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The place of *Homo floresiensis* in human evolution

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Summary - *Two main evolutionary scenarios have been proposed to explain the presence of the small-bodied and small-brained* Homo floresiensis *species on the remote Indonesian island of Flores in the Late Pleistocene. According to these two scenarios,* H. floresiensis *was a dwarfed descendent of* H. erectus *or a late-surviving remnant of a older lineage, perhaps descended from* H. habilis*. Each scenario has interesting and important implications for hominin biogeography, body size evolution, brain evolution and morphological convergences. Careful evaluation reveals that only a small number of characters support each of these scenarios uniquely.* H. floresiensis *exhibits a cranial shape and many cranial characters that appear to be shared derived traits with* H. erectus*, but postcranial traits are more primitive and resemble those of early* Homo *or even australopiths. Mandibular and dental traits show a mix of derived and primitive features. Unfortunately, many traits cannot be used to assess these two hypotheses because their distribution in* H. erectus*, early* Homo *(e.g.,* H. habilis*), or both is unknown.* H. erectus *ancestry implies evolutionary convergence on a postcranial configuration similar to australopiths and early* Homo*, which could be explained by a return to more climbing behaviors. Body size reduction as well as brain size reduction on a scale only rarely documented in mammals would also accompany the origin of* H. floresiensis *from a* H. erectus *ancestor.* H. habilis *ancestry implies parallel evolution of numerous cranial characters, as well as a few dentognathic traits. A pre-*H. erectus *ancestry also suggests an early migration to Southeast Asia that is as yet undocumented in mainland Asia, but minimal body and brain size reduction.*

Keywords - Homo floresiensis, *Evolutionary history, Hominin morphology, Convergence, Biogeography.*

Introduction

The authors of the 2004 announcement of a new hominin species, *Homo floresiensis*, on the Indonesian island of Flores suggested that: "The first hominin immigrants may have had a similar body size to *H. erectus* and early *Homo*, with subsequent dwarfing; or, an unknown small-bodied and small-brained hominin may have arrived on Flores from the Sunda Shelf" (Brown *et al.*, 2004, p. 1060). These two scenarios remain at the forefront of evolutionary hypotheses seeking to explain the presence of small-bodied and phylogenetically primitive hominins in this remote Southeast Asian locale during a time when modern *H. sapiens* are known throughout the Old World.

Although *H. floresiensis* is undoubtedly an evolutionary side branch without direct relevance for the evolution of *H. sapiens*, a better understanding of the evolution of *H. floresiensis* has important implications for hominin biogeography, evolutionary history and brain evolution. I will discuss evidence from the cranium, mandible, dentition, endocast and postcranial skeleton as it pertains to each of these evolutionary scenarios, and the implications of each scenario for the evolutionary history of this species.

Non-evolutionary ("pathological") explanations have also been posited for LB1, but these have not stood up to careful scrutiny. The proposed diagnoses, including Laron syndrome, "cretinism," and Down syndrome share certain clinical signs, including reduced stature and brain size, although in no case are the extremely small stature, brain size and other anatomical features of the Liang Bua hominins (e.g., the interlimb proportions, thick cranial bones) compatible with any of these pathologies (e.g., Falk *et al.*, 2009a; Brown, 2012; Baab *et al.*, 2015).

Background

Liang Bua cave is a large cave located on Flores in eastern Indonesia. Flores is one of the islands of Wallacea, a region known for low levels of terrestrial faunal diversity and high levels of island endemism (van den Bergh *et al.*, 2009). This pattern is the result of strong isolation barriers between the regions of Wallacea and Sundaland / the Asian mainland to the west, and Sahulland / Australia to the east. Even during the last glacial maximum there was no land connection between Flores and the islands to the west due to the deep straits between Flores and Sumbawa, as well as between Bali and Lombok (Lambeck & Chappell, 2001).

