



Conclusions: implications of the Liang Bua excavations for hominin evolution and biogeography

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ABSTRACT

Excavations at Liang Bua, on the Indonesian island of Flores, have yielded a stratified sequence of stone artifacts and faunal remains spanning the last 95 k.yr., which includes the skeletal remains of two human species, *Homo sapiens* in the Holocene and *Homo floresiensis* in the Pleistocene. This paper summarizes and focuses on some of the evidence for *Homo floresiensis* in context, as presented in this Special Issue edition of the *Journal of Human Evolution* and elsewhere. Attempts to dismiss the Pleistocene hominins (and the type specimen LB1 in particular) as pathological pygmy humans are not compatible with detailed analyses of the skull, teeth, brain endocast, and postcranium. We initially concluded that *H. floresiensis* may have evolved by insular dwarfing of a larger-bodied hominin species over 880 k.yr. or more. However, recovery of additional specimens and the numerous primitive morphological traits seen throughout the skeleton suggest instead that it is more likely to be a late representative of a small-bodied lineage that exited Africa before the emergence of *Homo erectus sensu lato*. *Homo floresiensis* is clearly not an australopithecine, but does retain many aspects of anatomy (and perhaps behavior) that are probably plesiomorphic for the genus *Homo*. We also discuss some of the other implications of this tiny, endemic species for early hominin dispersal and evolution (e.g., for the “Out of Africa 1” paradigm and more specifically for colonizing Southeast Asia), and we present options for future research in the region.

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Origins and affinities of *Homo floresiensis*

Hominins were present on the East Indonesian island of Flores by at least 880 ka (Morwood et al., 1998; Brumm et al., 2006; van den Bergh et al., 2009a), a time when *Homo erectus* was thought to be the only hominin species in East Asia. Previous researchers have, therefore, assumed that *H. erectus* was the first hominin to reach Flores (e.g., Verhoeven, 1968; Sondaar et al., 1994; van den Bergh et al., 1996; Morwood et al., 1998). For the same reason, in the initial description of *Homo floresiensis*, it was assumed that this endemic hominin species was the result of insular dwarfing of an ancestral *Homo erectus* population (Brown et al., 2004; also cf. Lyras et al., 2009) – in the same way that other large-bodied mammals have downsized on islands (Fig. 1; Lister, 1989; Lomolino, 2005; but see Niven, 2007; Meiri et al., 2008).

However, we favor an alternative hypothesis, based largely on the more detailed analyses of *H. floresiensis* skeletal remains from deposits spanning ~95 ka to ~17 ka (Table 1) presented in this

Special Issue and in other recent publications. Specifically, we propose that the individuals recovered from Liang Bua retain a wide-ranging suite of primitive morphological traits indicating that they may be descendants of a pre-*erectus* hominin species in Asia (Morwood et al., 2005; Argue et al., 2009; Brown and Maeda, 2009; Jungers et al., 2009a). We do not wish to imply that all aspects of *H. floresiensis* anatomy are plesiomorphic, depending on one's choice of outgroup. Argue et al.'s (2009) cladistic analysis corroborates the diagnosis and decision (Brown et al., 2004) to include the new species within the genus *Homo* rather than in *Australopithecus* (or a different genus). For example, relative tooth size, relative facial height, thickness of the cranial vault, endocast topography, aspects of the proximal femur, and orientation of the distal fibula are all features that distinguish the type specimen (LB1) from australopithecines. At the same time, there are relatively few unambiguous autapomorphies of *H. floresiensis* (Argue et al., 2009), and one of them, “obelionic depression,” appears instead to be a relatively common form of antemortem cranial molding known as positional plagiocephaly (Kaifu et al., 2009). Primitive features relevant to our preferred interpretation of *H. floresiensis* as a basal member of the genus *Homo* are summarized below.

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Figure 1. Endemic fauna on Malta included pygmy elephant, pygmy hippo, giant tortoise, and a large goose. These animals well illustrate the unbalanced nature of island faunas, the size changes that often occur, and the vulnerability of animals that have evolved in island isolation – once modern humans arrived on the island about 11 ka, endemic species quickly became extinct. (Photo from Adams, 1870).

