

The foot of *Homo floresiensis*

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Homo floresiensis is an endemic hominin species that occupied Liang Bua, a limestone cave on Flores in eastern Indonesia, during the Late Pleistocene epoch^{1,2}. The skeleton of the type specimen (LB1) of *H. floresiensis* includes a relatively complete left foot and parts of the right foot³. These feet provide insights into the evolution of bipedalism and, together with the rest of the skeleton, have implications for hominin dispersal events into Asia. Here we show that LB1's foot is exceptionally long relative to the femur and tibia, proportions never before documented in hominins but seen in some African apes. Although the metatarsal robusticity sequence is human-like and the hallux is fully adducted, other intrinsic proportions and pedal features are more ape-like. The postcranial anatomy of *H. floresiensis* is that of a biped¹⁻³, but the unique lower-limb proportions and surprising combination of derived and primitive pedal morphologies suggest kinematic and biomechanical differences from modern human gait. Therefore, LB1 offers the most complete glimpse of a bipedal hominin foot that lacks the full suite of derived features characteristic of modern humans and whose mosaic design may be primitive for the genus *Homo*. These new findings raise the possibility that the ancestor of *H. floresiensis* was not *Homo erectus* but instead some other, more primitive, hominin whose dispersal into southeast Asia is still undocumented.

Bipedalism is the derived hallmark of hominins^{4,5}, yet our understanding of its origins and subsequent evolution is incomplete. Associated postcranial elements are rare in the early part of the hominin fossil record^{5,6}, and relatively complete feet are rarer still. Although LB1 has been dated to the end of the Pleistocene^{1,3}, its feet shed new light on the evolution of bipedal gait and have important implications for hominin biogeography. The reassembled left foot is shown in Fig. 1 in both medial and dorsal view next to the associated right tibia and left femur.

It is possible to estimate the full length of LB1's foot (to the tip of the second digit) from the assembled partial foot, assuming a modern human template and using a regression analysis based on a large sample of complete modern human feet (Supplementary Fig. 1). The estimated skeletal length of LB1's left foot is 191 mm (95% prediction interval, 184–199 mm), indicating a fleshy-foot length⁷ of 196 mm (189–204 mm). As Fig. 1 shows, the foot of LB1 is very long relative to the femur and tibia. The ratio of fleshy-foot length to maximum femur length (280 mm in LB1; ref. 2) is 0.7 (0.68–0.73). The relative foot length in LB1 far exceeds the upper limits for modern humans of either average or short stature (Table 1) and instead overlaps with bonobos (*Pan paniscus*). It is also relatively longer than the estimate for *Australopithecus afarensis* (AL 288-1), which was based in part on an Early Pleistocene foot from Olduvai Gorge, Tanzania (OH 8)⁷. Because it is the distal-most segment in the lower-limb link system, a hominin foot of this relative length requires

compensatory kinematic adjustments at ankle, knee and/or hip joints to permit adequate clearance of the toes in the swing phase of walking and running (unless the toes were curled)⁸, and it probably places limits on running speed⁹. The relatively high foot-to-femur ratio, not unlike the high humerofemoral index², is driven primarily by an exceptionally short hindlimb (Supplementary Table 1).

The metatarsal robusticity sequence observed in LB1 follows the most common human formula, I > V > IV > III > II (refs 3, 10). The orientation of the virtually flat and mutually articulating surfaces of the entocuneiform and hallucal metatarsal indicate that the big toe was fully adducted and in line with the other metatarsals. However, in comparison with the lesser metatarsals, the hallucal metatarsal is short; its relative length falls below the range observed in modern humans but is within the range characteristic of chimpanzees (Fig. 2a). Dorsal extensions of the articular surfaces are evident on all metatarsal heads, and the distal hallucal metatarsal is squared off as in modern humans but not in apes, *A. afarensis*, *Paranthropus robustus*¹¹ or early *Homo* from Dmanisi, Georgia⁶. Sesamoid grooves are not evident on the distal joint surface of the hallucal metatarsal of LB1. Modern human-like dorsiflexion and stability at the metatarsophalangeal joints late in stance phase are implied, but load-sharing among the digits at toe-off was probably impacted by the relatively



Figure 1 | The foot and long bones of the type specimen of *H. floresiensis*. Medial (top) and dorsal views of the reassembled left foot of LB1, shown here with its associated right tibia and left femur.

