



New wrist bones of *Homo floresiensis* from Liang Bua (Flores, Indonesia)

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ABSTRACT

The carpals from the *Homo floresiensis* type specimen (LB1) lack features that compose the shared, derived complex of the radial side of the wrist in Neandertals and modern humans. This paper comprises a description and three-dimensional morphometric analysis of new carpals from at least one other individual at Liang Bua attributed to *H. floresiensis*: a right capitate and two hamates. The new capitate is smaller than that of LB1 but is nearly identical in morphology. As with capitates from extant apes, species of *Australopithecus*, and LB1, the newly described capitate displays a deeply-excavated nonarticular area along its radial aspect, a scaphoid facet that extends into a J-hook articulation on the neck, and a more radially-oriented second metacarpal facet; it also lacks an enlarged palmarly-positioned trapezoid facet. Because there is no accommodation for the derived, palmarly blocky trapezoid that characterizes *Homo sapiens* and Neandertals, this individual most likely had a plesiomorphically wedge-shaped trapezoid (like LB1). Morphometric analyses confirm the close similarity of the new capitate and that of LB1, and are consistent with previous findings of an overall primitive articular geometry. In general, hamate morphology is more conserved across hominins, and the *H. floresiensis* specimens fall at the far edge of the range of variation for *H. sapiens* in a number of metrics. However, the hamate of *H. floresiensis* is exceptionally small and exhibits a relatively long, stout hamulus lacking the oval-shaped cross-section characteristic of human and Neandertal hamuli (variably present in australopiths). Documentation of a second individual with primitive carpal anatomy from Liang Bua, along with further analysis of trapezoid scaling relative to the capitate in LB1, refutes claims that the wrist of the type specimen represents a modern human with pathology. In total, the carpal anatomy of *H. floresiensis* supports the hypothesis that the lineage leading to the evolution of this species originated prior to the cladogenetic event that gave rise to modern humans and Neandertals.

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Introduction

The discovery in 2003 of a partial hominin skeleton from the late Pleistocene deposits at Liang Bua on the Indonesian island of Flores sparked broad scientific and public interest (Brown et al., 2004; Morwood et al., 2004, 2005, 2009; see also Aiello [2010] for a recent review). The attribution of these remains to a new hominin taxon, *Homo floresiensis*, has received wide support due to the mosaic combination of primitive and derived features observable in its skull, endocast, and postcranium (Brown et al., 2004;

Morwood et al., 2005; Falk et al., 2005, 2007, 2009a,b; Argue et al., 2006, 2009; Tocheri et al., 2007, 2008; Larson et al., 2007, 2009; Gordon et al., 2008; Baab and McNulty, 2009; Brown and Maeda, 2009; Jungers et al., 2009a, b; Jungers and Baab, 2010; Kaifu et al., 2011). However, a few skeptics have argued that these skeletal remains represent modern *Homo sapiens* that exhibit a systematic growth disorder or pathology (Henneberg and Thorne, 2004; Jacob et al., 2006; Martin et al., 2006; Hershkovitz et al., 2007; Obendorf et al., 2008; Rauch et al., 2008; Oxnard et al., 2010) or can be alternatively explained by processes underlying normal human variation (Richards, 2006). Thus, two main debates have emerged in relation to *H. floresiensis*. The first involves whether these remains represent a hominin species distinct from modern *H. sapiens* or modern humans with atypical morphology

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due to disease, pathology, or disorder; the second acknowledges *H. floresiensis* as a valid taxon, but addresses whether or not this taxon evolved from *Homo erectus sensu stricto* (i.e., Asian *H. erectus*—the only other fossil hominin species currently known from Indonesia) and the specific evolutionary processes involved (Bromham and Cardillo, 2007; Niven, 2007, 2008; van Heteren and de Vos, 2007; van Heteren, 2008, 2011; van Heteren and Sankhyan, 2009; Baab and McNulty, 2009; Morwood and Jungers, 2009; Lyras et al., 2009; Jungers and Baab, 2010; Kaifu et al., 2011).

The wrist morphology of the *H. floresiensis* type specimen (LB1) has played a key role in addressing the first issue (Tocheri et al., 2007, 2008; Larson et al., 2009) but is not yet relevant to the second phylogenetic issue due to a lack of comparative evidence from *H. erectus sensu lato*. LB1's wrist bones include an intact capitate, scaphoid, and trapezoid, and portions of the lunare and hamate, all from the left side (Tocheri et al., 2007; Larson et al., 2009). Three-dimensional (3D) morphometric analyses of the intact bones indicate that the shared, derived shape and articular configuration of the radial side of the wrist exhibited by modern humans and Neandertals is not present in the carpus of *H. floresiensis* (Tocheri et al., 2007). The carpal complex of modern humans and Neandertals involves a palmar broadening and repositioning of the trapezoid along with concomitant changes to the surrounding bones, including novel enlargement of a palmarly-placed trapezoid-capitate articulation, and trapezoid and trapezium facets that engulf the full distoradial aspect of a somewhat supinated scaphoid tubercle. This derived complex of features is thought to facilitate obliquely oriented transarticular loading resulting from strong contraction of the thumb musculature during intensified manipulative behaviors (Lewis, 1989; Tocheri, 2007). Partial evidence of the derived complex is present in an ~800,000 year old capitate from the site of Gran Dolina (attributed to *Homo antecessor* by Lorenzo et al., 1999), but other earlier fossil hominin carpals and metacarpals attributed to *Australopithecus* spp. and *Homo habilis* suggest that the full complex was not yet present (Napier, 1962; Marzke, 1983, 1997; Lewis, 1989; Tocheri, 2007; Tocheri et al., 2008; Kivell et al., 2011). Given this evidence, the lineage that gave rise to *H. floresiensis* most likely predates the origin of the modern human/Neandertal-like radial carpal complex, suggesting that it is more than 800,000 years old (Tocheri, 2007; Tocheri et al., 2007, 2008). Hominins were present on Flores by one million years ago (Brumm et al., 2010), which is consistent with such a hypothesis of divergence.

