comparisons. While a variety of methods are available to replace missing data, all have limitations. In particular, overfitting and reduced variance can affect the generalizability of results, so our preference was to delete cases with missing data from statistical analysis. The distribution of all data sets, by sex and species/subspecies, were first examined graphically using normal probability and stem and leaf plots, and the Shapiro-Wilk statistic. Linear dimensions were normally distributed, but the P_3 module often violated distributional assumptions, with kurtosis and significant values for the Shapiro-

Wilk and Kolmogorov-Smirnov test statistics ($p < 0.01$). Significant differences in size and shape (proportions) were tested using one-way analysis of variance (ANOVA), with Bonferroni adjustment to protect against the Type I errors associated with multiple pair-wise comparisons. Results were considered statistically significant at $p < 0.05$.

Following Taylor and Groves (2003), basicranial length (basion-nasion) was used to standardize mandibular and dental dimensions in multivariate comparisons. Basicranial length was considered suitable, as our aim was to examine mandibular variation in size and shape that resulted from differences in relative size, not masticatory effort (Smith, 1993). We were also concerned with the broader behavioral and taxonomic associations of tooth size and mandibular morphology. Mandibular and dental dimensions were therefore considered in the context of indicators of body mass, relative limb proportions, and brain size in *H. floresiensis*, *H. sapiens*, and the small number of Plio-Pleistocene hominin skeletons for which there are comparable data, *H. erectus* specimens KNM-WT 15000 and Dmanisi D2600 (Walker and Leakey, 1993; Rightmire et al., 2006; Lordkipanidze et al., 2007; Martinón-Torres et al., 2008), and *A. afarensis* specimen A.L. 288-1 (Johanson et al., 1982; Kimbel et al., 2004). Comparisons of scaling trajectories in adults were examined using ordinary least squares (OLS) and reduced major axis regression (RMA). We preferred RMA to OLS regression where both the independent and dependent variables are measured with error (Smith, 1994), as is the case with most morphometric studies.

Elliptic Fourier components powerfully quantify variation in two-dimensional shapes (Lestrel, 1997), and have proved successful in discriminating the taxonomic associations of hominoid symphyseal contour data (Daegling and Jungers, 2000; Guy et al., 2008). Mid-sagittal symphyseal outlines of LB1 and LB6 were compared with those in *H. sapiens* and a range of Plio-Pleistocene hominins, using the procedures specified by Guy et al. (2008). Outlines were obtained from mid-sagittal CT scans, lateral radiographs adjusted for radiographic enlargement, casts sectioned at the midline, and, when we did not have access to the original specimens, the published literature (Bräuer and Schultz, 1996; Ward et al., 2001; Vekua et al., 2002; Kimbel et al., 2004). All symphyseal outlines were oriented in the occlusal plane and the scale held constant. For six of the modern *H. sapiens*, and for LB1 and LB6, outlines could be generated from radiographs, CT scans, and sectioned mandibles. Evaluation of the shapes produced by these different procedures using elliptic Fourier descriptors (EFDs) and principal components analysis (PCA), demonstrated that they were directly comparable. Processing of digital images, obtaining EFDs, and PCA of the normalized EFDs was conducted using SHAPE 1.3 (Iwata and Ukai, 2002).

The extent and pattern of multivariate differentiation between groups, probabilities of group membership, and the influence of individual variables on distributions were explored using discriminant function analysis (DFA) and PCA, with nine mandibular and dental dimensions (Table 1). The primary purpose of DFA is to predict group membership from a set of predictors. DFA assumes that groups are correctly identified and the final solution will maximize between-group variance, while minimizing within-group variance. The loading matrix of correlations between predictors and discriminant functions provides information on the relative contribution of predictors to group membership. PCA uses a single set of variables to discover if any of the variables form subsets (groups) that are relatively independent of each other. The factors generated by the PCA are based on correlated, as well as inversely correlated, subsets of variables, which may reflect underlying biological processes (Jackson, 1991; Chase et al., 2002). For the final multivariate comparisons, the sexes were pooled as the

individual male and female samples displayed very similar group-based distributions, and multivariate characteristics. We also considered that this would provide the most robust solution, given that the sex of the Liang Bua mandibles, and those of most other Plio-Pleistocene hominins, will never be beyond dispute. Statistical and graphical procedures were performed using SYSTAT 11 (Systat, 2002), PAST 1.34 (Hammer et al., 2001), and SPSS 14 (SPSS, 1990).

LB1

History

Most of the LB1 skeleton was excavated in August 2003 from Spit 59, Sector VII, at Liang Bua, with a charcoal based 14C age estimate for the skeleton of 18 ka, bracketed by a TL and IRSL age range of 36 ± 5–6.8 ± 0.8 ka (Roberts et al., 2009). Other post-cranial elements, including most of the right arm, were excavated from the adjacent Sector XI in the following field season (Morwood et al., 2005). Found at a depth of 5.9 m, within a layer of moist, dark-brown silty clay, the bones were extremely soft and unmineralized when found. Upon exposure to air they gradually hardened, becoming somewhat "chalky" and extremely fragile. The LB1 mandible was found close to its associated cranium, and tapho-nomic processes had resulted in some postmortem distortion and fracture. The mandibular corpus is broken at the junction of the right M_3–M_2, right P_3, and left I_2–C, the posterior right corpus and ramus are twisted slightly laterally, and the left condyle is incomplete (Figs. 1–4). This has not affected corpus and symphyseal dimensions, or the outlines that we use here, but will have altered bi-ramal measurements. After cleaning and reconstruction by Thomas Sutikna, the mandible would not occlude, or articulate precisely, with the maxillary dentition and cranial base, primarily due to distortion of the right ramus.

The dentition is complete, apart from the left P_4 and right I_1 that were not recovered. Interproximal facets on the adjacent teeth and compensatory mesial migration, suggest that the right P_4 was lost during life. The M_3s are both fully erupted, with occlusal wear and dentine exposure indicating adult status. This assessment is supported by the fusion of all postcranial epiphyses and complete external closure of the basioccipital synchondrosis. Based on the morphology of the associated pelvis, combined with other aspects of skeletal size and development, Brown et al. (2004) concluded that LB1 was female, as have Jungers et al. (2009). However, the skeletal and dental dimensions of LB1 are currently the largest of the Pleistocene-age adults at Liang Bua (Brown et al., 2004; Morwood et al., 2005; Larson et al., 2007b; Jungers et al., 2009),

Figure 2. Anterior views of the LB1 (top) and LB6 (bottom) mandibles.

which suggests that these assessments should still be treated with caution.

In December 2004, the hominin skeletal materials from Liang Bua were removed from Arkeologi Nasional, Jakarta, and taken to Gadjah Mada University by Teuku Jacob (Balter, 2004; Dalton, 2005a,b). An attempt was made to cast the LB1 mandible, which resulted in damage to surface bone. Filler was used to correct the visible damage, and external dimensions were altered due to the separation of cracks in the corpus and a corresponding increase in bigonial breadth. The deep cut marks now running along the lateral inferior corpus of the mandible are an artifact of the mold-making process (Fig. 5). The dimensions and morphology reported here
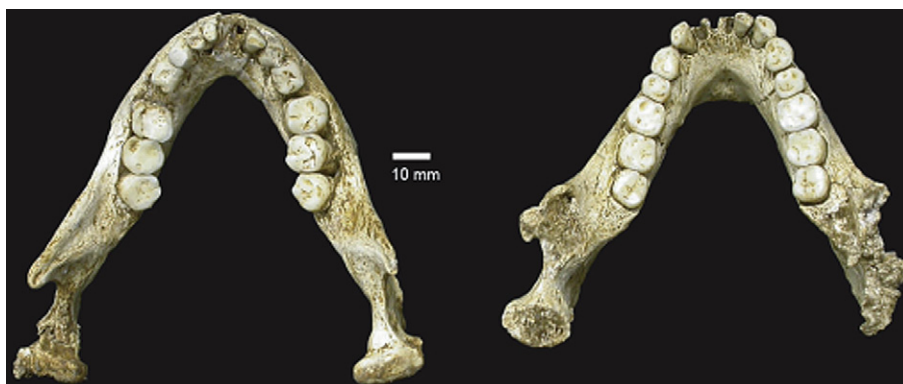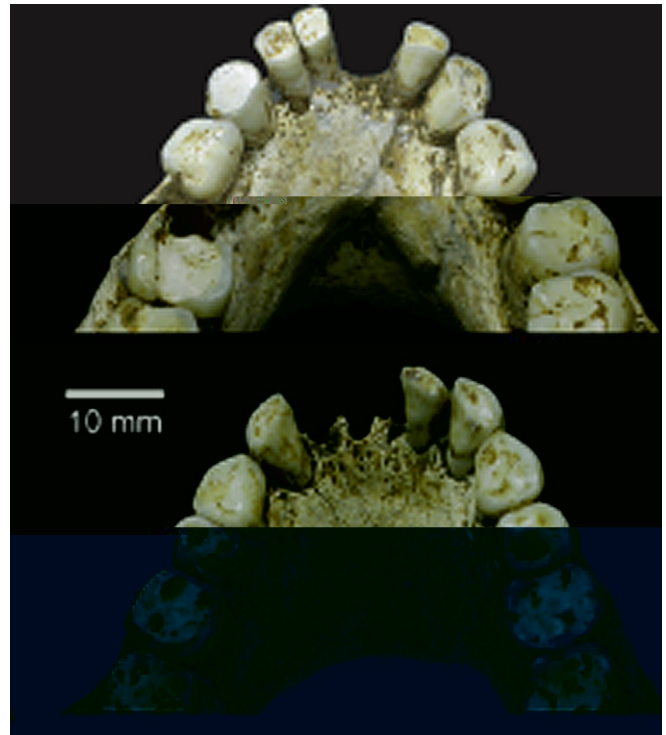

Figure 1. Occlusal views of the LB1 (left) and LB6 (right) mandibles.

Figure 3. Left lateral views of LB1 (top) and LB6 (bottom) mandibles.

Figure 4. Posterior symphyseal region and anterior dentition in LB1 (top) and LB6 (bottom).

were recorded prior to the LB1 mandible being removed from Jakarta, and are supported by CT scans, stereolithographic models, radiographs, and photographs.

Mandibular morphology

Analysis of linear dimensions of the LB1 mandible and comparative samples show that the mandibular dental arch is narrow anteriorly, long relative to its breadth, and the P_3–M_3 row is laterally convex rather than straight (Table 2, Fig. 1). Anteriorly, the symphyseal region is rounded, bulbous, and inferiorly receding (Brown et al., 2004) (Figs. 2–4). There is no evidence of a raised midline keel, mental tuberosity, mental fossae, or incurvature, as is usual in *H. sapiens* (Schwartz and Tattersall, 2000). However, several of the East Turkana early *Homo* mandibles (KNM-ER 820, KNM-ER 1482, and KNM-ER 1802) do have both a midline keel and mental trigone, but without incurvature, so there is no true chin (Wood, 1991). In the posterior symphysis, the alveolar planum inclines posteroinferiorly, there is a moderate superior torus, a deep and broad genioglossal fossa, and a low, rounded, and continuous inferior transverse torus (Simian shelf) (Fig. 4). In midline section, there is a marked posterior inclination of the symphyseal axis relative to the occlusal plane, and the overall morphology of the symphysis is similar to LH4 (Brown et al., 2004). However, the symphyseal morphology of Plio-Pleistocene hominins is highly variable, as demonstrated by comparison of Dmanisi D211, D2600, and D2735, and East Turkana KNM-ER 820, KNM-ER 992, KNM-ER 1482, KNM-ER 1802, and KNM-ER 1501 (Wood, 1991; Bräuer and Schultz, 1996; Van Arsdale, 2006; Rightmire et al., 2008) (Table 3). Some specimens of approximately similar date have a long and

inclined alveolar planum, and well-developed superior and inferior transverse tori, while others have a relatively featureless posterior symphysial surface (KNM-ER 1802, KNM-ER 1501). The symphyseal shape index of LB1 (symphyseal height/symphyseal thickness) is low in comparison to *H. sapiens* and close to the *H. erectus* and *A. afarensis* means (Fig. 6). This is a reflection of greater relative thickness of the symphysis in Plio-Pleistocene hominins and LB1 compared with *H. sapiens*, not necessarily a common morphological pattern.

If symphyseal robusticity ([symphyseal height*symphyseal thickness/external alveolar breadth at M_2]*100) is considered in relation to estimated body mass, then LB1 has a robust symphysis relative to body mass and is outside the range of small and large-bodied *H. sapiens*, as is A.L. 288-1 *A. afarensis* (Fig. 7). If body mass in Dmanisi *H. erectus* is estimated from the femoral head of D4167 that is probably associated with D2600, then D211 falls within the modern *H. sapiens* range of variation, but D2600 is hyper-robust, primarily due to its great symphyseal height. For symphyseal shape, D2600 is close to the modern human average (Figs. 6 and 8). The total cross-sectional area of the LB1 symphysis, measured from a scanned midline silicone impression in ImageJ, is 314.8 mm^2, with a perimeter of 73.7 mm. Examining the association between cross-sectional area and body mass may have provided some insight into masticatory behavior, but comparable data from *H. sapiens* and a range of Plio-Pleistocene hominins was not available. Unfortunately, radiograph (compression of three dimensional structures into two dimensional plane) and CT scan resolution were inadequate for documenting the thickness of cortical bone, defining the subperiosteal area, or the arrangement of trabecular bone in the symphysis with enough precision for calculating the cortical index (Daegling, 1989; Schwartz and Conroy, 1996) and cross-sectional geometric properties (Daegling, 1989; Daegling and Grine, 1991).

Comparison of the mid-sagittal symphyseal contours of LB1 with *H. sapiens* ($n = 37$), *H. erectus* ($n = 12$), and a sample of
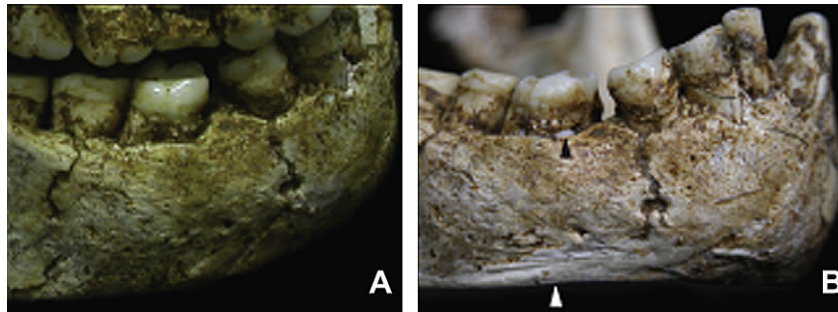
Figure 5. Detail of right lateral corpus of the LB1 mandible following cleaning and reconstruction in November 2003 (A), and after it had been returned to Arkeologi Nasional from Gadjah Mada University in February 2005 (B). Cut marks and fill in the inferior border (white arrow) and adhering impression material (dark arrow).

Plio-Pleistocene hominins ($n = 35$) using EFD and PCA reinforces the results obtained by Guy et al. (2008) (Fig. 7). Symphyseal shape in *H. sapiens*, including Melanesians and Late Pleistocene Australians, is distinct from australopiths, early *Homo*, and most *H. erectus*. LB1 falls outside the range of variation in *H. sapiens* and *H. erectus*, and is closest to A.L. 266-1 (PC1 0.129, PC2 −0.053), A.L. 330-5 (PC1

Table 2
Descriptive statistics for the *Homo sapiens* and *H. floresiensis* mandibles, crania, and femora.