Skull, teeth, and brain endocast

The two mandibles (LB1 and LB6) exhibit numerous primitive traits (Brown and Maeda, 2009). Most importantly, the corpus in both lower jaws is very robust and they lack a true mental eminence (“chin”). The mandibular symphyses, which are very thick for height, have superior and inferior transverse tori in cross-section (Brown et al., 2004; Brown and Maeda, 2009). Among ancient hominins, this trait occurs most commonly in australopithecines. The lower premolars are exceedingly and consistently primitive; all known mandibular third premolars of LB1, LB2, and LB6 present plesiomorphic crown and root morphologies (Morwood et al., 2004; Brown and Maeda, 2009), recalling teeth observed both in some australopithecines and in earliest *Homo* (Gómez-Robles et al., 2008). They bear no resemblance to retained deciduous first molars of modern humans (Falk et al., 2009a).

The brain of LB1 is only ~417 cc in volume, a value closer to apes and australopithecines than to early *Homo*. Endocast shape and

configuration do not appear to be consistent with microcephaly or other pathological syndromes (Falk et al., 2005, 2007, 2009). It does, however, appear to be derived in specific ways (e.g., expanded gyri in the region of Brodmann’s area 10 and in the orbitofrontal area), and was perhaps globally reorganized in comparison to similarly sized ape brains. Endocast size and shape are unlikely to have resulted simply from downsizing a *H. erectus* brain (Martin et al., 2006; but cf. Weston and Lister, 2009).

The cranial shape of LB1 fits the patterns of size-correlated changes in the skulls of the earliest fossils of *Homo* (Baab and McNulty, 2009). In other words, its overall shape is predicted relatively well by extrapolating the size-shape trajectories derived from a sample of early *Homo* skulls down to a skull the size of LB1. Furthermore, 3-D geometric morphometric findings corroborate other types of statistical shape analyses (e.g., Argue et al., 2006; Gordon et al., 2008). Notably, analyses of cranial shape in LB1 reveal no special affinities between the crania of LB1 and Southeast Asian *H. erectus* or small *H. sapiens* (Fig. 2). Despite the aforementioned plagiocephaly seen in LB1 and its correlated impacts on cranial symmetry and even dental occlusion (Kaifu et al., 2009), the degree of left-right asymmetry seen in LB1 is neither excessive nor a symptom of some unknown developmental abnormality (Jacob et al., 2006; Baab and McNulty, 2009).

Postcranium and body proportions

The relatively short clavicle and very low degree of humeral torsion in LB1 appear to represent an early, primitive stage in the evolution of hominin shoulders, and this pattern is probably retained from the primitive condition of early *Homo* in Africa (e.g., KNM-WT 15000) and at Dmanisi (Larson et al., 2007, 2009; Lordkipanidze et al., 2007). A similar inference can be made for the flaring ilia of the LB1 bony pelvis (Jungers et al., 2009b). The iliac blades project far laterally beyond the margins of the acetabulae in LB1, recalling the configuration seen in A.L.288-1 (*A. afarensis*) and the new Gona pelvis from Ethiopia (Simpson et al., 2008) but is quite different than humans afflicted with Laron Syndrome (Falk et al., 2009a).

The wrist bones of LB1 (and LB6) are similar to those found in apes, australopithecines, and *H. habilis* (Tocheri et al., 2007; Larson et al., 2009; Tocheri, pers. comm.). The trapezoid of LB1 lacks the derived “boot shape” and expanded palmar surface seen in all modern humans (including pituitary dwarfs and giants), and the capitates of both LB1 and LB6 are highly excavated, or waisted, along their radial aspects. As such, the carpals of *H. floresiensis* differ significantly from those found in more recent hominin species from the last 800 k.yr., including modern humans, Neanderthals, and *Homo antecessor* (Tocheri et al., 2007; Larson et al., 2009).

The foot of LB1 has a broad array of primitive traits that recall apes and some australopithecines (Jungers et al., 2009a,b). These features include relative foot length, relative hallux length, relative phalangeal length, intrinsic tarso-metatarsal proportions, and overall navicular anatomy (with a large medial tuberosity and a “pinched” lateral aspect). The foot of LB1 appears to lack a well-defined medial longitudinal arch as is typically found in the feet of modern humans and probably in *Homo erectus* (Bennett et al., 2009).

