



The affinities of *Homo floresiensis* based on phylogenetic analyses of cranial, dental, and postcranial characters[☆]



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ABSTRACT

Although the diminutive *Homo floresiensis* has been known for a decade, its phylogenetic status remains highly contentious. A broad range of potential explanations for the evolution of this species has been explored. One view is that *H. floresiensis* is derived from Asian *Homo erectus* that arrived on Flores and subsequently evolved a smaller body size, perhaps to survive the constrained resources they faced in a new island environment. Fossil remains of *H. erectus*, well known from Java, have not yet been discovered on Flores. The second hypothesis is that *H. floresiensis* is directly descended from an early *Homo* lineage with roots in Africa, such as *Homo habilis*; the third is that it is *Homo sapiens* with pathology. We use parsimony and Bayesian phylogenetic methods to test these hypotheses. Our phylogenetic data build upon those characters previously presented in support of these hypotheses by broadening the range of traits to include the crania, mandibles, dentition, and postcrania of *Homo* and *Australopithecus*. The new data and analyses support the hypothesis that *H. floresiensis* is an early *Homo* lineage: *H. floresiensis* is sister either to *H. habilis* alone or to a clade consisting of at least *H. habilis*, *H. erectus*, *Homo ergaster*, and *H. sapiens*. A close phylogenetic relationship between *H. floresiensis* and *H. erectus* or *H. sapiens* can be rejected; furthermore, most of the traits separating *H. floresiensis* from *H. sapiens* are not readily attributable to pathology (e.g., Down syndrome). The results suggest *H. floresiensis* is a long-surviving relict of an early (>1.75 Ma) hominin lineage and a hitherto unknown migration out of Africa, and not a recent derivative of either *H. erectus* or *H. sapiens*.

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1. Introduction

The taxonomic status of *Homo floresiensis* (Brown et al., 2004) has been controversial since the species was announced. The strata in which the remains were found are dated to between 65 ± 5 and 89 ± 7 thousand years ago (ka), while the ulna of Liang Bua 1 (LB1) is dated to between 86.9 ± 7.9 and 71.5 ± 4.3 ka and the ulna of LB6 is slightly younger (Sutikna et al., 2016). Fragmentary material from Mate Menge, Flores, dated at ~700 ka has also recently been discovered and provisionally referred to the *H. floresiensis* lineage (Brumm et al., 2016; Van den Bergh et al., 2016). Bones that have been placed in the *H. floresiensis* hypodigm have been interpreted in

three broad ways: 1) that *H. floresiensis* is a distinct species and derived from an early lineage of *Homo* (e.g., Brown et al., 2004; Falk et al., 2005; Morwood et al., 2005; Argue et al., 2006, 2009; Larson et al., 2007; Tocheri et al., 2007; Brown and Maeda, 2009; Jungers et al., 2009b; Brown, 2012); 2) that *H. floresiensis* is a distinct species, derived from Asian *Homo erectus* (Kaifu et al., 2011, 2015; Van den Bergh et al., 2016); and 3) that it is not a valid species, but is instead a pathological population of anatomically modern humans (i.e., *Homo sapiens*) that had genetic or metabolic disorders (e.g., Henneberg and Thorne, 2004; Jacob et al., 2006; Martin et al., 2006; Richards, 2006; Hershkovitz et al., 2007; Obendorf et al., 2008; Oxnard et al., 2010, 2012; Henneberg et al., 2014; for reviews to the contrary, see Groves, 2007; Aiello, 2010; Van Heteren, 2013). White (2010) mused that one might also want to consider the possibility that the unique anatomy and small body size might be the unusual result of founder effect and rapid genetic drift in a small population of modern humans colonizing Flores. However, modern humans

[☆] This paper is dedicated to the memory of our late friend and colleague, Professor Mike Morwood.

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have dwarfed repeatedly around the world and none converge on the unique proportions and anatomy of *H. floresiensis* (Jungers et al., 2016).

The hypothesis that *H. floresiensis* represents a modern human population with a genetic disorder has not withstood testing (Argue et al., 2006, 2009; Falk et al., 2007, 2009; Jungers et al., 2009b; Aiello, 2010; Brown, 2012; Baab et al., 2013, 2016; Van Heteren, 2013). The most recent iteration of these kinds of hypotheses proposes that LB1 had Down syndrome (Henneberg and Thorne, 2004). Baab et al. (2016), however, found minimal congruence between the phenotype of LB1 and clinical descriptions of Down syndrome, and that *H. floresiensis* remains a phenotypically unique, valid species with its roots in Plio-Pleistocene *Homo* taxa. We also test whether the phylogenetic position of *H. floresiensis* we obtained is attributable to Down syndrome, using similar reasoning to Dembo et al. (2015), who note that if Liang Bua 1 had Down syndrome, it should have characters diagnostic of this syndrome and characters that align it with *H. sapiens*.

Insular dwarfing has been invoked to explain the morphology of *H. floresiensis* from a *H. erectus*-like predecessor. The 'island rule' for insular dwarfing (Foster, 1964; Alcover, 1976; Sondaar, 1977; Dayan and Simberloff, 1998; Köhler and Moyà-Solà, 2004) stipulates that body size of mammals alters when a founder population reaches an island, becomes reproductively separated from its mainland group, and faces an environment different from those of its mainland sister species. For example, a smaller body size would be expected as a response to a limited food supply, and a larger size to the absence of predation (Foster, 1964). Studies that focus on this phenomenon have disputed the universality of this 'rule' (Sondaar, 1977; Heaney, 1978; Wassersug et al., 1979; Lawlor, 1982; Melton, 1982; Libois et al., 1993; Dayan and Simberloff, 1998; Meiri et al., 2008), but it remains the case that rapid insular changes in body size are very common (Millien, 2006).