Variable	*Homo sapiens*				*H. floresiensis*	
	n	mean	sd	CV	LB1	LB6
Symphyseal height	1110	33.7	3.87	0.11	28	28
Symphyseal thickness	592	15.0	2.15	0.14	15	17
Corpus height M_1	538	28.9	3.42	0.11	20.5	22.5
Corpus height M_2	557	27.3	3.29	0.12	24.5	23.5
Corpus thickness M_1	570	14.4	1.79	0.12	15	14
Corpus thickness M_2	596	15.8	2.02	0.12	15.5	15
Bicondylar breadth	919	118.4	7.92	0.06	(100)	–
Bigonial breadth	1065	99.2	8.83	0.08	(83)	71
Ramus minimum breadth	1192	34.9	5.00	0.14	36	36.5
M_2 external arch breadth	457	61.8	3.79	0.06	55	53
I_1 BL	540	5.8	0.52	0.08	5.7	–
I_2 BL	638	6.2	0.47	0.07	6.2	5.4
C BL	1210	7.8	0.69	0.08	7.9	6.7
P_3 BL	756	8.2	0.74	0.09	8.8	7.6
P_3 MD	756	7.0	0.67	0.09	10.4	8.5
P_4 BL	754	8.4	0.68	0.08	–	7.6
P_4 MD	754	6.9	0.59	0.08	–	6.3
M_1 BL	713	10.8	0.87	0.08	11.4	10.0
M_1 MD	713	11.0	0.64	0.06	10.1	10.1
M_2 BL	1181	10.6	0.92	0.08	10.7	9.7
M_2 MD	1181	10.5	0.72	0.07	10.1	10.3
M_3 BL	581	10.5	0.94	0.08	10	8.9
P_3 area (BL*MD)	756	57.6	9.24	0.16	91.5	64.6
P_4 area (BL*MD)	714	59.2	7.10	0.12	–	47.9
M_1 area (BL*MD)	713	120.8	16.89	0.14	115.1	101.1
M_2 area (BL*MD)	1181	112.6	17.88	0.15	108.0	99.9
P_3-M_2 crown area	544	350.5	47.1	0.13	372.5[d]	323.3
Symphyseal module (H/T)	518	2.26	0.30	0.13	1.86	1.64
Corpus module (H/T)	497	2.05	0.27	0.13	1.36	1.63
Symph. robusticity index[a]	508	815.6	156.6	0.19	763.6	935.4
Corpus robusticity index[b]	532	667.5	118.2	0.17	559.1	602.6
P_3 module (MD/BL)*100	756	84.4	2.49	0.03	118.1	111.8
P_4 module (MD/BL)*100	754	82.2	3.72	0.04	–	82.8
Maximum femur length	828	429.5	30.5	0.07	281	–
Max. femoral head breadth	799	43.4	4.14	0.09	31.5	–
Basion-nasion	637	115.7	6.74	0.05	81	–
Estimated body mass[c]	799	65.4	10.21	0.15	35.9	–
Humero-femoral index	732	71.9	2.15	0.03	86.4	–

[a] Symphyseal robusticity index = ([Symphyseal height*symphyseal thickness]/M2 arch breadth)*100.
[b] Corpus robusticity index = ([corpus height*corpus thickness]/M_2 arch breadth)*100.
[c] Body mass (kg) estimated from the mean of the three equations, based on prediction from femoral head diameter (Ruff et al., 1997).
[d] LB1 crown area estimate after addition of LB6 P_4 for missing LB1 P_4.

0.103, PC2 −0.050), and MAK-VP-1/12 (PC1 0.164, PC2 −0.014) *A. afarensis*. Variation in symphyseal shape within the *H. erectus* sample exceeds what has been reported for *H. sapiens* and *A. afarensis*, and living large-bodied hominoids (Daegling and Jungers, 2000; Sherwood et al., 2006; Guy et al., 2008). PCA of the EFDs indicates that, when compared with the *H. erectus* sample, the LB1 symphysis is closest in shape to Dmanisi D211 and Sangiran 5. However, the Dmanisi mandible has a prominent superior and inferior transverse tori and a deep genioglossal fossa, while Sangiran 5 does not. This highlights the potentially misleading results, which can be produced by cross-taxa comparisons using EFDs. Similar symphyseal outlines may not be associated with developmentally similar structures. For instance, both inferior transverse tori and prominent genioglossal spines may produce a raised section in the inferior third of the posterior symphyseal surface. While caution is required, in this instance the EFDs do emphasize the structural similarities between LB1, *A. afarensis*, and other Plio-Pleistocene hominins that share a symphysial profile that is inferoanteriorly receding, thick relative to height, with an extended alveolar planum, prominent inferior and superior transverse tori, and a deep genioglosal fossa. This pattern is not present in *H. sapiens* and currently known examples of Asian *H. erectus*.

Postmortem distortion of the right mandibular corpus has increased the anteroposterior curvature of the occlusal plane and inferior border of the corpus. A moderate lateral prominence lies lateral to the anterior third of M_1 making the corpus thickest at this location, with the ramus root inserting on the corpus above the lateral prominence. The superior lateral torus extends anteriorly from the lateral prominence as far as P_3, with a broad and shallow intertoral torus and poorly expressed inferior lateral torus. There are bilaterally double mental foramina located below P_3 and P_4, with the posterior foramina smaller in size and located more inferiorly (Fig. 3). Multiple foramina are a common feature of Asian *H. erectus*, a range of Plio-Pleistocene hominins, and are found at low frequency in our own species (Kieser et al., 2002). Compared to *H.sapiens*, the corpus is thick relative to its height, a trait shared by most pre-*H.sapiens* hominins (Table 3, Figs. 6 and 7). Relative to estimated body mass, LB1 has a robust mandibular corpus, but does not have the distinctive posterior corpus robusticity evident in A.L. 288-1, or australopiths more generally (Wood and Aiello, 1998). The relatively great corpus robusticity in LB1 is also apparent when the total cross-sectional area of the corpus at M_1 is compared with that in *H. sapiens* (Fig. 9). In Edo Period Japanese, there is a reasonable linear association between corpus cross-sectional area and femoral head diameter (body mass), with the two Liang Bua mandibles well outside the range of variation in this urban-agricultural sample. It may have been informative to extend this comparison to *H. sapiens* with different subsistence modes, as well as a range of Plio-Pleistocene hominins, but comparable data are not available.

Table 3
Mandibular characters that differentiate LB1 and LB6 from *Homo sapiens* and Plio-Pleistocene hominins.

	Liang Bua 1 and 6	*H. sapiens*	N. African *H. erectus*	Sangiran *H. erectus*	Chinese *H. erectus*	Dmanisi *H. erectus*	E. African early *Homo*	*A. africanus*	*A. afarensis*
Canine size	Small	Small	Small	Small	Small	Variable	Variable	Medium	Large
MD elongation of P3 crown	Yes	No	No	No	No	Variable	Yes	No	Yes
Complex P3 root morphology (multiple or Tomes')	Yes	No	No	Variable	No	Variable	Yes	Yes	Yes
Complex P4 root morphology (multiple or Tomes')	Yes	No	No	Variable	No	Unknown	Yes	Yes	Yes
M1 ≥ M2 > M3	Yes	Yes	Yes	Yes	Yes	Yes	No	No	No
Relatively wide alveolar arcade	No	Yes	Yes	Yes	Yes	No	No	No	No
Symphyseal axis strongly inclined	Yes	No	No	No	No	Variable	No	Yes	Yes
Mandibular corpus comparatively thin	No	Yes	No	Variable	Yes	Variable	No	No	No
Symphysis comparatively thin	No	Yes	Yes	Variable	Yes	Variable	No	No	No
Weak expression of posterior symphyseal structures	No	Yes	Yes	Yes	Yes	Variable	Variable	No	No
Broad extramolar sulcus	Yes		Yes	Yes	No	No	Yes	Yes	Variable
Ramus root anterior location (M1–M2)	Yes	No	No	No	No	Variable	Yes	Yes	Yes
Ramus root vertical location	High	Low	Intermediate	Low	High	Intermediate	High	High	High
Lateral corpus hollow	No	Yes	Yes	Variable	Yes	Variable	No	Variable	No

A thick corpus associated with a massive postcanine dentition has been seen as the result of the interplay of ontogenetic and evolutionary adaptations to masticatory forces, particularly in *Australopithecus* and early *Homo* (Wolpoff, 1975; Wood, 1978). While LB1 shares a similar cross-sectional corpus geometry to *Australopithecus*, and is megadont in comparison with *H. sapiens*, it lacks the huge, mesiodistally-elongated molar crowns that are a feature of australopiths, and to a lesser degree early *Homo* (Wood and Abbott, 1983; Wood, 1991; Brown et al., 2004). While a developmental and functional relationship between corpus and tooth dimensions makes sense, Plavcan and Daegling's (2006) intraspecific and interspecific study found few significant correlations, and no evidence of homogeneity of slopes among taxonomic groups. Root morphology and size, facial architecture, and masticatory force may be more important determinants of corpus robusticity than tooth crown size. Unfortunately, as Plavcan and Daegling (2006) pointed out, the allometric associations of hominin tooth root size and morphology are poorly understood. The total cross-sectional area of the corpus at the center of the right M$_1$, with allowance for alveolar recession resulting from periodontal disease, is 292.4 mm^2 with a perimeter of 67.8 mm (dimensions measured from a CT DICOM slice using OsiriX and ImageJ).

A transverse section at P$_3$ highlights the inferomedial progression of the corpus contour inferior to the level of the mental foramina. This reflects a continuation of the inferior retreat of the symphyseal region, and is strikingly similar to the pattern seen in *A. anamensis* and *A. afarensis* (Kimbel et al., 2006), but not Olduvai OH 13 and East Turkana early *Homo* that have a more vertical profile (Tobias, 1991; Wood, 1991). In *H. sapiens*, the contour of the lateral corpus adjacent to the foramina is usually concave, and the inferior border everted (Table 3, Fig. 10). Prominent canine jugae are not evident in LB1. On the medial aspect, the alveolar segment is somewhat raised and continuous with the superior transverse torus anteriorly. A well-developed lingual alveolar prominence, continuous with the superior transverse torus, has been argued to be a feature of African *H. erectus* (Rosas and De Castro, 1998), but is not present in the Sangiran or Zhoukoudian samples. There is no evidence of mylohyoid lines, with a smooth transition to the submandibular fossa. Anteriorly, the submandibular fossae constrict as they join the broad genioglossal fossa. Genial spines and foramina are present above the inferior transverse torus (Fig. 4).

In lateral aspect, the root of the ascending ramus is placed anteriorly, beginning near the interdental septum for M$_1$–M$_2$, and with the ramus obscuring most of the M$_3$ (Fig. 3). The root of the ramus is placed high on the corpus at the alveolar margin, rather than the typically more posterior and mid-corpus root position in *H. sapiens*. The extramolar sulcus is broad and shallow, opening anteroinferiorly lateral to M$_2$ (Figs. 1 and 2). The ramus is broadest inferiorly, thickened mediolaterally, and in lateral view the anterior border of the ramus and coronoid processes arch posteriorly, without the anteriorly bulging coronoid margin and mid-ramus "waisting" typical of *H. sapiens*, *H. erectus* (KNM-WT 15000, Dmanisi D2600 and D2735, and Ternifine), and the only well-preserved example of early *Homo* (KNM-ER 992) (Wood, 1991). In the occlusal plane, the coronoid process is higher than the condyle, and is directed posteriorly with the tip overlapping the mandibular notch. While the rami are not as massive as those in MAK-VP1-2, AL333-43b, and A.L. 822-1 *A. afarensis*, which also have a relatively narrower mandibular notch, the overall morphology in LB1 is more similar to australopiths than to *Homo* (White and Johanson, 1982; Wood, 1991; White et al., 2000; Rak et al., 2007) The better preserved right condyle has a maximum mediolateral and anteroposterior dimension of 18 mm and 9 mm, respectively, a condylar height of 24 mm above the occlusal plane, and a deep subcondyloid tubercle (17 mm superoinferior) continuous with the neck and superior surface of the condyle. The masseteric fossa is concave, the gonial region everted, and the gonial angle is 116° on the left side and 100° on the distorted right side.

Medially, the alveolar prominence is continuous with the crista pharyngea, and is somewhat tubular in form. The crista pharyngea continues unbroken until the tip of the coronoid process, as does the buccinator gutter that it defines (Fig. 11). Where the cristae pharyngea and endocondyloidea join, the alveolar plane is present as a raised, mediolaterally thickened surface that is continuous with the inferior border of the sigmoid notch, contrasting with the depressed surface of the alveolar plane common in *H. sapiens*, and KNM-WT 15000. The overall effect is of a very heavily reinforced superior ramus in LB1. A neurovascular groove passes through the endocondyloid crista, and bilateral superior pterygoid tubercles are present. The mandibular foramina are located within a broad, somewhat oval-shaped depression that extends to the triangular plane. The foramina are large, oval-shaped, and without a projecting lingular notch. The sulcus coli is cone-shaped and without sharp margins. Taken as a whole, the morphology of the area including and adjacent to the mandibular foramen is closer to *Pan* than it is to typical *Homo* morphology (Richards et al., 2003). The areas of insertion for the lateral and medial pterygoid muscles are deeply excavated and all of the septal insertions are clearly defined.
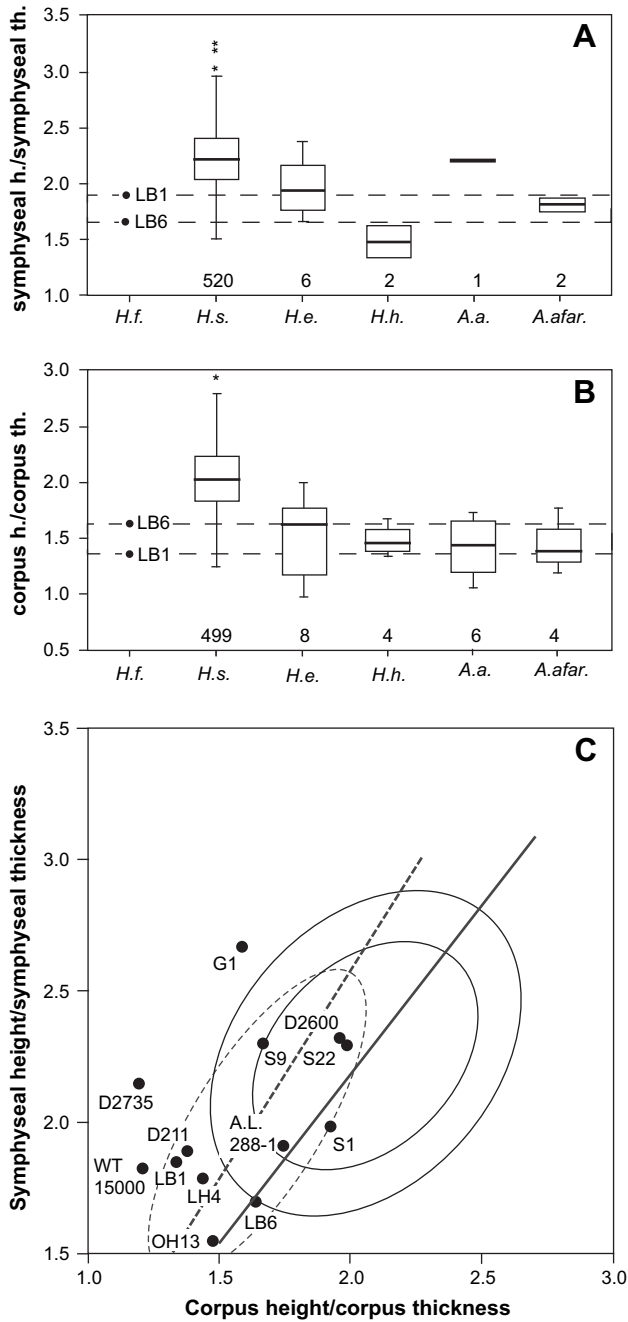
Figure 6. Symphyseal and corpus shape in *H. floresiensis* and Plio-Pleistocene hominins. (A) Box plots of the symphyseal module (symphyseal height/symphyseal thickness) distributions for *H. sapiens* (*H.s.*), *H. erectus* (*H.e.*), *H. habilis* (*H.h.*), *A. africanus* (*A.a.*), and *A. afarensis* (*A.afar.*) and values for LB1 and LB6 (*H. floresiensis, H.f.*). (B) Box plots of the corpus module (corpus height/corpus thickness) distributions for Plio-Pleistocene hominins and values for LB1 and LB6. (C) Scatterplot of the relationship between the symphyseal and corpus modules in large and small-bodied *H. sapiens*, and individual Plio-Pleistocene hominins, with sample confidence ellipses ($p > 0.68$ and $p > 0.90$) and reduced major axis regression slope. RMA for *H. sapiens* $n = 465$, slope $a = 0.977$, intercept $b = -0.15$, $r = 0.33$, error $a = 0.042$, error $b = 0.097$. Andaman Islanders (filled circles), $n = 10$, dashed RMA regression line and confidence ellipse ($p > 0.68$). *H. erectus* data are from Wood (1991), Kaifu et al. (2005a), Van Arsdale (2006), and PB (pers. obs.). *H. habilis* data are from Wood (1991), *A. africanus* data are from Charles Lockwood (pers. comm.), and *A. afarensis* data are from Kimbel et al. (2004, 2006).

