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The Primitive Wrist of *Homo floresiensis* and Its Implications for Hominin Evolution

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Whether the Late Pleistocene hominin fossils from Flores, Indonesia, represent a new species, *Homo floresiensis*, or pathological modern humans has been debated. Analysis of three wrist bones from the holotype specimen (LB1) shows that it retains wrist morphology that is primitive for the African ape-human clade. In contrast, Neandertals and modern humans share derived wrist morphology that forms during embryogenesis, which diminishes the probability that pathology could result in the normal primitive state. This evidence indicates that LB1 is not a modern human with an undiagnosed pathology or growth defect; rather, it represents a species descended from a hominin ancestor that branched off before the origin of the clade that includes modern humans, Neandertals, and their last common ancestor.

The debate over the affinity of the Late Pleistocene hominin fossils from the island of Flores has focused primarily on the craniodental remains of the first specimen (LB1) recovered from Liang Bua cave (1–6). LB1 is the holotype specimen of a new species, *Homo floresiensis* (1, 7), but some argue that it is a pathological modern human (4, 6). Here we examine the morphology of three wrist bones attributed to LB1 to test these competing hypotheses.

Wrist morphology can be a powerful indicator of phylogenetic relationships in Mammalia because of variation in the number and shape of

carpal elements and in the configuration of the articular surfaces (8–12). In primates, the trapezoid is the wrist bone situated directly proximal to the index finger. The modern human trapezoid is shaped like a boot (9, 13, 14), wherein the palmar half of the bone is radio-ulnarly and proximo-distally wide (Fig. 1). In contrast, other primates have a trapezoid that is more wedge-shaped with a narrow palmar tip and a wide dorsal base (9, 13–15). This difference between human and nonhuman primate trapezoid shape is concomitantly reflected by the shapes and articular configurations of the carpals that articulate with the trapezoid, and all of these carpals are derived in modern humans in comparison to those in other primates (Figs. 2 and 3) (9, 13). Upper Paleolithic *Homo sapiens* and Neandertals share these derived morphological features with modern humans, suggesting that they are most likely inherited from a recent common ancestor (13). A capitate attributed to *Homo antecessor* (16) and dated to ~0.8 million years ago (Ma) (17) also shares the derived condition (13, 16). Thus, the current paleontological evidence suggests that this complex of wrist features evolved by at least 800,000 years ago.

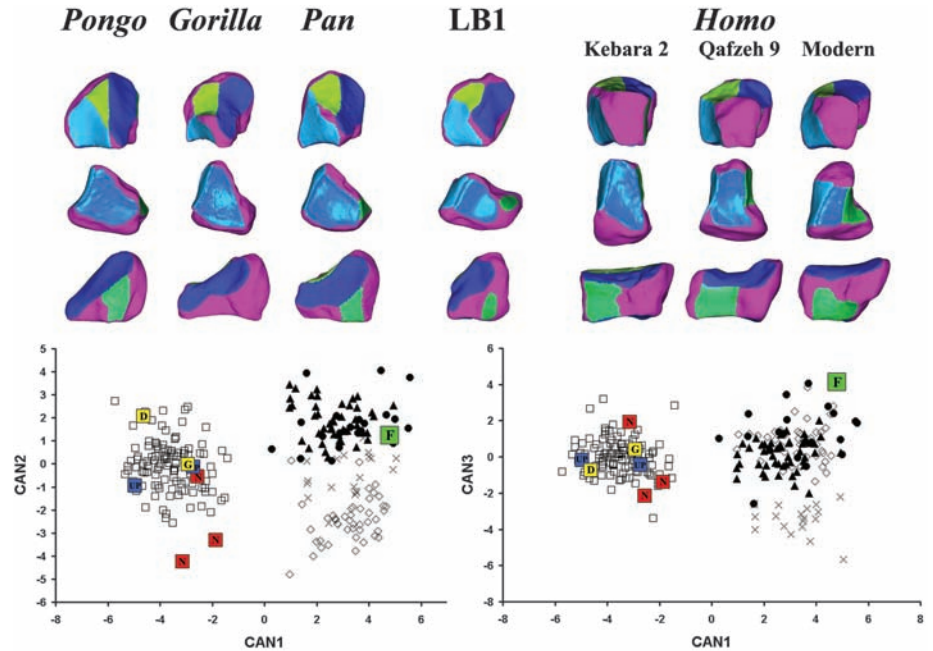
Three complete carpals—a trapezoid, scaphoid, and capitate—all of which are from a left wrist, were recovered along with the cranium, mandible, and additional postcranial material of LB1 in Spit No. 59 of Sector VII during the September 2003 excavation (fig. S1 and table S3) (1, 2, 18). Each is well preserved and shows no signs of pathology or abnormal development. As shown in Figs. 1 to 3, these three articulating bones display none of the shared, derived features of modern human and Neandertal carpals (13). Instead, they show the general symplesiomorphic pattern exhibited by all extant African apes, as well as fossil hominins that preserve comparable wrist morphology and date before 1.7 Ma (13, 19–22). Like other nonhuman primates, LB1's trapezoid is (i) wedge-shaped; (ii) the ulnar side of its second metacarpal articulation is oriented more sagittally (Fig. 1, top and bottom rows); (iii) its scaphoid articular surface is more triangular in shape (Fig. 1, middle row); and (iv) it lacks the expanded palmar non-articular area (Fig. 1, top row) and the more palmarly placed capitate articulation observed in modern humans and Neandertals (Fig. 1, bottom row). We quantified these shape differences using three-dimensional (3D) methods measuring the relative areas and angles of carpal articular surfaces (13, 14, 18, 23). Multivariate statistical analysis of these data distinguishes modern humans and Neandertals from the great apes, *Papio*, and LB1 (Fig. 1). Primarily, the trapezoids of modern humans and Neandertals are distinct in their shape and articular configuration as a consequence of the large expansion of palmar nonarticular area, which tends to square off the entire palmar half of the bone (Fig. 1, top row) (13).