The lower limb bones of two individuals (LB1, LB8) are shorter than those of the shortest known modern human pygmies, indicating a stature of 1–1.1 m, essentially the same as that of the shortest australopithecines such as AL 288-1 (Brown et al., 2004; Jungers et al., 2009b). The interlimb proportions of LB1, driven by the very short femora and tibiae (Fig. 3), resemble those of some australopithecines, including A.L. 288-1 (“Lucy”) (Morwood et al.,

Table 1
Inventory of fossils attributed to *Homo floresiensis* from the Liang Bua excavations on Flores, Indonesia.

Sector	Spit	ID	Element	Age (ka)	Age Rationale ^a
III	48	LB15/1	Mandibular 4th premolar	~69 ± 12	LBS3-4
III	51	LB15/2	Maxillary incisor	~69 ± 12	LBS3-4
IV	42D	LB2/1	Ulna, right	~74 ⁺¹⁴ / ₋₁₂	~LB-JR-8a
IV	43D	LB2/2	Mandibular 3rd Premolar, left	~74 ⁺¹⁴ / ₋₁₂	~LB-JR-8a
IV	47R	LB10	Pedal phalanx, Proximal 1st	~74 ⁺¹⁴ / ₋₁₂	~LB-JR-8a
IV	52L	LB11/1	Metatarsal fragment	~74 ⁺¹⁴ / ₋₁₂	~LB-JR-8a
IV	53L	LB11/2	Pelvic fragments	~74 ⁺¹⁴ / ₋₁₂	~LB-JR-8a
IV	54L	LB11/3	Pelvic and costal fragments	~74 ⁺¹⁴ / ₋₁₂	~LB-JR-8a
IV	58R	LB3	Radius, left	~74 ⁺¹⁴ / ₋₁₂	~LB-JR-8a
XI	42	LB4/1	Radius, left	>15.7–17.1, <17.1–18.7	>ANUA-23610 ^b , <ANUA-27117
XI	43	LB4/2	Tibia, right	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	46	LB5/1	Atlas	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	46	LB5/2	Metacarpal	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
VII	50	LB12	Manual phalanx, distal	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	51	LB6/1	Mandible	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	51	LB6/2	Radius, right	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	51	LB6/3	Ulna, left	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	51	LB6/4	Scapula, right	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	51	LB6/5	Metacarpal shaft	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	51	LB6/6	Pedal phalanx, Proximal	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	51	LB6/7	Manual phalanx, distal	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	52	LB6/8	Manual phalanx, proximal	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	52	LB6/9	Manual phalanx, middle	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	52	LB6/10	Manual phalanx, middle	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	52	LB6/11	Manual phalanx, distal	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	52	LB6/12	Manual phalanx, distal	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	52	LB6/13	Pedal phalanx, proximal	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	52	LB6/15	Pedal phalanx, middle	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	52	LB6/16	Manual phalanx, proximal	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	53	LB6/14	Mandibular 1st incisor	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
VII	54	LB13	Patella fragment	>15.7–17.1, <17.1–18.7	>ANUA-23610, <ANUA-27117
XI	56B	LB1/61	Manual phalanx, proximal	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
XI	57A	LB1/62	Manual phalanx, proximal	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
XI	57A	LB1/58	Phalanx, shaft fragment	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
XI	58A	LB1/50	Humerus, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
XI	58A	LB1/51	Ulna, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
XI	58A	LB1/52	Ulna, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
XI	58A	LB1/53	Fibula, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
XI	58A	LB1/54	Talus, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
XI	58A	LB8/1	Tibia, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/1	Cranium	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/2	Mandible	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/3	Atlas	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/4	Costal fragments	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/5	Clavicle, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/6	Ribs	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/7	Ossa coxae	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/8	Femur, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/9	Femur, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/10	Patella, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/11	Patella, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/12	Tibia, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/13	Tibia, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/14	Fibula, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/15	Talus, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/16	Navicular, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/17	Cuboid, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/18	Entocuneiform, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/19	Ectocuneiform, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/20	Mesocuneiform, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/21	Metatarsal I, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/22	Metatarsal II, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/23	Metatarsal III, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/24	Metatarsal IV, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/25	Metatarsal V, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/26	Navicular, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/27	Cuboid, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/28	Ectocuneiform, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/29	Metatarsal I, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/30	Metatarsal II, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/31	Metatarsal III, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/32	Metatarsal IV, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117