The hominin remains now assigned to *H. floresiensis* were recovered from Pleistocene deposits dated between ~18 and 74-95 ka (Brown *et al.*, 2004; Morwood *et al.*, 2004). Other terrestrial vertebrates recovered from these deposits include *Stegodon*, Komodo dragon, and smaller fauna, such as fish, frogs, snakes, rodents and bats. There is taphonomic and archaeological evidence for hunting or scavenging by *H. floresiensis* of young stegodonts, Komodo dragons and other fauna (Morwood *et al.*, 2004; van den Bergh *et al.*, 2009). Lithic tools associated with *H. floresiensis* are mostly simple pebble and flake tools, comparable to African Oldowan or Developed Oldowan assemblages, but with a small number of seemingly more sophisticated tools, such as blades (Morwood *et al.*, 2004; Moore & Brumm, 2009). Moore (2007) has suggested the few blades recovered were incidental byproducts of the basic reduction sequence used by *H. floresiensis* rather than evidence of advanced cognition sometimes associated with blade technology. Archaeological sites dated to 0.80-0.88 Ma (Mata Menge; Morwood *et al.*, 1998) and 1.02 Ma (Wolo Sege; Brumm *et al.*, 2010) from the Soa Basin of central Flores may be the ancestral population for *H. floresiensis*, which would allow for ~1 Myr of evolution in isolation. The absence of hominin fossils from the Soa Basin precludes taxonomic identification of this population. Also nearby are numerous *H. erectus* sites on the western Indonesian island of Java ranging in age from 0.27-0.55 to ~0.88 or possibly 1.5 Ma (Larick *et al.*, 2001; Hyodo *et al.*, 2011; Indriati *et al.*, 2011; Kaifu *et al.*, 2011b).

Evolutionary hypotheses

Perhaps the most notable characteristics of the Liang Bua hominin assemblage are the small stature and small brain size that are apparent in the fairly complete type specimen, LB1 (Brown *et al.*, 2004). Postcranial bones from other individuals are equally diminutive, if not a bit smaller (e.g., LB8) (Jungers *et al.*, 2009b). Although only one cranium has been recovered from the Liang Bua site, two mandibles (from the LB1 and LB6 individuals) are very similar in morphology and size (Brown & Maeda, 2009).

Evolutionary scenarios must explain the unique blend of anatomical features seen in the Liang Bua hominins. One hypothesis posits *H. erectus* as the ancestral population for *H. floresiensis* (Brown *et al.*, 2004), with subsequent island dwarfing. Within this broader scenario, different populations of *H. erectus* have been identified as being the likely stem population for the *H. floresiensis* lineage: early African *H. erectus* (i.e., *H. ergaster*) (e.g., Gordon *et al.*, 2008) and early Indonesian *H. erectus* (Kaifu *et al.*, 2011a). A second hypothesis positions the divergence of the *H. floresiensis* branch before the origin of *H. erectus*, making the ancestor an early *Homo* species such as *H. habilis* (e.g., Argue *et al.*, 2009).

On the surface, discerning between these two alternatives should be a straightforward exercise. If the Liang Bua hominins present traits that are derived for *H. erectus* compared to earlier hominins, then the likely evolutionary scenario is divergence from *H. erectus*. If the Liang Bua hominins exhibit traits that are more primitive than those observed in *H. erectus*, then this would suggest a pre-*H. erectus* divergence. In either case autapomorphic features likely reflect subsequent evolution. In reality, the situation is unlikely to be this clear cut. A quick survey of the literature indicates a mix of primitive and derived traits as well as some unique features. This contribution has three goals. The first is to sort characters from the skull and postcranial skeleton into one of three categories:

1) those that are shared between *H. floresiensis* and *H. erectus* (or later *Homo* species) to the exclusion of *H. habilis*,
2) those that are shared between *H. floresiensis* and *H. habilis* (or earlier hominins) that are more derived in *H. erectus*, and
3) those whose distribution in either *H. habilis* and/or *H. erectus* is unknown or is the same in both groups.

These characters must be evaluated critically with regard to their utility in determining *H. floresiensis* origins as 1) their status in early *Homo* and / or *H. erectus* is often unknown given the incomplete nature of the fossil record, 2) features may be variable within a given species, and *H. erectus* in particular has well-documented allometric, geographic and temporal variation (e.g., Baab, 2008), and 3) homoplasy may be common among closely related hominin species (Lieberman *et al.*, 1996; Collard & Wood, 2001). The final goal is to examine the implications of the two main evolutionary scenarios for hominin evolution.