The scaphoid and capitate of LB1 both exhibit the shapes and articular configurations that occur concomitantly with the primitive hominid trapezoid condition (13, 18), and multivariate analyses of these carpals provide similar results (Figs. 2 and 3). For example, LB1's capitate lacks the enlarged palmarly placed articular surface for the trapezoid observed in modern humans and Neandertals (9, 13) and, instead, shows the waisted neck characteristic of extant

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Fig. 1. (Top) Palmar (top row), proximal (middle row), and ulnar views (bottom row) of trapezoid morphology (the distal, palmar, and distal borders, respectively, shown toward the page top). All bones are scaled to approximately the same size and shown as from the left wrist. Articular surfaces are as follows: 2nd metacarpal (radial side), yellow; 2nd metacarpal (ulnar side), dark blue; capitate, green; trapezium, light blue; scaphoid, medium blue; nonarticular, pink. **(Bottom)** Plots of the canonical variables (CAN1 to CAN3) generated from 3D trapezoid shape analysis (13, 14, 18). CAN1 accounts for 76% of the variation, CAN2 accounts for 14%, and CAN3 8% (modern humans, open squares; *Pan*, closed triangles; *Gorilla*, open diamonds; *Pongo*, closed circles; *Papio*, X's; Upper Paleolithic *H. sapiens* (e.g., Qafzeh 9), blue squares (UP); Neandertals (e.g., Kebara 2), red squares (N); modern human pituitary dwarf, yellow square (D); modern human pituitary giant, yellow square (G); *H. floresiensis* (LB1), green square (F).



great apes and *Australopithecus* (Fig. 3, middle row) (20). Similarly, the articular surface for the trapezium on LB1's scaphoid does not extend out onto the scaphoid tubercle as it does in modern humans and Neandertals (Fig. 2, middle row) (13). However, LB1's scaphoid includes a fused centrale, as does the OH7 scaphoid from Olduvai Gorge (Fig. 2) (21, 24). Congenital fusion of these two carpal elements is a synapomorphy of *Gorilla*, *Pan*, and *Homo* (25), and the fossil evidence from LB1 and OH7 further indicates that fusion is the most likely primitive condition for all hominins.