Table 1 (continued)

Sector	Spit	ID	Element	Age (ka)	Age Rationale ^a
VII	59	LB1/33	Metatarsal V, right	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/34	Pedal phalanx, proximal	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/35	Pedal phalanx, Proximal	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/36	Pedal phalanx, Proximal	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/37	Pedal phalanx, Proximal	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/38	Pedal phalanx, Proximal	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/39	Pedal phalanx, middle	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/40	Manual phalanx, Middle	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/41	Pedal phalanx, Proximal	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/42	Manual phalanx, Middle	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/43	Pedal phalanx, distal	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/44	Scaphoid, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/45	Capitate, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/46	Hamate, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/47	Trapezoid, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/48	Manual phalanx, middle	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/49	Manual phalanx, distal	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/56	Pedal phalanx, middle	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/57	Pedal phalanx, distal	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/59	Metacarpal fragment	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	59	LB1/60	Lunate, left	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	61	LB8/2	Premolar	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
VII	62	LB1/55	Manual phalanx, Distal 1st	17.1–18.7, 17.9–19.0	ANUA-27116, 27117
XI	65B	LB9	Femur fragment	~18.2–19.7	~ANUA-31229
VII	69	LB14	Pelvis fragment (acetabulum)	>18.2–9.7, <41 ± 10	>ANUA-31229, <LBS7–46

^a For specific details regarding the dating samples used for the age estimates see Roberts et al. (2009: Table 1).

^b ANUA-23610 from Sector III is associated with the break-up of the Black Tuffaceous Silt that overlies the layers containing *H. floresiensis* material in Sectors VII and XI.

2005; Argue et al., 2006; Jungers, 2009). Currently, *H. floresiensis* is the only hominin species known outside Africa with this primitive body shape. The short hind limb also accounts for the relatively long foot of LB1 when standardized to femur length (Jungers et al., 2009a, Supplementary Online Material).

Affinities of *Homo floresiensis*

The first quantitative cladistic analysis of which we are aware that includes *H. floresiensis* (Argue et al., 2009) produces two equally parsimonious phylogenetic trees. Most importantly, both support the placement of the species as a basal member of the genus *Homo*, clearly lacking special affinities to Asian *H. erectus*. Most of the characters of this study are craniodental. We predict that similar quantitative, character-based analyses of the postcranium, with its numerous primitive morphologies, would further anchor this small-bodied species as a basal member of our own genus.

In sum, the suite of primitive traits revealed by numerous analyses in this Special Issue, along with previous and recently published studies indicate, collectively, that the ancestral population of *H. floresiensis* in Flores, and therefore earlier in continental Asia, may have been a habiline-like, or even more primitive hominin species. Pending further cladistic and other metric analyses, we propose that *H. floresiensis* presents plesiomorphic morphologies that include australopithecine-like body proportions, a small brain, and small body size (also cf. Ruff, 2009). We are also unaware of any systemic pathology that converts modern humans into phenotypes of their ancestors (cf. Falk et al., 2009a; Jungers et al., 2009c).

The earliest known hominins outside Africa occur at the ~1.8 Ma site of Dmanisi in Georgia. But the Dmanisi hominins, variously classified as very early *H. erectus/ergaster* or a new species, *H. georgicus* (Gabunia et al., 2000; Gabounia et al., 2002), were taller (>1.4 m) than *H. floresiensis*, had bigger brains (>600 cc), and apparently had “modern” interlimb proportions (Lordkipanidze



Figure 2. Skulls of 1.9 Ma *H. habilis* (A), 1.8 Ma *H. ergaster* from Dmanisi (B), and 18 ka *H. floresiensis* from Flores (C). Despite being separated by over 9000 km and almost 2 Ma, the early *Homo* and *H. floresiensis* skulls are still remarkably similar. (Photo credit: C. Stringer, Natural History Museum, London, UK.)