Dental morphology

All teeth are fully erupted and all crowns have marked occlusal and interproximal wear, with very little evidence of original cusp
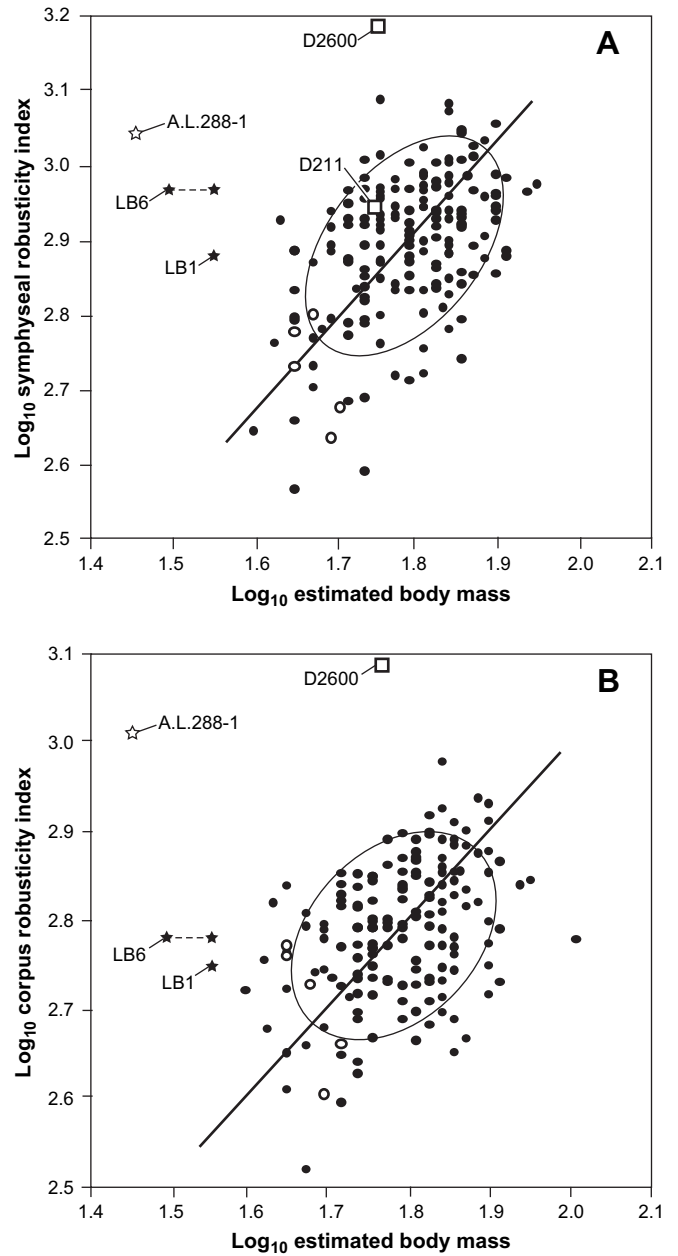
Figure 7. Scatterplots, RMA regression slopes, and sample confidence ellipses ($p > 0.68$) for the relationships between symphyseal robusticity and body mass (A), and corpus robusticity and body mass (B), in modern humans, LB1 and LB6, A.L. 288-1 (Johanson et al., 1982; White and Johanson, 1982; Kimbel et al., 2004), and Dmanisi D211 and D2600 (Bräuer and Schultz, 1996; Van Arsdale, 2006; Rightmire et al., 2008). Body mass was estimated from maximum femoral head breadth using the average of the three equations in Ruff et al. (1997). Range of body mass estimates for LB6 are based on data for LB1 and the smaller size of adult postcrania that may be associated with LB6. Body mass estimates for Dmanisi D211 and D2600 were calculated from the D4167 femur (Lordkipanidze et al., 2007). Reduced major axis regression (RMA) for the association between the symphyseal robusticity index and body mass (A), $n = 174$, slope $a = 1.191$, intercept $b = 0.761$, $r = 0.45$, err $a = 0.080$, err $b = 0.143$. RMA for the association between the corpus robusticity index and body mass (B), $n = 174$, slope $a = 0.973$, intercept $b = 1.045$, $r = 0.34$, err $a = 0.069$, err $b = 0.123$.

and fissure morphology preserved (Figs. 1 and 4). Interproximal facets on the adjacent P_3 and M_1, the occlusion and position of the right M_1, and occlusal wear on the opposing maxillary teeth, suggest that the right P_4 was lost antemortem, and not congenitally absent. The degree of occlusal wear is somewhat asymmetrical across the arch, and is a result of occlusion, with mastication

PC2

0.2
0.1
0.0
-0.1

D2600
S1   OH13
S6
CC28
KNM-ER 1802
KS1
A.L. 288-1
ZHH1
D211
S5   AR13   LB6   LB1
LH4

① ●
② ○
③ ■
④ □
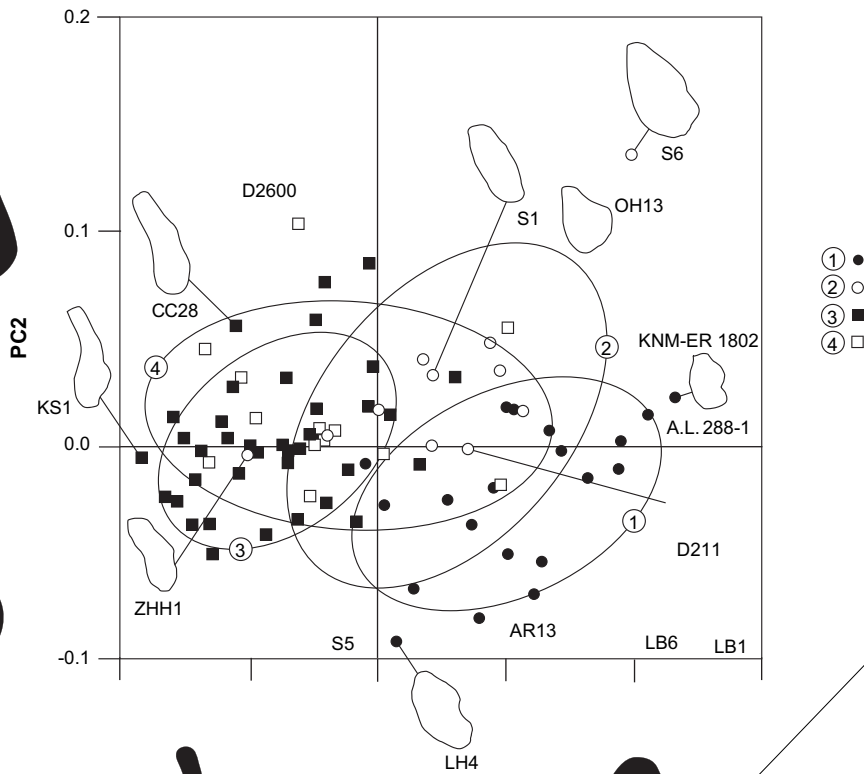
possibly favoring the left side of the arch. The maxillary P^4s are rotated (Brown et al., 2004) and the absence of a distal facet on the right M^2 indicates that the right M^3 did not come into occlusion (CT scans suggest that there may be a very small M^3 odontome within the alveolar bone). There is a well-developed Curve of Spee, which is exaggerated by post-mortem distortion on the right side. Individually, teeth have relatively horizontal planes of occlusal wear, rather than angled inferobucally on the P_3–M_2 crowns. Wear on the anterior mandibular teeth and associated maxillary dentition suggests an edge-to-edge incisal occlusion. There has been some compensatory mesial migration and eruption of the teeth. Impaction of food debris and calculus deposits have resulted in periodontal disease and alveolar recession around the molar tooth roots. Alveolar damage is most noticeable on the lingual margins of M_2–M_3, and the sublingual salivary ducts appear to have been relatively active. Where occlusal wear has exposed a cross-section through the enamel it is clear that the crowns have thick enamel. CT scans were used to indicate tooth root and alveolar morphology. Unfortunately, the resolution was too low to accurately measure enamel thickness, or any other tooth dimension.

The anterior part of the mandibular arch is extremely narrow (intercanine breadth is 14.5 mm) and the incisor tooth crowns are small in size, particularly mesiodistally, relative to the dimensions of the post-incisor dentition (Table 2). The remaining I_1 has smaller root and crown dimensions than either I_2, however, crown height and maximum breadth of the incisal area have been greatly

reduced through occlusal wear. The right I_2 is less worn and retains the inferior sections of the marginal ridges, which extend to the cervical margin and lingual fossa. Occlusal wear on the I_1 and right I_2 is fairly horizontal, while there is a slight "step" running mesiodistally across the occlusal surface of the left I_2.

Both canines have marked occlusal wear, with the wear facets angled distally. A larger area of dentine is exposed on the left side than the right, and crown heights are level with those of the adjacent I_2 and P_3. The exposed cross-sections through the crowns, combined with the remains of the marginal ridges on the lingual surface, suggest that well-defined marginal ridges were present. The preserved sections of these ridges have smooth lingual margins bordering shallow fossa. There is no evidence of a lingual ridge on either canine. CT scans demonstrated that both of the canines have a single conical root.

The P_3s have asymmetrical, mesiodistally-elongated crowns, with a slightly oblique orientation and broad distal talonid. While occlusal and interproximal wear has removed most details of crown morphology, it appears that the distal fovea was larger than the anterior, there was a strong distal marginal ridge, and the crowns were dominated by a large buccal cusp. Mesiodistally elongated, asymmetric P_3s are present in Miocene apes, early australopiths, and living apes. They clearly represent the primitive hominin condition, which changes to a derived, molarized, bicuspid, and symmetrical P_3 in later australopiths and early members of the genus *Homo* (Leonard and Hegmon, 1987; Wood and Uytterschaut,
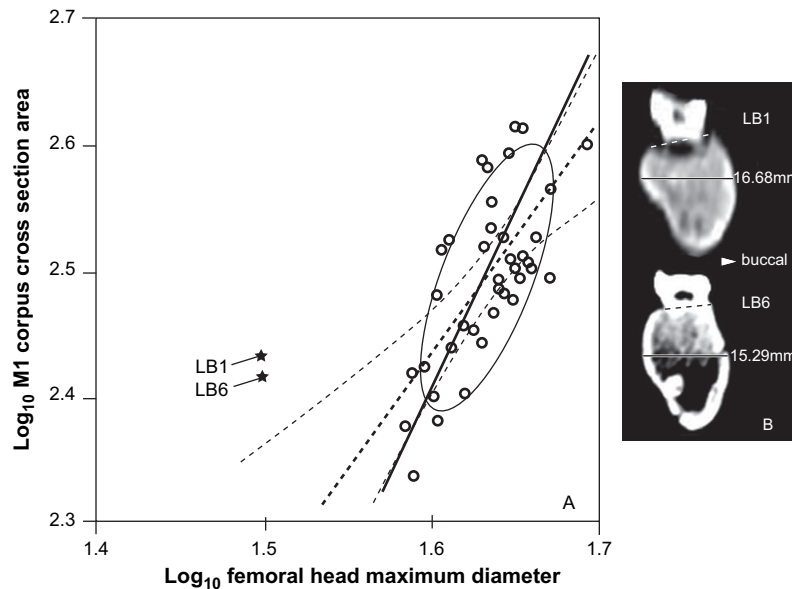
Figure 9. Scatterplot of the association between corpus cross-sectional area at M_1 and maximum femoral head breadth in *H. sapiens* and *H. floresiensis* (A), and CT scans of the LB1 and LB6 right corpora at mid-M_1 (B). Total subperiosteal corpus area was measured from scanned silicone molds, with the superior margin of the cross-section defined by a line connecting the medial and lateral alveolar margins (dashed lines in B). Cross-sectional areas for LB1 and LB6 were also measured from coronal plane CT slices. LB1 has periodontal disease that has removed alveolar bone from around the right M_1. The cross-section was corrected for this bone loss (dashed white line in [B]). RMA (heavy line) and CLS slopes, CLS confidence ellipse $p > 0.68$, and $p > 0.95$ CLS confidence bands (dashed lines). The modern *H. sapiens* are all from the Edo Period site of Ikenohata. Comparable data for other hominins is not currently available. Reduced major axis regression results for the *H. sapiens* sample, $n = 39$, $r = 0.68$, slope $a = 2.672$, intercept $b = -1.869$, conventional least squares regression $y = -0.497 + (1.832*x)$, SE $= 0.050$.

1987; Suwa et al., 1996; Kimbel et al., 2006) (Table 3). The LB1 P3s contrast with the derived condition in most *H. erectus* and *H. sapiens*, which is broadly similar to the P4 in shape, is usually bicuspid although with a larger buccal cusp, and in occlusal outline resembles the incisal outline of the canine. However, allowing for the effects of occlusal and interproximal wear, the details of crown shape, size, and location of the distal fovea and mesial ridge, and the prominence of the talonid in LB1, are also similar to Dmanisi D2735 and D211 (Martinón-Torres et al., 2008). Comparison of the size and shape of the Liang Bua P3 crowns place them outside the range of variation in our species (Fig. 12).