Van Heteren (2008) argued that the island dwarfing process in large animals typically produces paedomorphic characters, i.e. retention of juvenile characteristics. Van Heteren (2008) therefore tested for paedomorphic features in *H. floresiensis* and found that its orbital index falls within the range of *H. erectus* children but not *H. erectus* adults: in particular she proposed that the high orbital, dental, and brachial indices, low humeral and low tibial torsions, high gonial angle, and shortened lower limbs in *H. floresiensis* may be explained by paedomorphosis occurring in the dwarfing process of *H. erectus*, but that additional adaptations also occurred, such as the relatively small brain (to lower the daily energy requirements), while the relatively short legs and broad pelvis were adaptations to low gear locomotion and to increase stability on uneven ground (Van Heteren, 2012). There are numerous problems with this heterochronic explanation, including its generality. Paedomorphic hominids should have relatively large crania (Godfrey and Sutherland, 1996), and LB1's skull is remarkably small relative to any measure of body size. Moreover, no member of the genus *Homo* at any age of development has limb proportions comparable to LB1 (Jungers, 2013).

Lyras et al. (2009) performed a principal components analysis and cluster analysis of shape as represented by digitized landmarks of a stereolithographic replica of the LB1 cranium and of cranial casts of *H. erectus* Sangiran 17, *Homo habilis* KNM-ER 1813, and *Australopithecus africanus* STS 5; they calculated Euclidean distances among the specimens. Their results (Lyras et al., 2009: Fig. 3) show that *H. floresiensis* clusters with *H. habilis* on Function 1 (contrary to their interpretation that *H. floresiensis* clusters with *H. erectus*), while Function 2 and Function 3 do not discriminate between *H. sapiens*, *H. erectus*, *H. floresiensis*, or *A. africanus*. In their weighted pair group method of arithmetic means (Euclidean distances), however, *H. erectus* and *H. floresiensis* cluster.

Kaifu et al. (2011) undertook a detailed morphometric and morphological comparison of the LB1 cranium with *H. habilis* sensu lato (comprising KNM-ER 1470, KNM-ER 1590, KNM-ER 1805, KNM-ER 1813, KNM-ER 3732, KNM-ER 3735, KNM-ER 7330, OH 24), *H. erectus* sensu stricto (Sangiran and Trinil crania), and the Dmanisi group (putative *Homo georgicus*). Using 67 cranial characters that they observed on *H. floresiensis*, they tested four hypotheses: that *H. floresiensis* was descended from *H. habilis*, that it descended from the Dmanisi group, that it originated from something similar to early Indonesian *H. erectus* and subsequently dramatically dwarfed in body and brain size, and that *H. floresiensis* was not related to any of these species. Assessing the number of cranial characters that exclusively supported each hypothesis, they found that only three traits support a relationship between *H. floresiensis* and *H. habilis*; no characters exclusively support a hypothesis for a relationship between *H. floresiensis* and Dmanisi; and 17 characters supported, or are compatible with, the hypothesis that *H. floresiensis* was derived from early Javanese *H. erectus*. More recently, Kaifu et al. (2015) reiterated this hypothesis based upon a comparative study of the dentition. A re-evaluation of the endocranial value of 417 cc for LB1 (Falk et al., 2005) to 426 cc by Kubo and colleagues (2013), based upon micro-CT scans, led them to also prefer the view that *H. floresiensis* was an island dwarf form of *H. erectus*, while acknowledging the possibility that *H. floresiensis* may have dwarfed from a *H. habilis*-like species.

The island rule relates to changes in overall body mass and does not necessarily predict whether specific body regions would be most affected. Changes in body mass may be achieved in different ways, such as brain, gut, and kidney being traded-off against one another. Nor can we predict specific changes in brain volume or limb morphology after isolation on an island, because this will depend on the selective pressures involved (Niven, 2007). This notwithstanding, the question of allometric scaling of *H. erectus* in relation to *H. floresiensis* has been investigated and this explanation was abandoned early on by Morwood et al. (2005). Falk et al. (2005) showed that the brain:body size of *H. floresiensis* scales with australopith species, even though its endocranial shape is similar to Chinese *H. erectus* (Indonesian *H. erectus* was not examined). Gordon et al. (2008) scaled six cranial vault measurements to identify the best fit between the LB1 cranium and fossil hominin groups, finding that *H. floresiensis* scaled with *H. habilis*, Dmanisi hominin D2700, and Koobi Fora cranium KNM-ER 3733 (*Homo ergaster*), and not with *H. erectus* (Sangiran 17). Baab and McNulty (2009) explored the relationship between cranial size and shape, and showed that the morphology of the LB1 cranium is consistent with the expected shape for a very small specimen of archaic *Homo* and quite distinct from the modern human sample. The high humerofemoral index (limb proportions) for *H. floresiensis* has also been supposed to be a consequence of its extreme small body size, on the assumption that there exists a negative correlation between overall body size and limb length (e.g., Richards, 2006; Holliday and Franciscus, 2009). To test this hypothesis, Jungers (2009) examined limb proportions of a range of modern humans, including pygmoids, and *Australopithecus afarensis* (AL 288-1), *H. ergaster* (KNM-WT 15000), and *H. floresiensis*. He discovered that intraspecific covariation between limb proportions and body size in *H. sapiens* was statistically insignificant, so there is no evidence for a biological 'rule' relating body size to limb proportions; and that *A. afarensis* and *H. floresiensis* fell well outside the range of all human samples, including the small-bodied people. He tested this result in a number of ways; the results led him to conclude that the unusual limb proportions of *H. floresiensis* are not simply size-related allometries that follow a scaling model for modern humans (which in any case had little support), but can be explained as primitive re-tentions (also see Jungers et al., 2016).

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