Figure 3. The assembled skeleton of the type specimen of *Homo floresiensis* (LB1). (Photo credit: W.L. Jungers.)

et al., 2007). As such, we suspect that they represent a dispersal event that postdates that of the ancestral stock that ultimately gave rise to *H. floresiensis*. In other words, we hypothesize, based on geochronological, archaeological, and morphological data, that the *H. floresiensis* lineage exited Africa between 1.8–2.6 Ma – i.e., before



Figure 4. A full-body reconstruction of LB1 created by Elisabeth Daynès (© 2009, S. Plailly/E. Daynès – Reconstruction Atelier Daynès Paris).

hominins occupied Dmanisi, but after they began making stone artifacts (e.g., Semaw et al., 2003). This was a time when the extent of grassland savannah from Africa to China offered no barriers to faunal exchange (Dennell and Roebroeks, 2005; also cf. Hughes et al., 2008). Although Asia currently lacks hominin skeletal evidence, the two million year old stone artifacts reported in stratified context from Riwat in Pakistan fit this scenario (Dennell et al., 1998).

The prevailing model for early hominin evolution and dispersal, “Out of Africa 1,” assumes that the genus *Homo* originated in Africa at least 2.33 Ma (Kimbel et al., 1996); that *H. erectus sensu lato* was the first and only hominin species to disperse into Eurasia about 1.7–1.9 Ma (Zhu et al., 2008); and that the migrants were relatively large-brained and essentially modern in stature and body proportions (Antón and Swisher, 2004; Dennell and Roebroeks, 2005; Wells and Stock, 2007). The primitive anatomical traits of *H. floresiensis*, however, provide compelling evidence indicating just how little is known about when hominins first occupied Asia, the species involved, or what happened next. In fact, the Liang Bua evidence challenges nearly all key assumptions in the “Out of Africa 1” model, currently paradigmatic to our understanding of virtually all major hominin evolutionary innovations.

Implications for early hominin evolution and biogeography

Although major gaps exist in the Flores archaeological sequence, stone artifacts in stratified contexts show long term occupation on the island by premodern hominins between 880–680 ka at nine sites in the Soa Basin; at 193 ka near Liang Bua; and between 95–17 ka in