Derived morphology

The shapes of the LB1 cranium (Gordon *et al.*, 2008; Lyras *et al.*, 2009) and neurocranium (Baab & McNulty, 2009; Kaifu *et al.*, 2011a) are more comparable to *H. erectus* than *H. habilis*. LB1 does not show particular affinities with *H. habilis* fossils KNM-ER 1813 and OH 24 despite being closer in overall size to these fossils than most *H. erectus* specimens. LB1 particularly resembled the D2700 subadult from Dmanisi, but this is due in part to scaling patterns wherein the diminutive LB1 resembled other small *H. erectus*. Thick cranial bones also link LB1 to *H. erectus* but not earlier *Homo* species. However, this must be viewed as relatively weak support for *H. erectus* ancestry due to the small sample sizes for early *Homo*. Kaifu *et al.* (2011a) compared character state distributions of 67 craniofacial traits in LB1 and populations of Plio-Pleistocene *Homo*. They identified many traits in LB1 that appear to be derived for *H. erectus* relative to *H. habilis* (Tab. 1), including some that were present in LB1 and early African and Indonesian, but not Georgian *H. erectus* and others that were derived in LB1 and Sangiran/Trinil *H. erectus* compared to early African and Georgian *H. erectus*. They interpreted this pattern as most consistent with an early Indonesian ancestry for *H. floresiensis*.

Overall mandibular form was described as similar to early African/Georgian *H. erectus* (Morwood *et al.*, 2005), but with some more primitive features (see below). The scaling of the mandibular molars (M_1>M_2>M_3) is shared with *H. erectus* and *H. sapiens*, but not early *Homo*. The strongly inclined mandibular symphysis is shared with some Dmanisi *H. erectus* and gracile australopiths, but not early *Homo* or other *H. erectus* populations, including Indonesian ones (creating ambiguity in its interpretation).The mandibular molar crowns are less megadont than observed in early *Homo* and australopiths, while the well-developed lingual alveolar prominence is shared uniquely with African *H. erectus* (Brown & Maeda, 2009). Kaifu *et al.* (2015) identified the distolingual orientation of the transverse crest on the P_3 in LB1 as a shared derived feature with post-*H. habilis Homo*, including Dmanisi and African *H. erectus* populations.

The lack of postcranial elements that are clearly associated with early *Homo* and *H. erectus*, particularly Asian *H. erectus*, presents a distinct challenge to identifying traits shared between *H. erectus* and *H. floresiensis* exclusive of early

Tab. 1 - Characters identified by Kaifu **et al.** ***(2011a) that are shared between*** **H. floresiensis** ***and*** **Homo** ***species / populations (those in italics are less certain).***

H. FLORESIENSIS **SHARES THE FOLLOWING TRAITS WITH:**
H. erectus (but not *H. habilis*)
Moderately flexed occipital bone
Laterally flattened frontal squama with no eminence
Medially positioned external acoustic meatus
Thickened parietal bones
Moderately prominent nasal bridge
Shallow palate
Early African and Sangiran / Trinil *H. erectus* (but not Georgian *H. erectus* or *H. habilis*)
Laterally expanded parietals relative to cranial base
Suprameatal crest not laterally projecting
Low cranial vault relative to breadth
Well-developed frontal keel
Bulbous and laterally projecting ends of supraorbital torus
Flat basioccipital elevated relative to surrounding cranial base
Sangiran / Trinil *H. erectus* (but not Georgian / African *H. erectus* or *H. habilis*)
Temporal lines diverge posteriorly on parietals
Low and wide occipital squama
Flexed anteromedial corner of mandibular fossa
Small, pointed and medially directed mastoid process
Very narrow upper facial breadth
Absent or poorly defined vaginal process of styloid
Medio-laterally narrow mandibular fossa
Sharp protrusion of maxillary body beyond infraorbital surface with distinct infraorbital sulcus
Short facial height in infraorbital region

Homo. The broad, squared off distal end of the hallucal metatarsal in LB1 is more derived in the direction of *H. sapiens* than the condition documented for the Dmanisi *H. erectus* population (Jungers *et al.*, 2009a, 2009b; Pontzer *et al.*, 2010). However, the mid-Pleistocene Jinniushan foot had a more beaked distal hallucal metatarsal similar to the Baringo (KNM-BK 63) metatarsal, possibly belonging to African *H. erectus*, but overlapping *H. heidelbergensis s.l.* in time (Lu *et al.*, 2011). This suggests that a primitive distal hallucal metatarsal was retained through the Middle Pleistocene, making LB1 the outlier and not clearly aligned with any sampled extinct *Homo* taxon.