Direct examination, supported by CT scans and radiographs, also demonstrate that both P3s have bifurcated roots. The mesial root is conical in shape with a single nerve canal, and the distal root is broad and mesiodistally flattened with two nerve canals (Fig. 13). P3s with this root morphology, MB + D, are common in *A. afarensis* but rare in early *Homo* (Abbott, 1984; Wood et al., 1988). In the East Turkana early *Homo* mandibles, bifed P3 roots are present in KNM-ER 992 and KNM-ER 1482 (Wood, 1991). Some Indonesian *H. erectus* mandibular premolars also have bifurcated or Tomes' roots (Kaifu et al., 2005b), as does Dmanisi D2600 and D2735, the former having an exposed distal root which is flattened as in LB1 (Van Arsdale, 2006; Martinón-Torres et al., 2008). The reported bilateral incidence of MB + D P3s in modern *H. sapiens* is 3.5% (Shields, 2005).
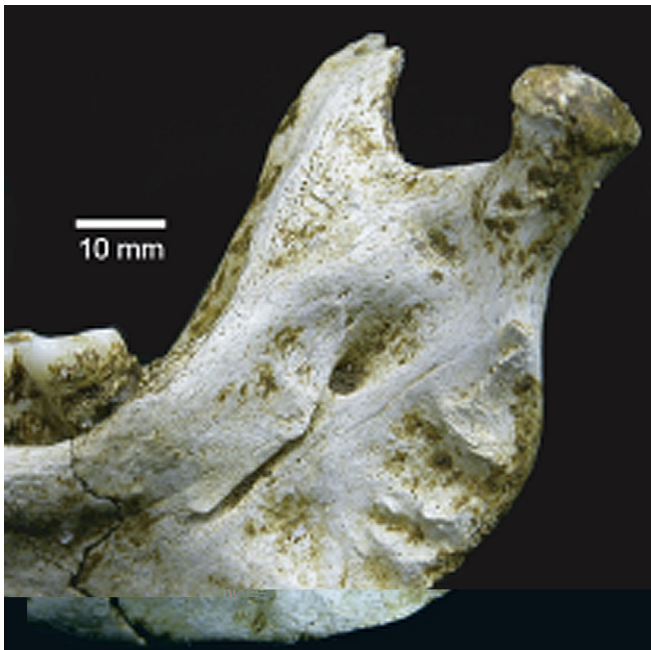
The only remaining evidence of P4s in LB1 is the preserved left alveolus, with the left P4 lost postmortem and the right during life. CT scans, and an impression of the P4 alveolus, indicate a Tomes' root with a strong mesiolingual grove and slight distobuccal groove, forming a C-shaped cross-section. There is some evidence that C-shaped Tomes' roots first appeared with *H. habilis*, with reduced postcanine crown and root dimensions compared with *Australopithecus*, but continued selection for a large root surface area (Shields, 2005; Wood et al., 1988). Shields (2005) found that Tomes' rooted P4s occur at a low frequency in *H. sapiens* (2.5%), and there was a developmental association between premolar crown size, root number, and root morphology.

All of the mandibular molar teeth are preserved in LB1. However, occlusal wear has removed evidence of cusp and fissure morphology, and interproximal wear has reduced the mesiodistal crown dimensions of all teeth. If tooth dimensions are adjusted for interproximal wear, all of the molars have mesiodistal dimensions that are similar to the buccolingual measurements for the same teeth. There is not a great deal of difference between the size of the molar teeth in each quadrant, and the size sequence for both mandibular and maxillary teeth in LB1 is M1 > M2 > M3. The LB1 molars do not have the mesiodistally elongated crowns present in australopiths and early *Homo*, where this is most evident in large M3 crowns, with M3 < M2 (Wood, 1991; Kimbel et al., 2004). Radiographs and CT scans indicate that the mesial and distal roots of both M_1s are widely divergent, but converge for M_2 and M_3.

Relative tooth size in LB1 was compared with variation in *H. sapiens* by examining the relationship between the size of the postcanine teeth (crown area P_3–M_2) and body mass (Table 2, Fig. 14). Tooth dimensions were corrected for mesiodistal wear and the LB6 P4 substituted for the missing P4s in LB1. Body mass was estimated from femoral head breadth (31.5 mm) using the average of the three equations in Ruff et al. (1997). For LB1, these provide estimates ranging from 31.4 kg to 41.3 kg, with an average of 35.9 kg. Globally, modern humans have broad regional patterns of relative limb proportions, body breadth, body mass, and average dental dimensions (Ruff, 1991, 2002). For postcanine tooth size, Australian Aborigines have absolutely and relatively larger teeth than the East Asian and European samples used here (Fig. 14). The relationship between postcanine size and body mass in LB1 is very close to what would be predicted for an Australian Aborigine of this body mass. For adult hominins that also have associated femora, A.L. 288-1 (whose femur head breadth is 28.6 mm) has a lower estimated body mass and substantially larger post canine tooth size than LB1, and larger-bodied Dmanisi *H. erectus* (D4167 femoral head breadth is 40 mm) falls on the edge of the $p > 0.66$ sample confidence ellipse of the Australians. These results contrast with those obtained previously (Brown et al., 2004), where relative tooth
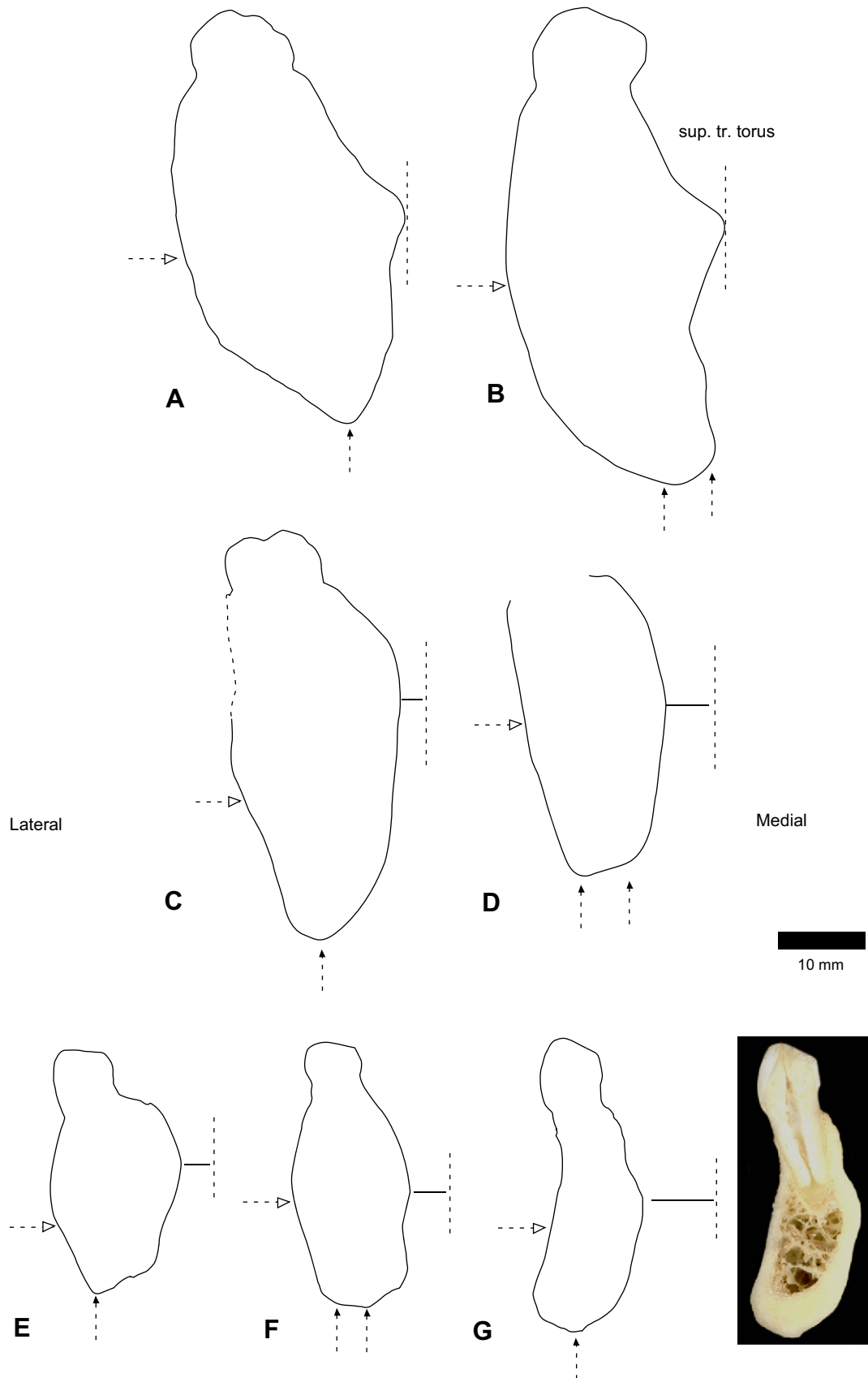
Figure 10. Outlines of modern human and Liang Bua left corpora at distal P$_3$. The superior transverse torus (sup. tr. torus) is a rounded buttress of bone marking the inferior margin of the internal (medial) alveolar surface. Stereolithographic models of the Liang Bua originals were sectioned at the position indicated by Kimbel et al. (2006), scanned directly into Adobe Photoshop, and the edges redrawn in Adobe Illustrator. A) *A. anamensis* KNM-KP 29281; B) *A. afarensis* KNM-KP 29281; C) *H. rudolfensis* KNM-ER 1802 reversed; D) *H. erectus* Sangiran 1 reversed; E) LB1; F) LB6; G) *H. sapiens* with original cross-sectioned surface. A and B redrawn from Kimbel et al. (2006). Hollow arrow indicates position of mental foramen, solid arrow inferior border, and hatched vertical line the midline. The position of the midline in Sangiran 1 was estimated from Sangiran 22, which preserves both sides of the arch.

Figure 11. The right medial ramus of LB1.

Figure 12. Bivariate plot of P$_3$ crown shape index (MD/BL*100) vs. buccolingual crown breadth for *H. floresiensis*, *H. sapiens*, *H. erectus* (Wood, 1991; Kaifu et al., 2005a; Van Arsdale, 2006; PB, pers. obs.), *H. habilis* (Wood, 1991), *A. africanus* (Kimbel et al., 2006), *A. afarensis* (William Kimbel, pers. comm.), *Pan paniscus*, and *Pan troglodytes troglodytes*, with *p* > 0.90 confidence ellipses and least squares regression slopes. *Pt* and *Pp* are separated on the basis of size and not shape.

size in LB1 was measured using the megadontia quotient of McHenry (1988), with lower body mass calculated from regression equations based on the stature of Jamaican school children (Aiello and Dean, 1990) and femoral cross-sectional area (McHenry, 1988). With less body mass (16–29 kg), LB1 was megadont (1.26–2.11) relative to *H. sapiens* (0.9) and *H. erectus* (0.9), but equivalent to estimates for *H. habilis* (1.9) (McHenry and Coffing, 2000). Therefore, depending upon how relative tooth size in LB1 is measured, LB1 is either within or outside the range in *H. sapiens* and *H. erectus*.

LB2

An isolated left P$_3$ was recovered from Sector VII, below the layer of "white" tuffaceous silts originally dated to 12–11 ka (Morwood et al., 2004), and described by Brown et al. (2004). The crown is asymmetric in shape, mesiodistally elongated, shares the triangular occlusal profile of the LB1 and LB6 P$_3$s, and has marked occlusal wear (Fig. 15). In common with LB1 and LB6, there is a well-developed talonid, occlusal wear, and what remains of crown morphology suggests a single, large buccal cusp, and the buccal surface of the crown continues to bulge outwards as it progresses apically towards the cemento-enamel junction. Unlike the other Liang Bua P$_3$s, the occlusal plane of wear is strongly oblique and angled distally, with relatively small interproximal facets. The root is broad and mesiodistally compressed, with two groves on the mesial and distal surfaces (lingual grooves deepest on both), and three nutrient foramina. In cross-section, the LB2 Tomes' root resembles a MB + D compressed into a single root, rather than C-shaped Tomes' root.

LB6

History and preservation

The LB6 mandible was excavated from Spit 51, Sector XI, at Liang Bua in September 2004. Based on its stratigraphic position below the layer of "white" tuffaceous silts dated to 12–11 ka, and above LB1 in Spit 58 (Morwood et al., 2004, 2005), the LB6 mandible dates to approximately 17 ka. Most of the right ramus, and parts of the

left coronoid process and condyle were damaged during discovery. When excavated, this mandible was undistorted, but taphonomic processes had resulted in a fracture through the corpus between the right P$_3$ and P$_4$ and left M$_1$ and M$_2$. These fractures did not affect the dimensions and morphological features discussed here. Bone preservation was similar to LB1. It is possible that some of the adult postcranial elements recovered from Spits 51–52 may be associated with the LB6 mandible. If so, LB6 would be a smaller adult than LB1 (Morwood et al., 2005).

The dentition is complete, apart from the central incisors and left I$_2$ that were not recovered from the excavation. Both of the M$_3$s are fully erupted, with occlusal wear and dentine exposure indicating adult status. Tooth size, and most of the linear dimensions of the LB6 mandible are smaller than LB1. The gonial region is also not everted and areas of muscle attachment on the lateral ramus are less rugose. Based largely on pelvic morphology, and dental and skeletal proportions, Brown et al. (2004) concluded that LB1 was most likely a female. However, as nothing is known about the expression of sexual dimorphism in *H. floresiensis* this conclusion remained tentative. The LB6 mandible, and its likely associated postcrania, are from a smaller individual than LB1. If we are correct about the sex of LB1, then LB6 is probably also female.

On November 2, 2004, the LB6 mandible was transferred to Gadjah Mada University, along with other skeletal remains from Liang Bua (Balter, 2004; Dalton, 2005a,b). During an attempt to cast this mandible, it was irreparably damaged. The symphysis was broken, the medial surface of the right ramus removed and poorly repaired (Fig. 16), and cut marks, glue, and filler are now a feature of the lateral corpus and ramus. This has altered the original arch dimensions, occlusion, and morphology of the symphysis and ramus. Data reported here are based on a limited number of dimensions and photographs recorded before LB6 left Jakarta, supplemented by measurements, photographs, radiographs, and CT scans recorded after the mandible was returned. Unfortunately, many of these observations can no longer be verified through reference to the original specimen.
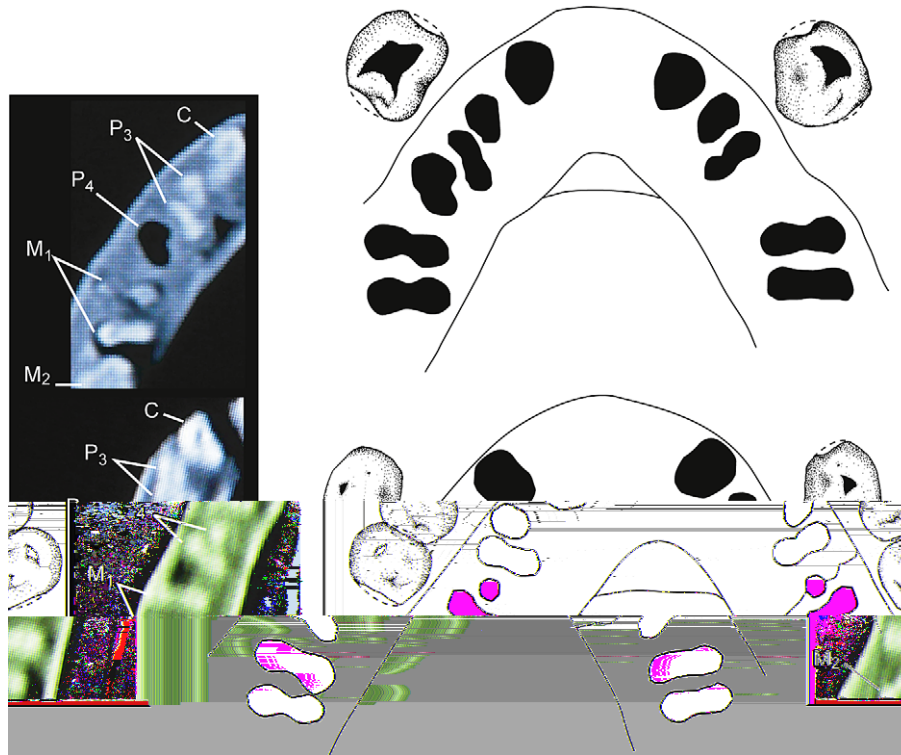
Figure 13. Orientation, number, and location of left C-M_1 tooth roots, and occlusal views of the associated premolars in LB1 (top) and LB6 (bottom), with dashed lines indicating crown dimensions prior to interproximal wear. Root location was documented from CT scans (left) and direct observation, with the cross-section orientated in the alveolar plane and approximately 8 mm inferior to the occlusal surface.