Although the trapezoid, capitate, and scaphoid of LB1 are strikingly similar to those of extant African apes and early hominins, LB1 is only one individual, and it remains to be demonstrated whether such primitive wrist anatomy is typical of the population sampled in late Pleistocene deposits at Liang Bua. In 2009, one of us (MWT) examined all unidentified bone material excavated in 2003 and 2004 from Sectors VII and XI at Liang Bua. Three additional carpal bones were identified; one is a mostly intact right capitate (LB20), and the other two are left and right partial hamates (LB21 and LB22). These carpals were excavated in 2004 and were recovered from between 4.95 and 5.15 m depth of Sector XI (Fig. 1). The stratigraphic unit from which the new carpals were recovered contained considerable hominin and non-hominin skeletal material, including the mandible and postcranial remains attributed to individual LB6. This unit is approximately 1 m above and 1 m south from where the LB1 partial skeleton was recovered and over 2 m beneath the layer of black tuffaceous silts (BTS)—the last erosion of which occurred at least 17,000 years ago (Morwood et al., 2009; Roberts et al., 2009).

Including a fragmentary left hamate (LB1–46) directly associated with the type specimen (Larson et al., 2009), there are now three *H. floresiensis* hamates (two left, one right) from Liang

Bua; thus, the remains of at least two individuals have been recovered for which wrist material is preserved. Although the new LB20 is a right capitate and that associated with the type skeleton (capitate specimen LB1–45) is a left, these two bones certainly represent different individuals. The new capitate is considerably smaller than LB1–45 and is most likely associated with the new hamates (LB21 and LB22) as it articulates well with the right hamate and was found in the same stratigraphic context. The LB21 and LB22 specimens are well matched in size and morphology, found in close proximity to one another, and probably come from the same individual. Although these new carpals have been given unique identification numbers (LB20, LB21, and LB22), their close association with remains attributed to specimen LB6 (mandible and postcranial elements including a metacarpal and manual phalanges; see Morwood et al., 2005; Larson et al., 2009) suggests that they probably belong to this individual.

Here we describe these additional *H. floresiensis* carpals from Liang Bua and present the first quantitative comparative analyses of their morphology. The taxonomic, phylogenetic, and functional implications of these specimens are considered along with further discussion of the previously published wrist bones of *H. floresiensis*. A secondary goal is to address specific concerns about the *H. floresiensis* wrist raised by other workers who support the position that the morphology of these carpal remains results from disease, pathology, or other abnormality.

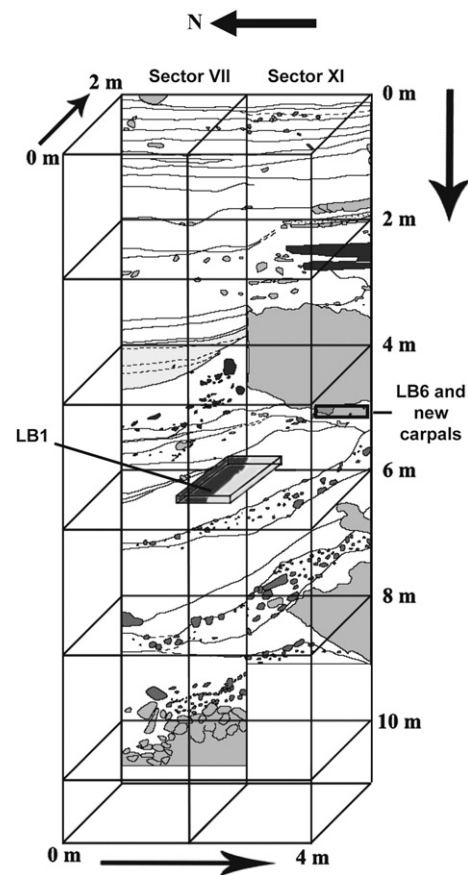


Figure 1. Stratigraphic context of the Liang Bua carpal specimens. The cranium, mandible, and postcranial material of LB1, including the wrist bones, were recovered in 2003 from Sector VII, whereas in 2004 more limb elements of LB1 were recovered from Sector XI (dark and light rectangles show the respective approximate positions of recovery). Elements attributed to a second, smaller individual (LB6) were recovered from spits 50–53 of Sector XI. The new carpals (LB 20, 21, and 22) also derive from these spits from sediments in the southeast corner of Sector XI (black rectangle).

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