Primitive morphology

Morphological evidence suggesting a pre-*H. erectus* ancestry for *H. floresiensis* includes traits seen in LB1 that are shared with early *Homo* or earlier hominins that are more derived in *H. erectus*. The overall profile of the mandibular symphysis is similar to that of australopiths (Brown & Maeda, 2009), including the absence of any the components of a chin (as defined by Schwartz & Tattersall, 2000) and a moderate superior torus separated by a broad genioglossal depression from a low inferior torus. The ascending ramus lacks the characteristic "waisting" seen in *H. sapiens* and *H. erectus*, and the overall ramus morphology, including the region around the mandibular foramen, has been described as more australopith-like than *Homo*-like. The profile of the corpus inferior to the P_3 accords more closely with that seen in early *Australopithecus* rather than early *Homo*. Brown & Maeda (2009) suggested that the narrow dental arcade of LB1/LB6 was shared with pre-*H. erectus* hominins, but this was disputed by Kaifu *et al.* (2011a), who demonstrated metrically that the LB1 arcade was wider than *H. habilis* and Dmanisi *H. erectus*, but overlapped early Javanese *H. erectus* populations.

Postcranially, the interlimb proportions of LB1 are clearly more ape-like and australopith-like than those of *H. erectus* (Jungers, 2009). Estimates of the OH 62 (*H. habilis*) humero-femoral ratio are controversial due to issues regarding reconstruction of the incomplete femur, and range from values that are even higher than those of LB1 and *A. afarensis* (Hartwig-Scherer & Martin, 1991) to nearly human-like values (Haeusler & McHenry, 2004). Regardless, LB1 has the primitive state of long upper limbs relative to lower limbs. Similarly, the ratio of cross-sectional strength of upper to lower limb in LB1 is similar to OH 62 and closer to chimpanzees than humans and *H. erectus* (Ruff, 2009; Jungers *et al.*, 2010).

The foot of LB1 can be compared to pedal and tarsal elements from early *Homo* / *H. erectus* from East Africa and *H. erectus* from Dmanisi, but there are no tarsal / pedal remains from Asian *H. erectus*. The prominent navicular tuberosity of LB1 is more primitive than that seen in OH 8 (assigned to either *H. habilis* or *Paranthropus boisei*). Jungers *et al.*'s (2009a,b) interpretation of the large navicular tuberosity as weight bearing led them to conclude that LB1 did not have a medial longitudinal arch. However, a more prominent plantar tuberosity was also described for the Middle Pleistocene Jinniushan individual and Neanderthals, both of which were interpreted as having medial longitudingal arches (albeit a low arch for Jinniushan) (Trinkaus, 1983; Lu *et al.*, 2011). Based on metatarsal torsion, Pontzer *et al.* (2010) concluded that the Dmanisi *H. erectus* population had a midfoot transverse arch and therefore a longitudinal arch. Metatarsal torsion also suggests that the OH 8 foot had a longitudinal arch (Pontzer *et al.*, 2010) and the navicular tuberosity is human-like (Susman & Stern, 1982). A longitudinal arch may also be present in *A. afarensis* (Ward *et al.*, 2011) and *A. sediba* (Zipfel *et al.*, 2011), but probably not *A. africanus* (Drapeau & Harmon, 2013). If these interpretations are correct, then the lack of a longitudinal arch in LB1 may be more primitive than the condition seen in early *H. erectus* and possibly *H. habilis* or even *Australopithecus*. However, the presence of an attachment site for the spring ligament in LB1, which supports the longitudinal arch in humans, and the presence of a navicular tuberosity in species interpreted as possessing an arch, both complicate this interpretation (Jungers *et al.*, 2009b), and both the presence of an arch and the taxonomic attribution of OH 8 are controversial (as reviewed in Griffin & Wood, 2006). The low degree of talar head torsion in LB1 is closer to the range for African apes than humans and fossils assigned to *H. erectus*. However, values for OH 8 reported by different workers fall near both ranges (compare 40^0: Day & Wood, 1968; and 28.5^0: Zipfel *et al.*, 2011).

Uncertain or shared morphology

Many of the anatomical details recorded for the Liang Bua hominins are shared with both *H. erectus* and early *Homo* or their distribution is unknown for one or both groups. These morphologies are not useful in establishing the evolutionary origins of this species.