Mandibular morphology

In overall size and morphology, and relative to comparative samples, LB6 has numerous detailed similarities to LB1 (Table 2, Figs. 1–4). However, with reduced tooth and corpus dimensions, it is probably from a slightly smaller adult. The mandibular dental arch is narrow anteriorly and long relative to its breadth. The axis of P_3–M_3 is straight, forming a more V-shaped dental arcade than in LB1, and in lateral view the inferior border of the mandible is not as arched as LB1. Similar to LB1, the anterior aspect of the symphyseal region lacks a raised midline keel, mental tuberosity, mental fossae, or incurvature, as are usual in *H. sapiens* (Schwartz and Tattersall, 2000). However, it is not as rounded, bulbous, and receding as in LB1. The posterior symphyseal regions of LB1 and LB6 are remarkably similar (Fig. 4). As in LB1, the alveolar planum of LB6 inclines posteroinferiorly. There is a moderate superior torus, a deep and broad genioglossal fossa, and the inferior transverse torus is low and rounded, rather than shelf-like, and there is a strong posterior angulation of the symphyseal axis. LB6 also shares the relatively thickened and robust symphysis of LB1, with a low symphyseal index compared with *H. sapiens* (Table 2, Figs. 6 and 7). The symphyses of these two mandibles are most similar to a range of Plio-Pleistocene hominins, including LH4 (White and Johanson, 1982) and KNM-WT 15000 (Walker and Leakey, 1993), and the symphyseal thickening and internal transverse tori are most similar to Dmanisi D211 and East Turkana KNM-ER 820 and KNM-ER 992 (Wood, 1991). However, within the Dmanisi sample, D211 has a mental eminence while D2735 does not (Bräuer and Schultz, 1996; Van Arsdale, 2006), and there is considerable variation in the East Turkana early *Homo* mandibles as well (Wood, 1991). The Liang Bua symphyses are unlike the geographically more proximate examples of *H. erectus* from Sangiran (Kaifu et al., 2005a) and Zhoukoudian (Weidenreich, 1936), which lack comparable internal buttressing.

Comparison of the mid-sagittal symphyseal contours of LB6 with *H. sapiens*, *H. erectus*, and a sample of Plio-Pleistocene hominins using EFD and PCA emphasizes the morphological similarity with LB1 (Fig. 8). LB6 falls outside the range of variation in *H. sapiens* and *H. erectus*, and is closest to A.L. 266-1 (PC1 0.129, PC2 −0.053), A.L. 330-5 (PC1 0.103, PC2 −0.050), and MAK-VP-1/12 (PC1 0.164, PC2 −0.014). These results are contrary to the unsupported claims made by Jacob et al. (2006) that indicate that the LB1 and LB6 mandibles show no substantial deviations from *H. sapiens*, and LB6 has no traits that are unknown amongst modern Australomelanesians. If symphyseal robusticity in LB6 is considered in relation to the body mass estimate of LB1, LB6 is more robust than LB1, also outside the range of *H. sapiens*, and approaching the relative robusticity of *A. afarensis* (A.L. 288-1).

The LB6 mandibular corpus was originally undistorted and extremely well preserved. A moderate lateral prominence lies lateral to the M_2s, more posterior than in LB1, making the corpus thickest at this location. The ramus root inserts on the corpus at the posterior margin of the lateral prominence. The superior lateral torus extends anteriorly from the lateral prominence as far as P_3, and the intertoral torus and inferior marginal torus are more defined than in LB1. There are multiple mental foramina bilaterally, three on both sides, located below P_3 and P_4, with the posterior foramina smaller in size and located more inferiorly than the anterior pair. A shallow groove separates the foramina from the inferior border, and, as in LB1, the bone surface above the foramina is not depressed. Compared to *H. sapiens*, the corpus is thickened relative to its height (Fig. 6), a trait shared by LB1 and most pre-sapiens hominins, and, similar to LB1, robust relative to body mass (Table 2, Figs. 7 and 9). Canine jugae are more pronounced than in LB1, although still only slightly raised. Medially, the alveolar segment is not as tubular in form as in LB1, but is continuous with the superior transverse torus anteriorly. As in LB1, mylohyoid lines
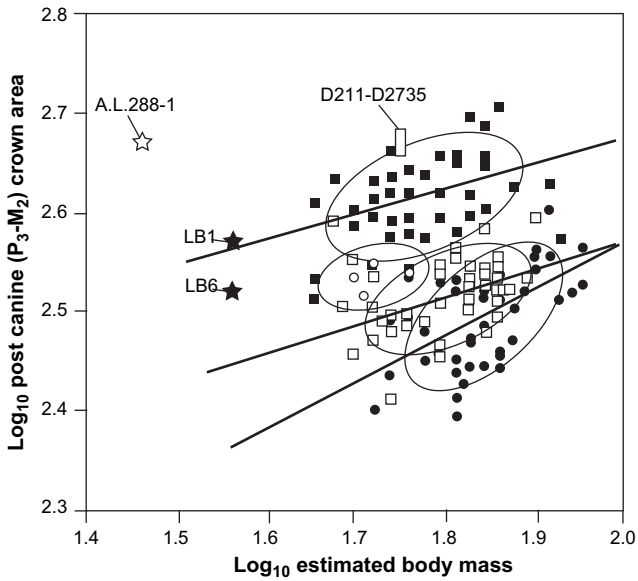
Figure 14. Bivariate plot of the relationship between mandibular post canine crown area and estimated body mass in *H. sapiens*, LB1 and LB6, Dmanisi D211 and D2735, and A.L. 288-1. Least squares regression slopes and sample confidence ellipses ($p > 0.68$), with all data transformed to Log_{10}. Body mass in LB6 estimated from LB1. Variation in post-canine crown area at Dmanisi based on mandibles D211 and D2735, as tooth wear and tooth loss prevents the measurement of crown area in D2600 (Van Arsdale, 2006; Martinón-Torres et al., 2008). Body mass calculated from maximum femoral head breadth using the average of the three equations in Ruff et al. (1997), with the Dmanisi D4167 femur used for D211 and D2735. Conventional least squares regression results for the *H. sapiens* samples: Australia $n = 41$ $y = 2.139 + (0.268{*}x)$, $r = 0.43$, SE = 0.039; East Asia $n = 42$ $y = 2.002 + (0.285{*}x)$, $r = 0.46$, SE = 0.032; and Europe $n = 44$ $y = 1.631 + (0.407{*}x)$, r = 0.55, SE = 0.041. Australian solid squares, East Asia hollow squares, Europe-Africa solid circles, and Andaman Islanders hollow circles.

are not present, with a smooth transition from the alveolar segment to the submandibular fossa. Anteriorly, the submandibular fossae constrict and arch superiorly as they join the broad genioglossal fossa. Genial spines and foramina are present above the inferior transverse torus.

The mandibular corpus robusticity index for LB6 is slightly higher than LB1, robust relative to *H. sapiens*, but, as in LB1, it does not have the distinctive posterior corpus robusticity evident in A.L. 288-1 and other australopiths (Fig. 7). In a small modern *H. sapiens* sample (Edo Period Japanese), there is a positive linear association between corpus cross-sectional area at M_1 and femoral head diameter. From these limited data, it appears that as body mass

increases, so does the size of the mandible. Using the LB1 femoral head dimension, both LB1 and LB6 are well outside the human range of variation and their mandibular corpora have larger cross-sectional areas than would be predicted for *H. sapiens* of this body size. The total cross-sectional area of the corpus at the center of the right M_1 is 265.5 mm^2 with a perimeter of 65.2 mm (dimensions measured from a CT DICOM slice using OsiriX and ImageJ).

In lateral aspect, the ascending ramus obscures most of the M_3, and the extramolar sulcus, which is broader than in LB1, opens anteroinferiorly lateral to M_2. The left ascending ramus is more complete than the right, but there is postmortem damage to the coronoid process and condyle. The ramus is broadest inferiorly, thicker mediolaterally than in LB1, and in lateral view the anterior border of the ramus and coronoid processes arch posteriorly as in LB1. Reconstruction of the right condyle gives a condylar height of approximately 22 mm above the occlusal plane. The remaining fragment of right condyle has a maximum mediolateral dimension of 17 mm and is without the associated deep subcondyloid tubercle found in LB1. In contrast to LB1, the masseteric fossae is flat to slightly concave and the gonial region is only slightly everted. The gonial angle measures 116° on the left side, as in LB1.

On the medial aspect of the ramus, the alveolar prominence has a flatter profile than in LB1, but is also continuous with the crista pharyngea. The anterior border of the crista pharyngea is incomplete and it is not clear if it has the same form as in LB1 (Figs. 11 and 16). As in LB1, where the crista pharyngea and endocondyloidea join, the alveolar plane is present as a raised, mediolaterally thickened surface that is continuous with the inferior border of the sigmoid notch. Mediolateral thickening of the ramus, both at the ramus root and alveolar plane, is greater than in LB1, and the ramus is extremely robust. A slight neurovascular groove passes through the endocondyloid crista, and a prominent superior pterygoid tubercle is present on the preserved left side. The remaining mandibular foramen, sulcus coli, and lingular notch are morphologically similar to LB1. The areas of insertion for the lateral and medial pterygoid muscles are deeply excavated, although to a lesser degree than in LB1, and all of the septal insertions are clearly defined. While the LB6 mandible is smaller in some dimensions than LB6, posterior to M_2 the impression is of greater robusticity, particularly in the superior ramus and neck of the condyle.

Dental morphology

All teeth are fully erupted, and while most crowns have marked occlusal and interproximal wear, the extent of occlusal wear is less than in LB1. This is particularly true for P_4 and M_3, suggesting that
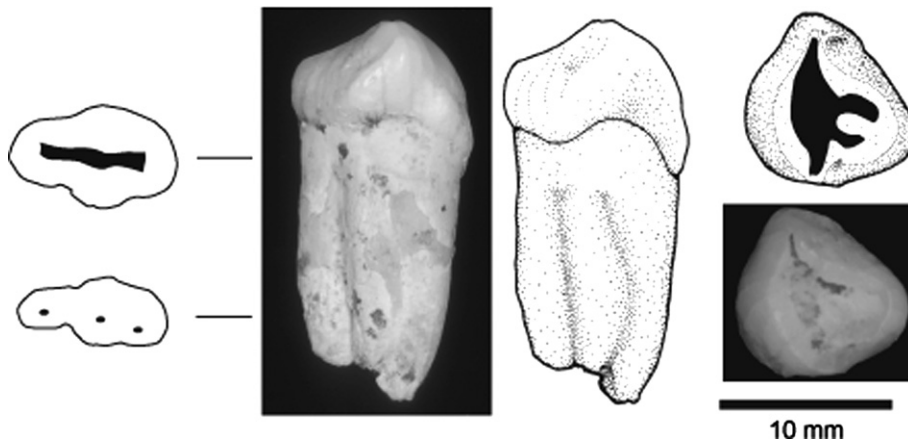
Figure 15. Mesial and occlusal views of the LB2 isolated right P_3, and cross-sections of the root showing root form.
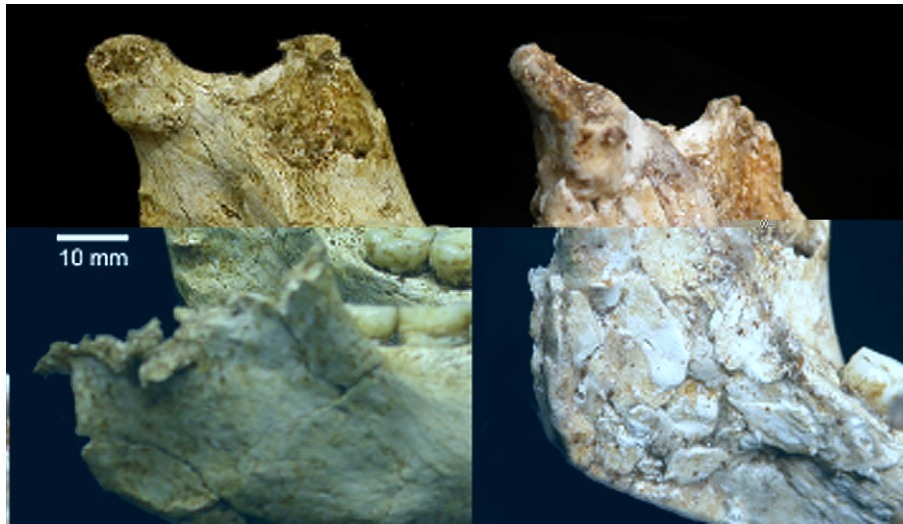
Figure 16. Comparison of the original preservation of the left medial ramus of LB6 (left), with its appearance upon return to Arkeologi Nasional in February 2005. During an attempt to cast the mandible at Gadjah Mada University, the medial and lateral surfaces of the ascending ramus were separated, presumably when the medial surface adhered to the mold. The fragmented remains of the medial surface were not all returned to their correct anatomical position, and some sections are replaced by filler.

LB6 is from a younger adult individual than LB1. While occlusal wear is less than in LB1, little useful morphological information remains. Unlike LB1, the Curve of Spee is only slight, but the heliocoidal plane of wear is similarly developed. Occlusal wear on the canines and the remaining portion of I_2 is greater than we would have expected given the degree of occlusal wear on the other teeth. Relatively great anterior tooth wear is also present in LB1, with an apical abscess associated with the alveolus for the missing maxillary right I^2. There is some evidence of vascular proliferation in the alveolar bone surrounding the incisor teeth, but there is no indication of the periodontal disease associated with the molar teeth of LB1. Wear on the anterior mandibular teeth suggests an edge-to-edge anterior occlusion. There has been some compensatory mesial migration of the postcanine teeth to maintain tooth contacts. Where occlusal wear on M_1 has exposed a cross-section through the enamel, it is clear that the crowns have thick enamel. Although the resolution was inadequate for quantification, CT scans and radiographs of LB1 and LB6 also suggest enamel thickness in the *Homo* range.