The consistent carpal shape differences between human and nonhuman primates are the result of differences in the cavitation of the carpal mesenchyme during embryonic development (18, 26). In modern humans, the trapezoid, capitate, and trapezium arise in the mesenchyme in essentially their adult form by the 11th week of development, long before the processes of chondrification and ossification are complete, and the remaining carpal elements achieve their distinctive shapes shortly thereafter (26). Because of the timing of carpal formation, dysostoses (i.e., errors in cell patterning) or disruptions (i.e., through exposure to toxic substances or infection) may result in malformation of the initial carpal shape (27, 28). However, the transient characteristics of such disturbances most often produce localized skeletal shape abnormalities (e.g., individual bones are affected) that are not typically associated with skeletal dwarfism (27, 28). In contrast, dysplasias usually involve systemic errors in ossification and growth, frequently resulting in dwarfism (27, 28). The genes that result in dysplasias, however, do not normally become expressed until after normal shape formation of the carpal mesenchyme (27). Although skeletal dysplasias may include carpal

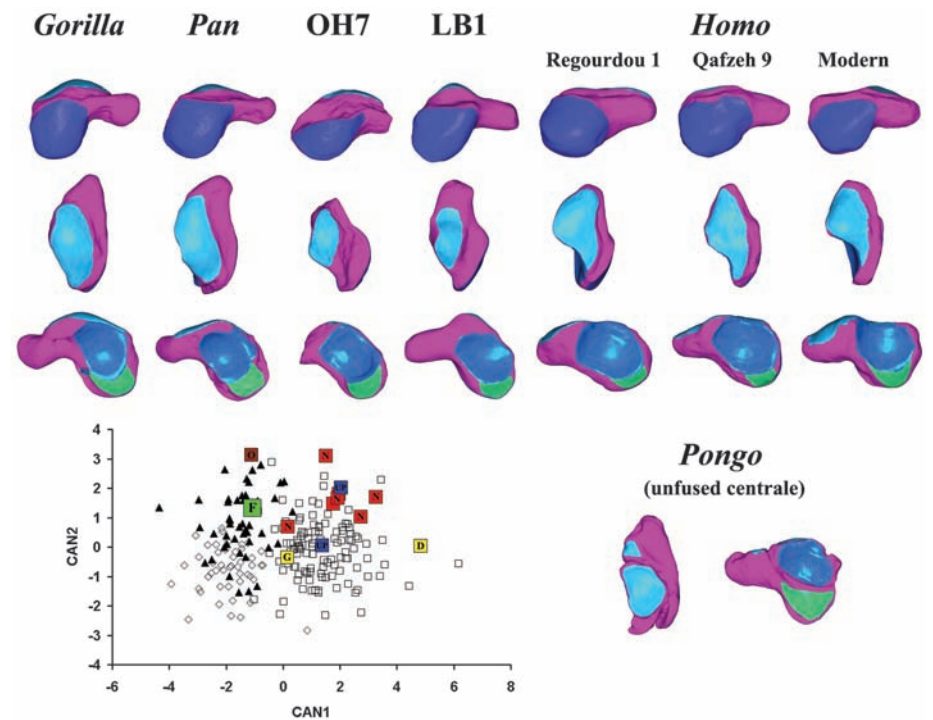


Fig. 2. (Top) Radial (top row), distal (middle row), and ulnar views (bottom row) of scaphoid morphology (the distal, palmar, and distal borders, respectively, shown toward the page top). All bones are scaled to approximately the same size and shown as from the left wrist. Regourdou 1 is a Neandertal. Articular surfaces are as follows: radius, dark blue; trapezium-trapezoid, light blue; capitate, medium blue; lunate, green; nonarticular, pink. **(Bottom left)** Plot of the canonical variables (CAN1, CAN2) generated from 3D scaphoid shape analysis (13, 18). CAN1 accounts for 89% of the variation, CAN2 accounts for 11% [symbols as in Fig. 1 plus *H. habilis* (OH7), brown square (O)]. **(Bottom right)** The separate centrale (the primitive condition in primates) is shown articulated with the scaphoid in *Pongo*.

and digit abnormalities related to ossification errors, as well as various forms of microcephaly (27), none are known to result in abnormal carpal

morphology that closely mimics a plesiomorphic state. Our diverse modern human sample includes a pituitary dwarf (USNM 314306) and a