Kaifu *et al.* (2011a) identified at least 20 cranial traits present in LB1 that are also found in *H. habilis* and some *H. erectus* populations, including weak or no development of the coronal and sagittal keels, a weak angular torus, a long temporal squama with a short parietomastoid suture, presence of a postglenoid process, a shallow mandibular fossa, and an indistinct supraorbital sulcus. Falk *et al.* (2009b) documented numerous features of the LB1 endocast that are derived for hominins relative to apes, and compared LB1 favorably with *H. erectus* rather than several ape and hominin species, including *A. africanus* (Falk *et al.*, 2005). Unfortunately, early *Homo* was not included in the comparative sample. The robust mandibular corpus relative to estimated body mass seen in LB1 is common in Plio-Pleistocene *Homo* (Brown & Maeda, 2009). Asymmetric and mesiodistally-elongated P_3 crowns documented for LB1 and LB6 are common in some australopiths, early *Homo*, and while rare in *H. erectus*, are seen at Dmanisi (Brown & Maeda, 2009; Kaifu *et al.*, 2015). The P_3 with a bifurcated root seen in LB1 and LB6 is common in australopiths, but also observed in some early *Homo* and *H. erectus*. LB1 presents a P_4 with a Tomes' root. The P_4 of LB6 was described as two-rooted (MB + D pattern; Brown & Maeda, 2009) or as Tomes' form (Kaifu *et al.*, 2015). Shields (2005) suggested that c-shaped Tomes' roots first appear in *H. habilis* coincident with tooth size reduction in this group, but while Tomes' rooted P_3's are documented in early *Homo*, Tomes' rooted P_4's are uncommon in the hominin fossil record (Wood *et al.*, 1988). However, both single and double-rooted P_4's are present in African early *Homo*, African *H. erectus* and Indonesian *H. erectus* (Wood *et al.*, 1988; Kaifu *et al.*, 2005) and in fact occur with equal frequency in *H. habilis* and older Sangiran *H. erectus* (Kaifu *et al.*, 2015).

The carpal bones of the Liang Bua hominins have many features also observed in australopiths and apes, but not in Neanderthals and modern humans, such as a wedge-shaped trapezoid, and a capitate with a waisted neck and a scaphoid facet that extends onto the neck in a J-hook shape (Tocheri *et al.*, 2007; Orr *et al.*, 2013). Carpal morphology is unknown in early *Homo* and *H. erectus*. LB1/LB6 share low humeral torsion and a low claviculohumeral ratio with *H. erectus* as well as earlier hominins (Larson *et al.*, 2007; Larson, 2009; Churchill *et al.*, 2013; Roach *et al.*, 2013). The glenoid fossa faces laterally rather than cranially in KNM-WT 15000 and LB6, but may face more cranially in the Dmanisi hominins (Lordkipanidze *et al.*, 2007; Larson, 2009), although this discrepancy may be due to measurement differences (Larson, 2009). The transverse orientation of the scapular spine of LB6 and KNM-WT 15000 (Larson *et al.*, 2007) is derived relative to African apes and most australopiths (Green & Alemseged, 2012), with the exception of KSD-VP-1/1 (*A. afarensis*) whose value is between that of LB6 and KNM-WT 15000 (Haile-Selassie *et al.*, 2010). Therefore, LB1 shoulder girdle anatomy is broadly congruent with the condition found in *H. erectus* (allowing for some intraspecific variation), but unknown in early *Homo*.

Of the >11 known tali from East and South Africa, the best contenders for attribution to early *Homo* include KNM-ER 813, Omo 323-76-898, and possibly OH 8 (e.g., Gebo & Schwartz, 2006 and references therein). However, the latter may belong to *P. boisei*, as noted above. Tali typically attributed to *H. erectus* include the African KNM-ER 803 (fragmentary) and KNM-ER 5428 and the Georgian D4110 fossils (Pontzer *et al.*, 2010; Boyle & DeSilva, 2015). The shallow dorsal trochlear groove of LB1, derived in the direction of *H. sapiens*, is found in representatives of both groups. The ape-like flaring of the lateral malleolar facet appears to be conserved in most pre-*H. sapiens* fossils including D4110. The hallux is quite short relative to the other metatarsals, which is more ape-like than human-like, but this pattern is similar to that seen at Dmanisi (Jungers *et al.*, 2009a, 2009b; Pontzer *et al.*, 2010). The halluces of the LB1 and Dmanisi feet are adducted, as are those of the hominins (*H. erectus*?) that made the 1.4 and 1.5 Ma footprints at Illeret (Bennett *et al.*, 2009), in contrast to the primitive abducted hallux seen in basal hominins (Lovejoy *et al.*, 2009) and the Late Pliocene Burtele foot (Haile-Selassie *et al.*, 2012), or the intermediate degree of abduction documented for australopiths (e.g., Stern & Susman, 1983; Clarke & Tobias, 1995; but see Latimer & Lovejoy, 1990; McHenry & Jones, 2006). Yet, not all early hominins had abducted halluces as attested to by the 3.6 Ma Laetoli footprints (Raichlen *et al.*, 2010). The OH 8 (*H. habilis*?) toe was adducted (e.g., Susman, 1983), so this may represent a shared derived feature of *H. floresiensis* and *Homo* more broadly , but perhaps some pre-Homo species as well.. The iliac flaring of the pelvis is present in australopiths, but also *H. erectus*, *H. heidelbergensis sensu lato* and Neanderthals (Arsuaga *et al.*, 1999; Simpson *et al.*, 2008). Low tibial torsion in *H. floresiensis* (5-7^{0}) appears comparable to the condition at Dmanisi (1^{0}), but much lower than that of African *H. erectus* (KNM-WT 15000: 34^{0}) or later *Homo* species (Wallace *et al.*, 2008; Jungers *et al.*, 2009a; Pontzer *et al.*, 2010), but I could find no information about this feature in *H. habilis*.