With the exception of the right I_2, all of the LB6 incisors were lost postmortem. The remaining lateral incisor is smaller than the corresponding tooth in LB1 and has more of the original crown height preserved. The crown is reasonably symmetrical, tapering fairly evenly from incisal edge to the cervix. The labial surface is smooth and without developmental lines. Lingually, there is a well-developed cingulum, the marginal ridges are poorly defined, and the surface is without a clearly demarcated lingual fossa. The mesial third of the occlusal surface has had a piece of enamel chipped off, probably during life.

Both canines are preserved, have smaller crowns than LB1, but are morphologically very similar. They have moderate occlusal wear, with the occlusal surfaces angled distally, and level with the adjacent I_2 and P_3. The exposed cross-sections through the crowns, combined with the remains of the marginal ridges on the lingual surface, suggest that well-defined marginal ridges were present. The preserved sections of these ridges have smooth lingual margins bordering shallow fossae. There is no evidence of a lingual ridge on either canine. CT scans demonstrated that both of the canines have a single conical root.

The P_3s are smaller than those in LB1, but share the asymmetrical and mesiodistally elongated crowns, with the broad distal talonid and dominant buccal cusp, of the LB1 and LB2 premolars. In occlusal view, the crowns have a triangular outline and slightly oblique orientation relative to the P_4–M_3 axis, although to a lesser degree than in LB1. Taking into consideration the extent of occlusal wear, details of crown morphology, including dominance of the lingual cusp, size and location of the distal fovea and marginal ridges, and development of the talonid are all similar to Dmanisi D2735 and D211 (Martinón-Torres et al., 2008). In common with LB1 and LB2, comparison of the size and shape of the LB6 P_3 crowns place them outside the range of variation in our species (Fig. 12). CT scans and direct observation demonstrate that both P_3's have bifurcated roots, with the MB + D pattern found in LB1 (Fig. 13).

Both P_4s are preserved in LB6, although with little evidence of original cusp relief and fissure detail. They are relatively large premolars, somewhat molariform, and with a subrectangular, slightly asymmetrical occlusal outline (Figs. 1, 4, and 13). On the buccal surfaces of both premolars there is evidence of a shallow buccal groove, and in occlusal view, the crown is broader mesial to the groove than distally, with a prominent distolingual marginal ridge. When unworn, these teeth probably had a small distobuccal cusp separated from a much larger mesiobuccal cusp. Whether or not there were mesial and distal cusps on the talonid portion of the crown is less certain. Differentiation between the crown shape and occlusal morphology of the LB6 P_3s and P_4s is extremely similar to Dmanisi D2735 and D211 (Martinón-Torres et al., 2008). Asymmetry between the premolar crowns is also common in East Turkana early *Homo*, with KNM-ER 992 and KNM-ER 1802 having extremely molariform P_4s (Wood, 1991). However, in early *Homo* from East Turkana and Olduvai (OH 13), the P_3 crowns are more clearly bicuspid and without the mesiodistal elongation of the Liang Bua and Dmanisi premolars. CT scans and direct observation indicate that the LB6 P_4s have double roots, with the MB + D form found in the LB1 and LB6 P_3s (Fig. 13). In the majority of anthropoid primates, excluding *H. sapiens*, mandibular P_4s usually have two roots, as does *A. afarensis*, *A. boisei*, and some specimens of early *Homo* (Abbott, 1984; Wood and Uytterschaut, 1987; Shields, 2005). In *H. sapiens*, variation in root number is greater for P_3 than P_4, but Shields (2005) found that double rooted premolars are extremely uncommon for both tooth classes (P_3: 3.5%, P_4: 1.7%), and MB + D was not found in his P_4 sample. Having single rooted P_3s and P_4s as the normative condition makes *H. sapiens* unique amongst

higher primates, just as the presence of multiple roots distinguishes *H. floresiensis* from most representatives of the genus *Homo*.

All of the mandibular molar teeth are preserved in LB6. However, occlusal wear has removed details of cusp and fissure morphology, and interproximal wear reduced the mesiodistal crown dimensions of all teeth. If tooth dimensions are adjusted for interproximal wear, all of the molars have mesiodistal dimensions that are similar to the buccolingual measurements for the same teeth, with a size sequence of M1 ≥ M2 > M3. LB6 has a slightly smaller postcanine dentition than LB1 but whether or not body mass was also lower is uncertain. While there were extremely small adult postcranial bones excavated from Spit 51 at Liang Bua (LB6/2 right radius, LB6/3 left ulna, and LB6/4 right scapula) in close association with the LB6 mandible, whether or not they are from the same individual is unproven (Morwood et al., 2005; Larson et al., 2007b; Jungers et al., 2009). However, where duplicate skeletal elements are preserved, all of the isolated adult postcrania from Liang Bua have smaller dimensions than those in LB1 but share distinctive morphological details (Brown et al., 2004; Morwood et al., 2005; Jungers et al., 2009). Using estimates of body size and limb proportions from LB1, LB6 is less megadont than LB1 and has a smaller crown area than would be predicted for an Australian Aboriginal of similar body mass (Fig. 14). This is in contrast with A.L. 288-1, which is absolutely and relatively large-toothed compared with the *H. sapiens* range of variation.

Statistical results

Pan

The univariate, principal components (PCA), and discriminant function (DFA) analyses of mandibular variation in the genus *Pan* are available in the Supplementary Online Materials.

Homo

In the DFA of the *Homo* sample, the *H. sapiens* pooled-sex sample was subdivided into three broad geographical groups: 1) Australia and Melanesia, 2) East Asia, and 3) Europe and Africa. Our interest was not in the morphological relationships, or distances between these groups, but in variation within *H. sapiens* compared with *Pan*, and comparison of the Liang Bua mandibles with contemporary and modern humans. DFA of the pooled-sex *H. sapiens* and *H. floresiensis* data set employed the same nine linear dimensions as used in the *Pan* DFA and PCA. Missing data reduced the multivariate data set from 2063 to 318, with all of the African Pygmies excluded due to either a damaged symphysis or incomplete dentition. The analysis included 318 cases, and none were identified as multivariate outliers with $p < 0.001$. Evaluation of statistical assumptions of linearity, normality, and homogeneity of variance-covariance matrices indicated that the analysis was robust. Three discriminant functions were calculated with $\chi^2 = 525.4$, $p = 0.000$ (68.1% variance). There was still a strong association between groups and predictors after the removal of the first function, with $\chi^2 = 212.4$, $p = 0.000$ (20.5% variance), and also after the second function ($\chi^2 = 80.3$, $p = 0.000$, 11.4% variance). The loading matrix of correlations between variables and discriminant functions indicated that the best predictors for distinguishing between the pooled-sex *H. sapiens* groups were tooth dimensions (P_3 mesiodistal length, M_2 buccolingual breadth), which set apart the large toothed Australian-Melanesian group from the other two (Fig. 17). For the second function, bigonial breadth and corpus height were the strongest predictors, but this did not separate the modern human groups. LB1 and LB6 obtained function scores that placed them well outside the human range of variation.

They combine relatively large teeth, particularly LB1, with small corpus height and bigonial dimensions. Mahalanobis distances between the two Liang Bua mandibles, and the group centroid for closest alternate group (Australian-Melanesian) were LB1 $D^2 = 132.1$ and LB6 $D^2 = 56.6$. Both Liang Bua mandibles are more than twice the distance from *H. sapiens* than bonobos are to chimpanzees (*Pan paniscus-Pan troglodytes schweinfurthii* $D^2 = 24.5$, *Pan paniscus-Pan troglodytes troglodytes* $D^2 = 25.8$).

Discriminant function analyses of the size-adjusted data based on basicranial length reduced the distance between LB1 and LB6, but did not greatly alter the dispersion and distance between the modern human groups (Fig. 17). Three discriminant functions were calculated with $\chi^2 = 437.6$, $p = 0.000$ (88.4% variance). There was still a significant association between groups and predictors after the removal of the first function, with $\chi^2 = 18.7$, $p = 0.016$ (11.6% variance). Correlations between predictors and functions were highest for M_1 buccolingual breadth and arch width at M_2 for function 1, and minimum ramus width for function 2. The Australian-Melanesian group remained distinctive due to relatively large dental dimensions. The second function isolated the Liang Bua mandibles from the *H. sapiens* groups, with LB1 and LB6 sharing a relatively thickened corpus, broad ramus, and mesiodistally elongated P_3. In the size-adjusted DFA, Mahalanobis distances between the Liang Bua mandibles and the closest alternate group centroid (Australian-Melanesian) were only slightly reduced (LB1 $D^2 = 64.8$, LB6 $D^2 = 53.6$). This is in marked contrast to the *Pan* adjusted DFA, where the Mahalanobis distances between *Pan paniscus* and *Pan troglodytes* were much smaller, and dispersion greatly reduced (Table S6).

Principal components analyses of the pooled-sex *H. sapiens* and *H. floresiensis* data set employed the same nine linear dimensions as used in the *Pan* PCA and DFA. As in the DFA, missing data reduced the multivariate data set from 2067 to 318. Analysis of the raw data extracted three components with eigenvalues >1. The first component (38.0% of variance) had a strong size component, with the highest loadings for symphyseal height, corpus height, bigonial breadth, and ramus minimum breadth. For the second component (17.3% of variance), P_3 mesiodistal length, M_1 buccolingual breadth, and M_2 arch breadth were the most influential variable loadings (Table 4). Generally, small mandibles obtained negative scores on Factor 1 and positive scores on Factor 2, if combined with small tooth and broad arch dimensions. For instance, the Australian-Melanesian sample has larger average symphyseal, corpus, bigonial, and tooth dimensions. In this, they contrast with the East Asian sample. The two Liang Bua mandibles are outside the range of modern human variation as a result of combining a robustness of the tooth-bearing segment and tooth size. They contrast with the Andaman Islanders who have the relatively small mandibular dimensions that would be predicted from their body mass (maximum femoral head diameter: Andaman, $n = 17$, mean = 36.8 mm, sd = 2.42; modern humans without Andamans, $n = 778$, mean = 43.6 mm, sd = 3.99; LB1, 31.5 mm) (Fig. 18). Using the size-adjusted data set, the PCA extracted three factors with eigenvalues >1.0. With the exception of arch breadth at M_2, loadings for the first component (31% of variance) were of a similar magnitude, with relatively small mandibles obtaining a larger positive factor score. For the second factor (15.5% of variance), the highest loadings are for symphyseal and corpus height, P_3 mesiodistal length, and corpus thickness. Size-adjustment removed the shape differences between the modern human groups, producing a relatively homogeneous distribution. The two Liang Bua mandibles do not share the pattern of size and shape associations found in *H. sapiens*, remain outside the range of modern human variation, and contrast with the morphological pattern in small-bodied members of our species (Figs. 17 and 18).
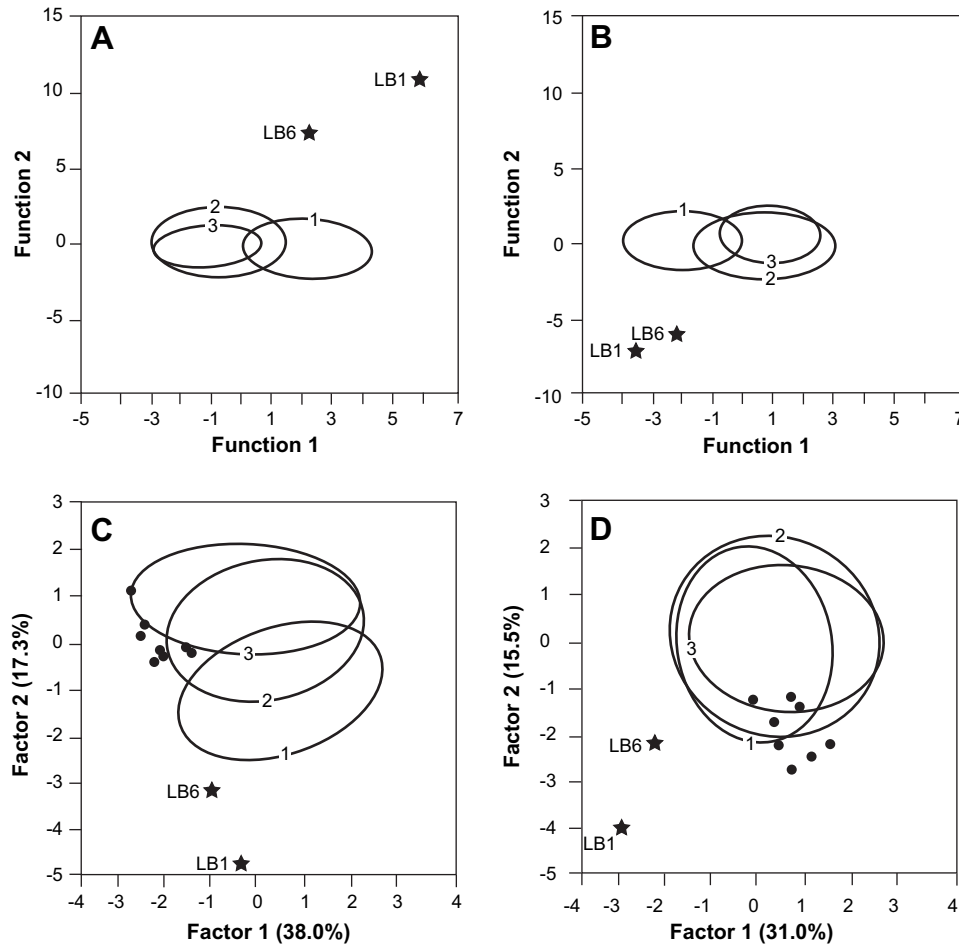
Figure 17. Bivariate plots of the unadjusted (left) and size-adjusted (right) pooled-sex *H. sapiens* and *H. floresiensis* DFA (top) and PCA (bottom) analyses, with the sample distributions represented by sample confidence ellipses ($p > 0.90$). Ellipse labels: Australian and Melanesian group (1), East Asian group (2), and European-African group (3). In the PCA plots, the location of the small-bodied Andaman Islanders are indicated by filled circles.

Discussion

H. floresiensis as a developmentally abnormal *H. sapiens*

The combined morphology of the symphyseal region, corpus, ascending ramus, and premolars in the LB1 and LB6 mandibles places them outside the range of variation in both *H. sapiens* and Asian *H. erectus*. Differences between LB and *H. sapiens* include the angulation and thickness of the symphysis, presence of superior and inferior transverse tori with a deep and broad genioglossal fossa, a transversely thickened corpus, lateral corpus contour, premolar crown and root morphology, and robusticity of the tooth-bearing segment. Critics of the status of *H. floresiensis* as a novel species have argued that mandibles with a similar size and morphology to LB1 and LB6 are found in living Australomelanesians (Jacob et al., 2006; Richards, 2006), or modern humans with a range of developmental disorders (Martin et al., 2006a; Hershkovitz et al., 2007).