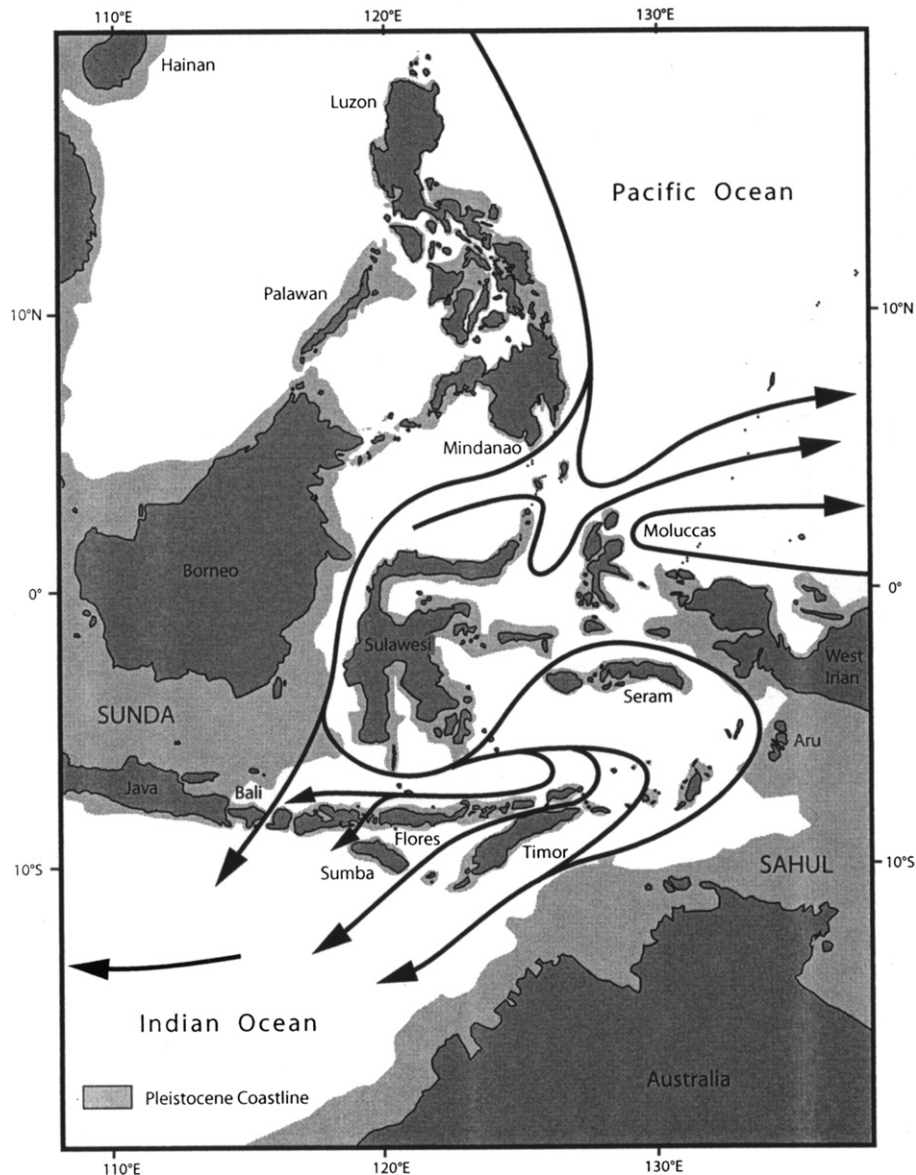


Figure 5. The predominant ocean currents in Southeast Asia flow from north to south – the “Indonesian Throughflow” (after Kuhnt et al., 2004).

Liang Bua (Morwood et al., 1998,2004; O’Sullivan et al., 2001; Moore, 2005; Brumm et al., 2006; Brumm, 2007; Moore and Brumm, 2007; Moore et al., 2009; Westaway et al., 2009). Furthermore, these stone artifact assemblages show continuity in flaking technology and artifact types throughout the sequence, with particular emphasis on production of radial cores (or Mode 1 “discoids” [Moore et al., 2009]), as found in the earliest Oldowan stone artifact assemblages in East Africa (Semaw et al., 2003). Claims by some critics that stone artifacts found with *H. floresiensis* at Liang Bua are so sophisticated that modern humans must have made them are, therefore, ill-founded (e.g., Martin et al., 2006; cf. Moore et al., 2009). In contrast, evidence for use of mollusks and symbolic behaviors symptomatic of modern humans, such as use of pigments, personal adornments, and formal disposal of the dead, is conspicuously absent from levels containing skeletal evidence for *H. floresiensis*. However, these materials occur in overlying deposits (Morwood et al., 2004; van den Bergh et al., 2009b). What is clear from the archeological and paleontological remains at Liang Bua is that modern human hands and modern human-sized brains are not needed to produce core and flake technologies (Tocheri et al., 2007; Falk et al., 2005,2009).

The fossil record on Flores is far from complete, but it confirms that the island was always a difficult colonization prospect: few land animals reached the island, and those that did establish themselves, such as *Stegodon*, rodents, and Komodo dragon, exhibit long-term phylogenetic continuity associated with traits characteristic of insular evolution. In fact, apart from a single varanid species, no new immigrants or extinctions are apparent in the sequence between a faunal turnover 900 ka in the Soa Basin and 17 ka at Liang Bua (van den Bergh et al., 2009a,b). Given these circumstances, the arrival of hominins by 880 ka was probably the result of an extremely rare event, such as a tsunami. In such a scenario, a small colonizing group could have accidentally crossed to the island while clinging to a natural raft of vegetation or an up-rooted tree washed out to sea (Smith, 2001; also cf. de Queiroz, 2005).

On the basis of both cultural and biological evidence, therefore, we suggest that the early hominins already present in the Soa Basin by 880 ka are likely to have experienced undisturbed, long term phylogenetic continuity. Moreover, these early hominins were probably directly ancestral to *H. floresiensis* – in much the same way that *Stegodon florensis florensis* in the Soa Basin was directly



Figure 6. Two million years ago, animals on Sulawesi included giant tortoise and a primitive, pygmy “elephant” with four tusks. (Drawings courtesy of Hans Brinkerink.)

ancestral to *Stegodon florensis insularis* at Liang Bua. During this time span, the *Stegodon* population on Flores underwent a ~30% reduction in body size (van den Bergh et al., 2009a). Associated hominins probably arrived on Flores with relatively small bodies, but may also have downsized further as an adaptation to specific conditions on the island. However, we do not believe it is likely that such a reduction in body size, if it did occur, could explain the numerous plesiomorphic skeletal features of *H. floresiensis*. Modern humans have “dwarfed” to pygmy size repeatedly and independently around the world, including Southeast Asia, and there is no hint of correlated evolutionary reversals in body shape or bony morphology (Migliano et al., 2007; Jungers, 2009; Jungers et al., 2009a; Perry and Dominy, 2009; but see Holliday and Franciscus, 2009). Human pygmies bear no meaningful resemblance to *H. floresiensis* (Fig. 4) save for small body mass.