Ancestry of *H. floresiensis* and implications for the evolutionary history of hominins

Traits shared among *H. floresiensis*, *H. erectus* and early *Homo* are uninformative as to whether the lineage leading to *H. floresiensis* branched off before or after the origin of *H. erectus*, but confirm its assignment to the genus *Homo*. *H. rudolfensis* seems an unlikely ancestor as the most distinctive aspects of the face and the large dentition are not present in the Liang Bua hominins. Thus, the most likely ancestors for *H. floresiensis* are *H. erectus* and *H. habilis* (or a closely related species). It is currently difficult to confidently discern between these two because *H. floresiensis* shares features with *H. erectus* to the exclusion of early *Homo*, but, conversely, also shares primitive features with earlier hominins that differ from the more derived condition in *H. erectus* or *H. sapiens*.

Cladistics

A cladistic analysis of *H. floresiensis* based on 60 (mostly cranial) characters indicated that *H. floresiensis* diverged before the emergence of *H. erectus* (Argue *et al.*, 2009). Bootstrap support for the tree nodes was low, and when *H. floresiensis* was forced into a clade with the Dmanisi population or with *H. habilis*, the trees were only 2 or 3 steps longer than the shortest tree, respectively. There was less support for a *H. floresiensis* – *H. erectus* sister group relationship, although only two characters excluded *H. floresiensis* from the clade that included *H. erectus* – radiofemoral index and a confluent supramastoid crest and inferior temporal line. I confess that I am uncertain about the robustness of these results given these observations.

Evolutionary convergences

Given the assignment of *H. floresiensis* to the genus *Homo*, the most primitive aspects of morphology (i.e., australopith- but not *Homo*-like) must be evolutionary convergences rather than primitive retentions. Perhaps a primitive mandibular ramus and symphysis re-appeared due to a shift toward more forceful mastication in *H. floresiensis* (Brown & Maeda, 2009). The primitive navicular tuberosity morphology and the absence of a longitudinal arch may also be reversals depending on how the anatomy of the OH 8 foot is interpreted, and if the OH 8 foot in fact belongs to *H. habilis*. Brain size also represents a "reversal" as it is smaller than both *H. erectus* and early *Homo*.

If *H. erectus* was the ancestor of *H. floresiensis*, then the human-like limb proportions of *H. erectus* were altered such that the lower limb became foreshortened relative to the upper limb and the relative robusticity of the upper limb increased relative to the lower limb. It is possible to speculate that a return to more arboreal behaviors on Flores was a catalyst for these postcranial changes since these are traditionally linked to greater climbing capabilities. Yet, the stiff foot, adducted hallux, and uncurved phalanges do not particularly support this locomotion mode.

If *H. habilis* was the ancestor of *H. floresiensis*, then many features of the cranium (and some dentognathic traits) evolved in parallel in *H. floresiensis* and *H. erectus*. Specifically, overall cranial shape as well as features such as thick parietal bones, a low and wide occipital squama with moderate flexion, and a shallow palate are shared in the two species. Further, reduction of the crown size of the mandibular molars, scaling of the molars (M_1>M_2>M_3), and a few mandibular traits would also be homoplasies in *H. floresiensis* and *H. erectus*. Although it is unclear what single selective pressure would result in parallel evolution of all of these features in both species, it is possible that not all of these features were the independent objects of selection. Cranial shape is integrated across hominins (Lieberman *et al.*, 2002; Bookstein *et al.*, 2003; Gunz & Harvati, 2007) and "robust" cranial features are both intercorrelated and covary with cranial shape within *H. sapiens* (Lahr & Wright, 1996; Baab *et al.*, 2010). This leaves open the possibility that multiple cranial traits shared between *H. erectus* and *H. floresiensis* arose via selection on one or a few traits via integrating mechanisms. If *H. habilis*, or a closely related form, was ancestral to both *H. floresiensis* and *H. erectus*, then similar selective pressures might be expected to produce a parallel outcome given the similar starting point.