Statements about mandibular morphology in Austral-omelanesians concentrate on the claim that the absence of a chin is not a valid species-defining characteristic, as 94% of living Rampasasa people on Flores have neutral or negative chins (Jacob et al., 2006). However, these authors confuse the external soft-tissue appearance of a receding chin in living people with the absence of the skeletal elements of a chin (Fig. 19), and a neutral or negative chin was never a species characteristic of the *H. floresiensis* holotype

(Brown et al., 2004). For the anterior symphysis, the relevant trait is "mandibular symphysis without chin and with a posterior incli-nation of the symphyseal axis" (Brown et al., 2004:1055). While Australomelanesians sometimes present a receding symphyseal profile they also maintain the elements of a bony chin (Jacob, 1967; Larnach and Macintosh, 1971; Brown, 1989). In this, and in all other respects, their mandibles are those of modern humans and distinct from those of *H. floresiensis*. Photographs of small-bodied living people, with a stature of 140-150 cm, modern human limb proportions and brain volumes, is not evidence that Rampasasa pygmies, or Australomelanesians more broadly, have the

Table 4
Variable loadings for the first two components in the unadjusted and size-adjusted *Homo sapiens*, LB1, and LB6 PCA.

	Unadjusted data		Size-adjusted data	
	Component 1	Component 2	Component 1	Component 2
Symphyseal height	0.780	0.008	0.679	−0.512
Symphyseal thickness	0.565	−0.126	0.645	−0.097
Corpus height	0.789	−0.141	0.566	−0.691
Corpus thickness	0.463	0.022	0.508	0.373
Bigonial breadth	0.678	−0.361	0.518	−0.119
M_2 arch breadth	0.451	−0.425	0.223	0.106
M_1 buccolingual	0.496	0.678	0.645	0.272
P_3 mesiodistal	0.303	0.804	0.593	0.587
Ramus min breadth	0.628	0.036	0.504	0.250
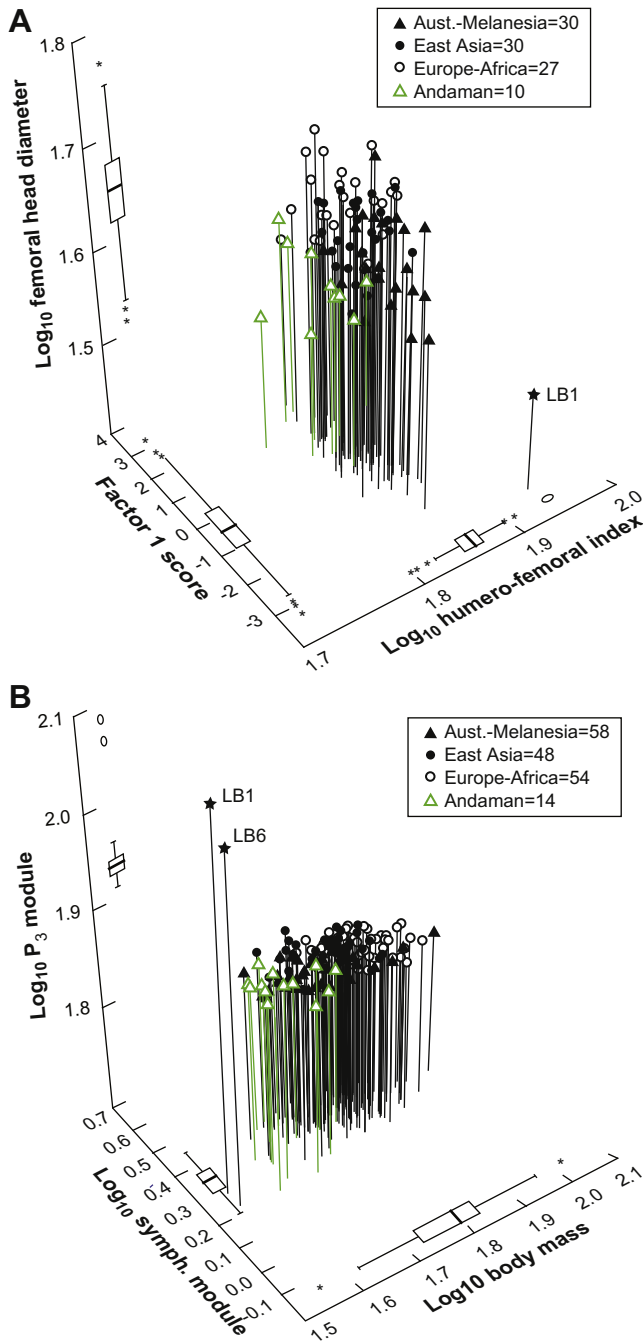
Figure 18. Association between mandibular and postcranial dimensions in large-and small-bodied *H. sapiens* and *H. floresiensis*. (A) Scatterplot of the association between the humero-femoral index, size-adjusted PC1 scores, and maximum femoral head diameter in *H. sapiens* and LB1, with box plots of the variable distributions. LB1 is separated from the *H. sapiens* distributions by its high humero-femoral index, low-negative PC1 scores, and small femoral head dimension. (B) Scatterplot of the association between estimated body mass, symphyseal module, and P_3 module in *H. sapiens*, LB1, and LB6, with box plots of the variable distributions. The body mass estimate for LB6 is based on LB1. LB1 and LB6 are distinguished from the *H. sapiens* distributions by their low body mass, low symphyseal modules, and high P_3 modules.

osteological characteristics of *H. floresiensis* (Jacob et al., 2006). There is an associated claim made by Jacob et al. (2006) that the LB6 mandible falls within the human range of variation and does not share the characteristics that distinguish LB1. This statement is not supported by morphological and statistical comparisons of the LB1 and LB6 mandibles, which clearly share the same set of distinctive

characteristics, both lying outside the range of variation in *H. sapiens* (Brown et al., 2004; Morwood et al., 2005).

Comments that LB1 may represent a microcephalic dwarf modern human also refer to the chin region (Martin et al., 2006b; Hershkovitz et al., 2007). Martin et al. stated that the absence of a chin is a "key feature, which gives the visual impression of primitive morphology in LB1" (Martin et al., 2006a: 1124), and later, "a small jaw with deviant development of the chin" is common in microcephalics, and the mental eminence may be "weak or lacking" (Martin et al., 2006a: 1140). The authors did not provide any skeletal evidence in support of their claims, and the microcephalic they illustrated has a prominent chin, with a thin vertical symphysis, and without superior and inferior transverse tori on the posterior surface. However, they cited Dokládal (1958) as providing evidence of a microcephalic having a small mandible with a weak chin. Small size is not a characteristic of the Liang Bua mandibles, neither LB1 nor LB6 have a weak chin, and the microcephalic described by Dokládal (1958: Fig. 2) has a prominent chin, and nothing in common with LB1 apart from a small cranial volume. This would have been obvious if Martin et al. (2006a) had provided an illustration of the specimen to which they referred. Apart from brain volume and disputed aspects of endocast morphology (Falk et al., 2005b, 2006, 2007; Holloway et al., 2006; Martin et al., 2006a), Martin and colleagues have been unable to provide evidence of a microcephalic modern human that replicates the symplesiomorphic and unique characteristics of *H. floresiensis* in any respect.

A more targeted suggestion that LB1 might be developmentally abnormal was recently made by Hershkovitz et al. (2007), who argued that it displayed the distinctive characteristics of Laron Syndrome (LS) (Laron, 2004). There is a large clinical literature on primary GH resistance or insensitivity, most of it stimulated by the pioneering research of Zvi Laron, who was one of the co-authors in Hershkovitz et al. (2007). It is therefore surprising that the trait list these authors provided is not supported by the clinical literature, is not diagnostic of LS, and for the most part not identifiable in LB1. The majority of people who have been identified as having LS are of Jewish or Mediterranean origin, with most belonging to consanguineous families. The clinical indicators include delayed development, head with protruding forehead, saddle nose and "sunset look," very thin diploë, undeveloped facial bones and mandible, a small chin, reduced facial height, a head which appears large for the body but may have a circumference 2–3 sd smaller than average or be in the low normal range, stature between 4 and 10 sd below average, thin long bone shafts and underdeveloped muscles, short limbs for trunk length, extremely small hands and feet (acromicra), and spinal stenosis (Laron, 1995, 2004; Schaefer et al., 1994; Kornreich et al., 2002; Laron et al., 2006). Apart from short stature, none of these are found in LB1 (Brown et al., 2004; Morwood et al., 2005). Hershkovitz et al. (2007) made particular reference to the small size of the LS mandible, with a small or double chin. These are also not features of the LB1 and LB6 mandibles, which are robust and without a bony chin. Most surprisingly, Hershkovitz et al. (2008) *in errata* to their earlier publication (Hershkovitz et al., 2007) provided a lateral x-ray of a child that they declared has Laron Syndrome. While a scale is not present, cranial and dental morphology is distinct from LB1 (Brown et al., 2004) and the mandibular symphysis (particularly when the contrast of their image is adjusted in Adobe Photoshop) is vertical, without superior and inferior transverse tori, with a thin alveolar component and a projecting chin.

Form and function

In fossil and extant apes, for a given jaw length, larger forms have significantly more robust symphyses and corpora than smaller
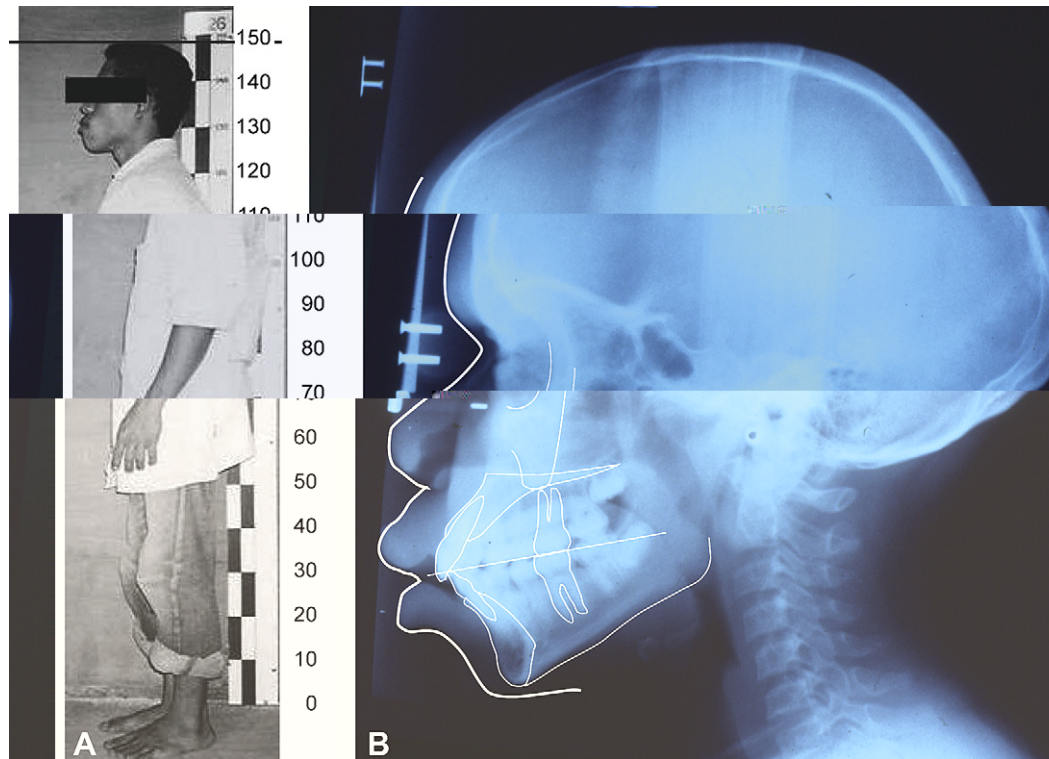
Figure 19. (A) Rampasasa pygmy from Flores, approximately 1.48 m tall, with modern human limb proportions and head size, and receding symphyseal profile. Jacob et al. (2006) argued that this was evidence of the absence of a chin in the Rampasasa and Australomelanesians more generally. However, a lateral radiograph (B) of an Australomelanesian demonstrates that despite the appearance of a receding chin given by the external soft tissue, the underlying symphyseal morphology indicates a projecting mental tuberosity and incurvature. Compared with *H. floresiensis*, the symphysis is also tall and relatively vertical, with a thin alveolar component, and without posterior tori. Figure 19A reproduced with permission of the Proceedings of the National Academy of Science USA.

forms (Ravosa, 2000; Taylor 2002). Ravosa (2000) argued that this is probably linked to size-related increases in dietary toughness, which in turn causes elevated mandibular loads, or more extended periods of load. Similarly, in fossil hominins, relatively megadont and large jawed forms (*Australopithecus* and *Paranthropus*) have significantly more robust mandibular bodies than in later *Homo* (Chamberlain and Wood, 1985; Wood and Aiello, 1998), with tooth wear data suggesting that the former were more reliant on tougher, fracture resistant foods than early *Homo* (Ungar, 2004; Scott et al., 2005; Ungar et al., 2006). Explanations of the link between mandibular form and function in primates have highlighted the importance of symphyseal and corpus morphology, and compact bone distribution, in providing enhanced resistance to bending and shearing stress during mastication (Hylander, 1984; Hylander et al., 1987; Daegling, 1989, 2007; Daegling and Grine, 1991; Hylander and Johnson, 1994; Schwartz and Conroy, 1996; Daegling and Hylander, 1998; Daegling and McGraw, 2007). Experimental investigations indicate that during unilateral mastication the primate balancing side corpus undergoes parasagittal bending, which instigates dorsoventral shear at the symphysis. Simultaneously, axial twisting of the corpus, and "wishboning" of the corpus and symphysis, result from the interaction of working-side bite force, and muscle activity on the working and balancing sides. Increased resistance to distortion at the symphysis is provided by superior and inferior transverse tori, labiolingual thickening, and greater vertical depth (Hylander, 1984), and for the corpus, greater depth and buccolingual thickening (Hylander, 1988; Daegling, 1989; Hylander and Johnson, 1994).

In general, these areas of structural reinforcement distinguish the mandibles of all Pliocene hominins from most members of the genus *Homo*. While *H. floresiensis* has an absolutely and relatively smaller postcanine dentition than A.L. 288-1, it shares aspects of symphyseal and corpus shape and robusticity, which also distinguish it from Pleistocene *H. erectus* and *H. sapiens*. Just as a variety of dietary and ecological models have been proposed for the masticatory distinctions between Miocene apes, *Australopithecus*, and early *Homo* (Jolly, 1970; Kay, 1985; Aiello and Wheeler, 1995; Teaford and Ungar, 2000; Aiello and Wells, 2002), they may be equally relevant to the contrasts between *H. sapiens* and *H. floresiensis*. Correlations between the morphology of the tooth-bearing segment and the physical properties of various diets has been investigated (Ravosa, 2000; Taylor, 2002; Vinyard and Ryan, 2006; Daegling and McGraw, 2007), and it has been argued that the relatively elevated torsional moments in *Paranthropus* and *Australopithecus* produced a different structural response to later *Homo* (Hylander, 1988; Daegling and Grine, 1991; Teaford and Ungar, 2000), with the distinctive corpus and symphyseal morphology in australopithecines a reaction to fibrous foods and high masticatory loads. While the link between mandibular form and function is broadly accepted, a study of functional morphology and masticatory stress in sympatric colobines provides a caution against cross-taxa predictions (Daegling and McGraw, 2007), with dietary differences not reflected in mandibular morphology. However, morphological differences between *H. floresiensis* and *H. sapiens* mandibles greatly exceed those within the Colobinae, and surely highlight increased resistance to structural failure in the symphysis and corpus in *H. floresiensis* relative to *H. sapiens*.