Implications of Liang Bua and future research

Finding skeletal remains of the Soa Basin tool-makers continues to be one of our group's research priorities. Such evidence would provide the means to test competing hypotheses about the phylogeny of *H. floresiensis*, would have major implications for the evolutionary history of hominins on the island, and would be ~880 ka closer in time and evolutionary development to the ancestral species that first exited Africa. Because of the unique circumstances of Flores as a refuge for faunal lineages long extinct elsewhere, Middle Pleistocene hominin skeletal evidence from the island has leveraged significance, perhaps with paradigm-changing implications for early hominin biogeography and ancient dispersal events in Asia generally. It could also open up a Pandora's Box of other hominin biogeographic and evolutionary possibilities at apparent odds with the various and generally accepted “Out of Africa” scenarios. We submit that there is no other region in Southeast Asia with such proven potential for shedding light on the dawn of the genus *Homo* and the radiation of its member species.

We also emphasize that, given its geographic position 400 km east of continental Asia with intervening islands, Flores cannot have been the only island in the region visited and perhaps settled by early hominins. If such populations persisted long enough, it is conceivable that other endemic hominin species evolved in isolation – and await discovery. On the basis of geographical proximity alone, Sumbawa to the west and Sulawesi to the north are the most

likely immediate source islands for hominins reaching Flores. However, the predominant ocean currents in island Southeast Asia flow strongly from the Pacific Ocean in the north to the Indian Ocean in the south, i.e., the “Indonesian Throughflow” (Fig. 5; Kuhnt et al., 2004), which would have facilitated north to south movement of animals drifting or swimming between islands, while impeding west to east movements. This is clear when the fossil records from a north to south transect of islands in the region, from Sulawesi to Timor, are compared.

Around two million years ago, the earliest terrestrial animals known from the fossil record in Southwest Sulawesi, the Walanae Fauna, comprised giant tortoise, crocodile, a pygmy *Stegodon*, a type of pygmy “elephant” with four tusks and *Loxodonta*-like molar cusps, and a primitive pig with large upper canines (Fig. 6; van den Bergh, 1999). In the course of the Pleistocene, both pygmy elephants were replaced by large-bodied immigrants – an advanced, hypsodont *Elephas* sp. and *Stegodon* spec. B (van den Bergh, 1999). Further south, reaching Flores was much more difficult and the range of large animals present there at 900 ka is a much-diminished subset of the Pliocene megafauna of Southwest Sulawesi: a pygmy *Stegodon* (*S. sondaari*), the giant tortoise, and the Komodo dragon, with the latter being derived from a dispersal of varanids across Australasia by the Miocene (Morwood et al., 1998; Molnar, 2004). The same limited range of large animals – *Stegodon*, giant tortoise, and a giant varanid – occurs further to the southeast on adjacent Timor in the Pleistocene fossil deposits of the Atambua Basin (Verhoeven, 1968; Hooijer, 1971, 1972a,b).

On the basis of island geography, ocean currents, and the fossil record, we argue that the first hominins to reach Flores most likely came from the north, specifically from Sulawesi. The required sea crossing is now ~300 km, but at times of low sea level “Greater Sulawesi,” including Selayar Island, would have approached to within 80 km of Flores, and the fossil record indicates that animals did make this crossing, albeit infrequently: *Stegodon florensis* on Flores is more closely related to *Stegodon* spec. B from Southwest Sulawesi than to *S. triganocephalus* from Java (van den Bergh, 1999; van den Bergh et al., 2009a). For all the above reasons, fieldwork programs are in-progress to establish when (and which) hominins first arrived on Sulawesi, as well as their evolutionary history and faunal impacts. Hopefully, this research will also provide further evidence for the evolutionary history of *H. floresiensis*, and the nature and timing of early hominin dispersals in Asia.

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