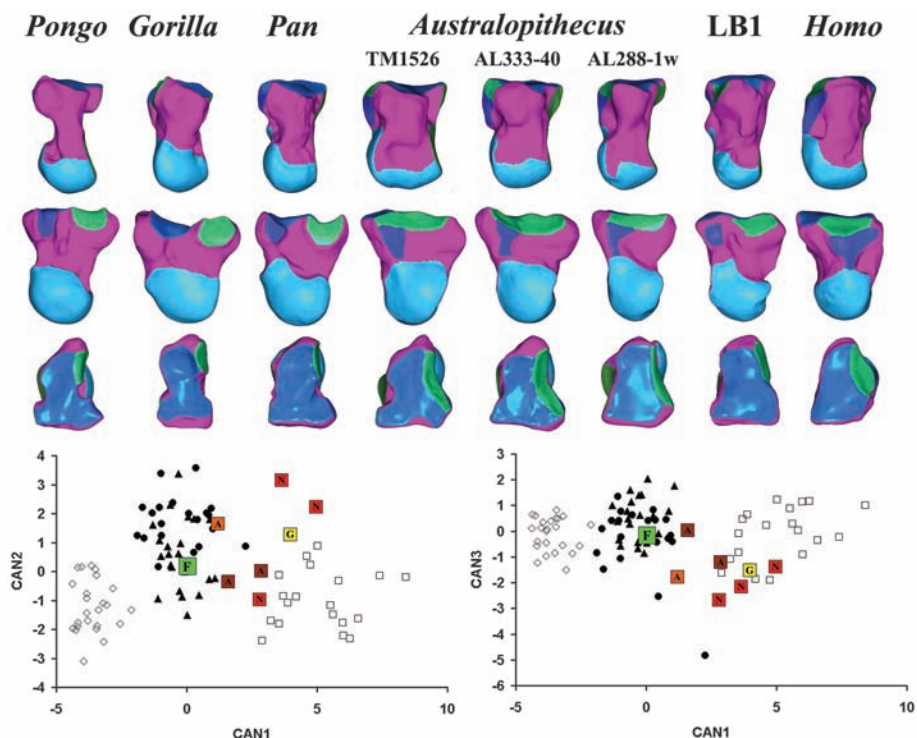


Fig. 3. (Top): Palmar (top row), radial (middle row), and distal views (bottom row) of capitate morphology (the distal, distal, and palmar borders, respectively, shown toward the page top). All bones are scaled to approximately the same size and shown as from the left wrist. Articular surfaces as follows: trapezoid, dark blue; scaphoid-lunate, light blue; 3rd metacarpal, medium blue; 2nd metacarpal, green; nonarticular, pink. **(Bottom)** Plots of the canonical variables (CAN1 to CAN3) generated from 3D capitate shape analysis (18). CAN1 accounts for 86% of the variation, CAN2 accounts for 13%, and CAN3 1% [symbols as in Fig. 1 plus *A. africanus* (TM1526), orange square (A); *A. afarensis* (AL333-40 and AL288-1w), brown squares (A)].

pituitary giant (USNM 227508) (tables S1 and S2). Both show normal modern human carpal shapes and articular configurations despite their abnormal sizes, demonstrating that LB1's wrist morphology is not the result of allometric scaling, errors in metabolism, or a skeletal growth disorder.

Our analyses support hypotheses that LB1 is descended from a hominin ancestor that migrated out of Africa before the evolution of the shared, derived wrist morphology that is characteristic of modern humans, Neandertals, and their last common ancestor. The association of LB1 with direct evidence of stone flaking technology comparable to that found at Oldowan or other Lower Paleolithic sites throughout the Old World (29) provides additional support for the hypothesis that the earliest hominins to use and make stone tools retained primitive hominin wrist morphology (13, 21, 30, 31). The structurally modified wrist of modern humans and Neandertals probably evolved sometime between 1.8 and 0.8 Ma (13). These structural modifications form a morphological complex that may represent an adaptation for better distribution of forces radio-ulnarly across the wrist to facilitate the full commitment to tool-related manipulative behaviors that arose in the

hominin lineage leading to modern humans and Neandertals (13).

The wrist morphology of LB1 may ultimately help falsify or support specific hypotheses regarding the phylogenetic position of *H. floresiensis* (1, 5, 7). Unfortunately, no carpals are attributed to *Homo erectus* sensu lato, which is otherwise well represented in the fossil record between 1.8 and 0.8 Ma, with the exception of a partial lunate from Zhoukoudian (32). However, if hominin carpals that date within this period of time are discovered, their primitive or derived morphology will allow a firmer assessment of their phylogenetic relationship to other Pleistocene hominin species, such as modern *H. sapiens* and *H. floresiensis*.

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