Body size reduction

Stature and body mass estimates for *H. floresiensis* and Plio-Pleistocene *Homo* species are in Table 2. I am unaware of any body mass estimates for Asian *H. erectus* based on postcranial dimensions. Ranges are wide for both parameters for most species. If the OH 62 stature estimate for *H. habilis* of 118 cm is correct, then the LB1 stature of ~106 cm would require only a small decrease from a *H. habilis* ancestor. *H. erectus* ancestry implies a considerable reduction in height ranging from 51-79 cm (African), 37-58

Tab. 2 - Stature and body mass estimates for *H. floresiensis* and Plio-Pleistocene *Homo* based on postcranial dimensions.

SPECIES AND INCLUDED FOSSILS	STATURE (CM)	BODY MASS (KG)
Homo floresiensis	>100-109	33, 36
LB1	101-109	33, 36 (range: 30-41)
Homo habilis	118	31-33
OH 62	118	33, 25
OH 8		31
OH 35		31.8
KNM-ER 3735		*46*
Homo rudolfensis	147-152	46-61
KNM-ER 1472	*150, 149-152*	*52, 47, 50*
KNM-ER 1481	*148, 147-151*	*61, 46, 57*
African *Homo erectus*	157-180	51-68
KNM-ER 736	180	68, 62
KNM-ER 737	157-167	52
KNM-ER 803	150	
OH 34	157-162	51
OH 28	165-171	54
KNM-ER 3228		67, 64
BSN49/P27 (Gona)		*33, 40*
KNM-WT 15000	*163 / 185*	*78, 68*
KNM-ER 1808	*181*	63, 59
KNM-ER 803	*150*	
Georgian *Homo erectus*	143-164	40-53
D4167 / D3901	145-164	53, 48-50
D3442 (1st metatarsal)	143	40
Asian *Homo erectus*	141-158	
Zhouk I	150, 141	
Zhouk IV	150, 154	
Ngandong B	158	
Trinil I	*163, 170*	
Trinil II	*167*	
Trinil III	*162*	

Estimates are from lower limb elements only based on reported values from the literature, with different estimates for the same fossils separated by commas (Santa Luca, 1980; Feldesman & Lundy, 1988; Leakey *et al.*, 1989; McHenry, 1991; McHenry, 1992; Hartwig-Scherer, 1993; Ruff & Walker, 1993; Ruff *et al.*, 1997; Antón *et al.*, 2007; Lordkipanidze *et al.*, 2007; Simpson *et al.*, 2008; Jungers & Baab, 2009; Aiello, 2010; Graves *et al.*, 2010; Ruff, 2010b). *H. floresiensis* stature estimates provided by B. Jungers pers. comm. based on the femur and the femur+tibia using modern human pygmies as the reference population. *Italics* imply uncertainties about the estimate or the taxonomic attribution of the fossil.

cm (Georgian) or 35-64 cm (Asian). The point estimates for body mass in LB1 based on lower limb elements are 33 and 36 kg, which are close to the *H. habilis* estimates and below those for *H. rudolfensis* and *H. erectus.* The average body mass of *H. erectus* implies a substantial body mass decrease from a *H. erectus* ancestor. However, if Gona accurately reflects the small end of the body range for *H. erectus* (Simpson *et al.*, 2008; Ruff, 2010a), then even a *H. erectus* ancestor may not imply a great deal of body mass reduction.

Brain evolution

EV in *H. erectus* varies from 646-1251 cm^3, considerably larger than that of LB1. Martin *et al.* (2006a, 2006b) argued that applying intraspecific brain:body scaling relationship to the "average" *H. erectus* predicts body masses ranging from <0.001 to 11.8 kg (and 6 kg using just the Dmanisi subsample) based on an EV of ~400 cm3 for LB1. They interpreted this to mean that non-pathological scaling mechanisms (e.g., island dwarfing) were unlikely to have resulted a LB1 hominin. The intraspecific scaling relationship for humans used by Martin *et al.* (2006b) was based on a single, modern population from Denmark.

Kubo *et al.* (2013) revised the LB1 EV upward to 426 cm^3 and used a geographically variable human sample to estimate the brain:body scaling relationship in humans. When this relationship was applied to *H. habilis* and early Indonesian *H. erectus*, the predicted brain masses for a hominin the size of LB1 were 447-449 cm^3 and 522-585 cm^3, respectively. Therefore, if early Indonesian *H. erectus* was the source population for *H. floresiensis*, an additional 10-29% of brain size reduction occurred above and beyond that predicted by intraspecific scaling. Weston & Lister (2009) provide a rare example of insular dwarfing on this scale (~30%) for Malagasy hippopotamuses.