Most recently, a study of dental topography in early *Homo* and *A. afarensis*, including comparison with *Pan troglodytes troglodytes* and *Gorilla gorilla gorilla*, found that there were consistent patterns of slope and relief produced by occlusal wear within taxa. Differences between these two hominin taxa were as great as between

the living apes, indicating similar degrees of difference in diet (Ungar, 2004). Ungar suggested that the major dietary difference between these early hominins may have been in fallback foods, with *A. afarensis* emphasizing harder, more brittle foods, and early *Homo* tougher, more elastic foods (Ungar, 2004). A microwear study has also indicated that there were substantial trophic differences between *P. robustus* and *A. africanus*. Unfortunately, post depositional abrasion (King et al., 1999) of occlusal surfaces in East African hominins may prevent broadening of the microwear comparison to include a substantial early *Homo* sample. Postmortem damage will also be an issue in the recovery of meaningful microwear information from the Liang Bua teeth.

While *H. floresiensis* has a structurally robust corpus and symphysis, and is somewhat megadont in comparison to most *H. sapiens*, the size of the molar teeth, facial height, and prognathism do not follow the australopithecine pattern (Brown et al., 2004; Kimbel et al., 2006), and it is not possible to confuse one with the other. However, LB1 and the developmentally younger LB6, both have marked occlusal and interproximal tooth wear suggesting forceful mastication. For both LB1 and LB6, the plane of molar occlusal wear is flat, similar to hunter-gatherers like the Inuit and Plio-Pleistocene hominins (Wood, 1991), rather than the high attrition angled wear in Mesolithic agriculturalists (Smith, 1984). In LB6, details of occlusal morphology are preserved on both M3s, and dentine is not exposed, indicating a younger adult than LB1. Comparison of occlusal wear in LB6 with a known age Australian series (Richards and Brown, 1981; Molnar and Molnar, 1990; Richards and Miller, 1991) suggests a maximum age in the early 20s, or perhaps younger if different growth trajectories are applicable (Dean, 2000; Dean et al., 2001). Interproximal wear, resulting from the vertical movement of contacting proximal surfaces as a response to occlusal forces (Kaidonis et al., 1992), is advanced relative to occlusal wear in LB6, as well as in LB1. As interproximal wear is most probably a result of force vectors moving the teeth (Kaidonis, 1995), rather than abrasives in the food bolus, this is consistent with a tough, fibrous diet requiring powerful mastication. Apart from the bones of *Stegodon* and Komodo dragon, some of which have cut marks (van den Bergh et al., 2009), there is little direct trophic evidence from the Pleistocene deposits at Liang Bua. While there are thousands of rodents, and some may have been consumed by *H. floresiensis*, their presence in the cave could equally have been part of their normal life cycle. Most of the *Stegodon* are infants, and would have been preferred prey for large Komodo dragons (*Varanus komodensis*) (Jessop et al., 2006), and relatively easy targets for an active hominin (van den Bergh et al., 2009). The mastication of uncooked meat, with low crowned hominin molars, would require prolonged and forceful chewing and may have contributed to the interproximal wear in LB1 and LB6.

Some additional evidence of dietary preference, particularly in LB1, may be provided by oral health status. Both LB1 and LB6 are free of dental caries, but there is heavy dental calculus with associated periodontal disease and alveolar recession in the posterior dental arch of LB1. The formation of static plaque deposits and calculus is multifactorial, and periodontal disease is common in pre-Neolithic and post-Neolithic human populations (Arensberg, 1996; Eshed et al., 2006) and in some species of wild primate. Amongst the Gombe Reserve chimpanzees, periodontal disease is ubiquitous in older individuals (Kilgore, 1989), and all adult Virunga gorillas have pronounced calculus buildup, alveolar resorption, and eventual tooth loss (Lovell, 1990). In wild, non-carnivore, mammal populations, the frequency of periodontal disease is linked to diet (Sone et al., 2005), and Crovella and Ardito's (1994) survey of oral pathologies in wild primates found that heavy tartar deposits were most common in folivorous colobines. Although there is evidence of meat eating, apart from dental calculus in LB1, there is no direct

evidence of the vegetative component of the *H. floresiensis* diet. Given the relativity of risks involved (Hawkes et al., 1991), and the likelihood that infant *Stegodon* may have only been a seasonal resource, we assume that plant foods dominated. It is presently unknown which edible plant species may have been available during the late Pleistocene of Flores but further paleoenvironmental reconstruction, and isotope analysis (Sponheimer et al., 2005a,b), may narrow the focus.

Origins and evolution

The distinctive mandibular morphology of LB1 is associated with many other distinctive attributes, including an estimated stature of only 109 cm (Brown et al., 2004), an endocranial volume of 385–417 cm^3 (Brown et al., 2004; Falk et al., 2005b; Holloway et al., 2006), an estimated brain weight/body mass ratio similar to *Pan* and *A. afarensis* (Brown et al., 2004; Falk et al., 2005b), a humerus and ulna that are both long relative to the lengths of the femur and tibia, and distinct from known limb proportions in the genus *Homo* (Morwood et al., 2005; Lordkipanidze et al., 2007; Brown, in preparation-b), a pelvis, femur, and basicranium indicative of obligate bipedalism (Brown et al., 2004; Jungers et al., 2009), long bone relative shaft robusticity overlapping *Pan* and *A. afarensis* and distinct from small-bodied *H. sapiens* (Morwood et al., 2005; Brown, in preparation-b), carpal morphology shared with *Australopithecus* and African apes but not *H. sapiens* and Neanderthals (Larson et al., 2007b; Tocheri et al., 2007b), a relatively short clavicle and a humerus with a low torsion angle as in KNM-WT 15000 (Morwood et al., 2005; Larson et al., 2007b) and Dmanisi (Lordkipanidze et al., 2007), and a cranial and facial morphology with a distinctive combination of symplesiomorphic, shared-derived, and unique traits (Brown et al., 2004; Argue et al., 2006; Baab et al., 2007; Brown, in preparation-a). Where duplicate elements are preserved in other hominins from the Liang Bua Pleistocene layers (e.g., the LB6/3 left ulna and LB8 left tibia), they present the same distinctive postcranial morphology observed in LB1 (Brown et al., 2004; Morwood et al., 2005; Jungers et al., 2009). Several questions arise from this unprecedented combination of traits in an island population of Late Pleistocene hominins from eastern Indonesia. For the most part, they concern the seemingly incongruous issues of time and geography.

When initially described, it was emphasized that *H. floresiensis* was most probably the result of an extended period of island evolution on Flores, from a larger-bodied and larger-brained *H. erectus* ancestor. Flores is a small (14,000 km^2), tectonically unstable island, located only 8° south of the equator, and more arid than islands further to the west. During the Pleistocene, the only large predator was the Komodo dragon and mammal body size complied with expectations under the island rule. An impoverished island fauna, with no evidence of succession or replacement, indicated that Flores was isolated for most of the Pleistocene (van den Bergh et al., 2009). *Homo erectus* was present on Java and hominins had reached Flores by 840 ka (Morwood et al., 1998). While there is continuity in artifact production methods between Mata Menge and the Late Pleistocene deposits at Liang Bua (Moore and Brumm, 2007, this issue), it remains unknown whether or not the initial hominin founder population was large-bodied *H. erectus*, or small-bodied members of a different species. Historically, modern human populations of extremely small average stature were found in rainforest habitats in the equatorial zone of Africa, Asia, and Melanesia (Bandler, 1880; Kroeber, 1919; Evans, 1937; Cavalli-Sforza, 1986). Explanations for the small body size of these people generally focus on thermoregulatory advantages for life in a hot and humid forest, either through evaporative cooling (Roberts, 1973) or reduced rates of internal heat production (Shea and

Bailey, 1996). In the absence of agriculture, these rainforests may have offered a more limited supply of calories for hominins (Bailey and Headland, 1991) and may also have favored smaller body size (Peters, 1983; Schmidt-Nielsen, 1984). With this background, one of us (PB) argued that *H. floresiensis* was a possible example of insular dwarfing, either on Flores, or another island in Southeast Asia, where the local environmental conditions placed small body size at a selective advantage. Subsequently, further discoveries enabled the exploration of postcranial scaling trajectories (Morwood et al., 2005), and the identification of symplesiomorphies not shared with *H. erectus*, which made this species an unlikely ancestor of *H. floresiensis*.

If *H. floresiensis* is not a dwarfed descendent of *H. erectus*, what do its skeletal and dental remains reveal about its likely evolutionary history? The current state of knowledge distinguishes *Australopithecus* from middle-late Pleistocene members of the genus *Homo* through limb proportions (Richmond et al., 2002; Reno et al., 2005; Green et al., 2007), size of the postcanine dentition (McHenry, 1984), mandibular premolar crown and root morphology (Abbott, 1984; Wood and Uytterschaut, 1987; Wood et al., 1988; Kupczik et al., 2005), endocranial volume (Tobias, 1991; Kappelman, 1996), the functional anatomy associated with locomotion and use of the hand (Stern and Susman, 1983; McHenry and Berger, 1998; Clarke, 1999, 2000; Stern, 2000), and perhaps body height and encephalization quotient (Jerison, 1973; Jungers, 1988; McHenry, 2002). For early *Homo*, while poor preservation continues to foster debate, the postcranial remains of OH 7, OH 8, OH 10, and OH 35 are suggestive of limb proportions similar to *A. afarensis* (Johanson et al., 1987; Hartwig-Scherer and Martin, 1991; Richmond et al., 2002), and foot and hand function, which has been interpreted as consistent with enhanced climbing ability (Marzke, 1997; Susman, 1998; McHenry and Coffing, 2000). This contrasts with the available evidence for *H. erectus*, which indicates derived reduced post canine tooth size, endocranial volumes greater than *Australopithecus* and overlapping *H. sapiens*, greater body height than *Australopithecus*, and relative limb proportions and obligate bipedalism like *H. sapiens* (Weidenreich, 1937, 1941, 1943; Day, 1971; Walker and Leakey, 1993; Kaifu et al., 2005b; Rightmire et al., 2006; Van Arsdale, 2006; Lordkipanidze et al., 2007).

Homo floresiensis combines characters from several of these taxa (Collard and Wood, 2007), and deciphering its phylogenetic relationships depend upon the weighting assigned to adaptively significant traits like brain volume and neural organisation, limb proportions and joint function, and masticatory biomechanics, with potential future arguments over the contribution of homoplasy, parallelism, and reversal (Lockwood and Fleagle, 1999). This is made more difficult by the currently limited time depth to the Flores hominin fossils, and the complete absence of comparable evidence from anywhere else. While we are certain that *H. floresiensis* was a small-brained, tool making, hominin biped, with australopithecine-like limb proportions, the origins of this species remain obscure. Until recently, it was generally accepted that the first hominin to leave Africa was *H. erectus* (Antón, 2003), with the 1.77 Ma Dmanisi hominins morphologically representative of the first emigrants (Gabunia and Vekua, 1995; Bräuer and Schultz, 1996; Gabunia et al., 2000; Gabounia et al., 2002; Lordkipanidze and Vekua, 2002; Vekua et al., 2002; Rightmire et al., 2006; Lordkipanidze et al., 2007).

As the Dmanisi site contains crania, mandibles, and some associated postcrania, it provides a rare opportunity to explore the adaptive morphology of early *H. erectus* in some detail, as well as providing greater context for the combination of characters in *H. floresiensis*. The Dmanisi crania are less derived than Asian *H. erectus*, have small endocranial volumes between 600 cm^3 and

780 cm^3, and there is ongoing uncertainty about their taxonomic status, e.g., *H. habilis*, *H. erectus*, or something else (Vekua et al., 2002; Rightmire et al., 2006). Most recently, Lordkipanidze et al. (2007) concluded that the postcrania did not possess the full suite of derived locomotor traits apparent in African *H. erectus* and later hominins. While the association between the adult humerus (D4507), femur (D4167), and tibia (D3901) seems a little uncertain as to whether or not they are from a single individual, their stature is in the range of 145–166 cm, limb proportions (humerus/femur) are close to the modern human average and contrast with *A. afarensis* and *H. floresiensis*, long bone shafts are robust as in *Australopithecus* and *H. floresiensis*, medullar canals are narrow like *H. erectus* but not *Australopithecus*, *H. floresiensis*, or *H. sapiens*, and the humeri have the low torsion evident in *H. floresiensis*. The D3901 tibia is not as robust as LB1, and has a straighter shaft without the midshaft oval-shaped cross-section present in *H. floresiensis* and *Pan*.

While the Dmanisi and Liang Bua postcrania share some features that are not common in *H. sapiens*, the larger endocranial volumes, derived limb proportions, and greater body mass and height of the Dmanisi hominins suggests that, in terms of morphology, they are further removed from Pliocene *Australopithecus/H. habilis* than *H. floresiensis*. If established interpretations of the significance of brain size, limb proportions, and locomotor behavior in our lineage are meaningful, then the ancestors of *H. floresiensis* left Africa well before those who arrived at Dmanisi. Whether or not these putative ancestors of *H. floresiensis* had the megadont masticatory adaptations of australopiths, or were smaller-toothed like later *Homo*, is unknown. It is possible that reduced molar size in *H. floresiensis* relative to *Australopithecus* may be an example of homoplasy, with independent evolution in the *H. sapiens* and *H. floresiensis* lineages. There is, of course, little evidence to support any of these suggestions, but if the latter is correct, then Asia may have had a more complex role in the evolution of our bipedal relatives than previously thought (Dennell and Roebroeks, 2005). Perhaps the ebb and flow of hominin Plio-Pleistocene dispersal witnessed, at different times, both out of Africa and out of Asia.

Conclusions

The Late Pleistocene hominin mandibles from Liang Bua are morphologically and metrically distinct from those in large-bodied and small-bodied *H. sapiens*, including modern humans from the same geographic region and microcephalics. Both mandibles share symplesiomorphic characters with *Australopithecus* and early *Homo*, including the posterior inclination of the symphyseal axis, presence of superior and inferior transverse tori, no mental tuberosity or incurvature, symphysis and corpus dimensions that are robust relative to body mass, mesiodistally elongated P$_3$s with double roots, and a posteriorly arching anterior ramal border, which are either not present, or are very uncommon, in *H. erectus* and *H. sapiens*. Biomechanical adaptations in the Liang Bua mandibles, while not as extreme as in australopiths, suggest a similar adaptation to high masticatory loads. While there is only limited trophic evidence from Liang Bua, and the vegetative component of the diet is unknown, meat was a component in the diet. When mandibular morphology is considered with the cranial and postcranial evidence, particularly in relation to relative limb proportions, skeletal robusticity, wrist function, brain size, and scaling trajectories, then it is unlikely that the Liang Bua hominins are insular dwarfed descendants of *H. erectus*. We believe that the Liang Bua hominins arrived on Flores in the middle Pleistocene, essentially with the skeletal and dental characteristics that distinguished them until they became extinct at approximately 18 ka.

Comparison with Dmanisi *H. erectus* suggests that the Liang Bua hominin lineage left Africa before 1.8 Ma, and possibly before the evolution of the genus *Homo*. We believe that these distinctive, tool making, small-brained, australopithecine-like, obligate bipeds moved from the Asian mainland through the Lesser Sunda Islands to Flores, before the arrival of *H. erectus* and *H. sapiens* in the region. They apparently survived in isolation until the end of the Pleistocene.

Acknowledgements

Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jhevol.2009.06.002.

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