Montgomery (2013) demonstrated the LB1 brain and body masses are consistent with scaling relationships based on mainland and island primate species rather than intraspecific scaling. However, most body mass estimates based on a *H. erectus* ancestor for LB1 were below 33-36 kg. Together, this suggests that while brain:body mass scaling may not present an impediment to the theory of island dwarfing for *H. floresiensis*, it does implicate selection specifically for reduced brain mass rather than just small body size.

Biogeography

A pre-*H. erectus* ancestry for *H. floresiensis* has important repercussions for hominin biogeography. The oldest hominin site known outside of Africa in Dmanisi, Georgia, contains fossils of early *H. erectus*. The presence of a *H. habilis* lineage on Flores may imply an earlier and as of yet undocumented migration out of Africa prior to the origin of *H. erectus* at 1.9 Ma. Alternatively, if the ancestor of *H. floresiensis* was not *H. habilis* but another closely related early *Homo* species that is yet undiscovered in Africa, or if *H. habilis* persisted in Africa longer than is currently documented, then the migration could have occurred at a later time. In either case, the late Pliocene / early Pleistocene hominin paleontological record would be incomplete.

If *H. floresiensis* was descended from Indonesian *H. erectus*, then probable ancestral populations can be found on nearby Java. However, there has been a suggestion that the regional ocean currents, which are primarily north to south (the "Indonesian Throughflow") would have limited eastward migration of hominins and that a more likely place to look for the ancestors of *H. floresiensis* is north, on Sulawesi (Morwood & Jungers, 2009) which does not currently have any fossil hominin sites. Interestingly, some of the craniodental and mandibular evidence (Morwood *et al.*, 2005; Gordon *et al.*, 2008; Baab & McNulty, 2009; Lyras *et al.*, 2009) points to an earlier *H. erectus* population as the possible ancestor, although this pattern is complicated by the confounding effect of size (Kaifu *et al.*, 2008; Baab, 2010) such that similarities between the LB1 cranium and smaller African / Georgian *H. erectus* individuals may not imply an especially close phylogenetic relationship. However, if correct, this implies an earlier migration of a more primitive population of *H. erectus* to Southeast Asia than is currently documented on Java.

Conclusions

Establishing whether the *H. floresiensis* lineage diverged from *H. erectus* or an earlier *Homo* species remains challenging due to uncertain distributions of characters in *H. erectus* or early *Homo* and conflicting signals from the remaining characters, some of which appear primitive and others derived for *H. erectus*. I suggest that the postcranial traits that are seemingly more primitive in *H. floresiensis* than *H. erectus* may represent convergences on the early *Homo* or australopith morphology, possibly due to the reintroduction of climbing in the locomotor repertoire of *H. floresiensis*. Similarly, the australopith-like features of the mandible may be due to a functional shift to tougher foods on Flores. I find these explanations marginally more palatable than parallel evolution of many more cranial traits, as well as few mandibular and dental traits, in *H. floresiensis* and *H. erectus* as the majority are not clearly linked to functional roles. Greater clarity regarding the evolutionary history of *H. floresiensis* may come from a more complete understanding of conditions under which evolutionary convergence occur, and the functional underpinnings and morphological integration of cranial anatomy in Plio-Pleistocene *Homo*. Future fossil discoveries of early *Homo* and *H. erectus* will undoubtedly refine our knowledge of character state distribution in *Homo* and provide additional evidence regarding the origin of *H. floresiensis*. More detail concerning the local environment of Flores may provide additional insights into possible selective pressures shaping *H. floresiensis* morphology.

A *H. erectus* ancestry accords better with the current biogeographical evidence, but implies some degree of body size reduction and more marked brain size reduction. Insular dwarfism is known to occur in mammals on islands, including primates, although I interpret the scale of brain size reduction in LB1 as indicative of selection specifically for a small brain in addition to small bodies. Ancestry from an early African/Georgian, rather than Indonesian, *H. erectus* population would entail less body/brain size reduction, but implies that a more primitive population inhabited Southeast Asia than currently documented in the fossil record. *H. erectus* ancestry also implies evolutionary reversals, particularly in the postcranial skeleton, that may themselves be informative about behavioral and functional alterations that occurred along this lineage, as already discussed.

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