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Table 1 | Relative fleshy-foot length in LB1, humans and apes*

Species	N	Mean	Standard deviation	Range
<i>Homo sapiens</i> †	34	54.2	2.5	49.3–58.9
<i>Homo sapiens</i> (pygmy)‡	10	54.5	2.1	50.7–56.7
<i>Homo floresiensis</i> (LB1)	1	70.0	—	67.5–72.9§
<i>Pan paniscus</i>	8	73.9	3.2	68.4–77.2
<i>Pan troglodytes</i>	36	82.5	4.9	72.3–95.9

N, sample size.

* $100 \times (\text{fleshy-foot length}/\text{femur length})$.

† Data from ref. 7 (Cleveland Museum of Natural History).

‡ Sample includes small-bodied individuals from Africa, the Andaman Islands and South America in the collections of the Natural History Museum, London, and the American Museum of Natural History, New York.

§ 95% prediction interval.

short hallux and long foot of LB1 (ref. 12). At $5\text{--}7^\circ$ (lateral), the degree of torsion of the distal tibia of LB1 relative to its proximal platform is at the lower end of the observed human range; despite the short hallux, therefore, there is no indication that the foot of LB1 was too in¹³.

The forefoot of LB1 is disproportionately long in comparison with modern humans. Relative to tarsal length (proximal talus to distal entocuneiform), the lesser metatarsals are long and fall outside the observed limits of our modern human sample (Supplementary Fig. 2). The proximal pedal phalanges also contribute to the long forefoot of LB1. As a percentage of corresponding metatarsal lengths, the proximal pedal phalanges of LB1 are longer than those observed in modern humans, and instead more closely resemble those in some chimpanzees (Fig. 2b). The proximal pedal phalanges of LB1 have robust bases and midshafts, and they lack the hour-glass shape characteristic of modern humans. They are also moderately curved, with included angles ranging from 16.8° to 26.8° ; the second value is beyond the range documented for modern humans and resembles some australopithecines¹⁴. Modern humans have short, straight toes¹⁵; short toes reduce the torques and bending stresses of ground-reaction forces in bipedalism and serve to reduce mechanical work in running¹⁶. The proximal pedal phalanges of LB1 lack this derived design feature, and thus probably experienced habitually high stresses (as further suggested by the presence of osteophytes on several of the phalanges)³. Their exceptionally high levels of robusticity also indicate that LB1 was unshod (Supplementary Table 2).

Of all the tarsal bones of LB1, the navicular is the most primitive in shape (Fig. 3a). The navicular tuberosity is large and projecting, and the lateral edge of the bone is pinched, producing a wedge-like effect seen in australopithecines and great apes but not in modern humans or OH 8 (ref. 17). The entocuneiform facet is well separated from the enlarged tuberosity, and there is no contact facet for the cuboid (a variable feature in modern humans). As in great apes and australopithecines, the medial longitudinal arch was probably weakly developed or absent in LB1 (refs 15, 17) and the navicular tuberosity was probably weight-bearing¹⁸. LB1's navicular affinities are corroborated by a statistical analysis of shape by means of geometric morphometrics (Fig. 3b, Supplementary Table 3 and Supplementary Fig. 3). The first two principal components of three-dimensional (Procrustes) shape coordinates reveal complete separation of modern humans from great apes. The left and right naviculars of LB1 and two of the three australopithecine naviculars group with African apes; OH 8 is more similar in shape to modern humans.

The talus of LB1 (Supplementary Information Fig. 4) is similar to modern humans in some features (for example, the neck angle is 23° , the body is slightly wedge-shaped and the dorsal trochlear groove is shallow with subequal margins)¹⁹, but it departs towards ape-like morphology with a very low degree of talar head torsion (at 26° , it is two to four standard deviations below mean values for modern humans)²⁰. A three-dimensional geometric morphometric analysis shows that LB1's talus falls outside of and between the envelopes for modern humans and African apes; it is 'intermediate' in shape, as are the tali of OH 8 and KNM-ER 1476a (Supplementary Figs 5 and 6).

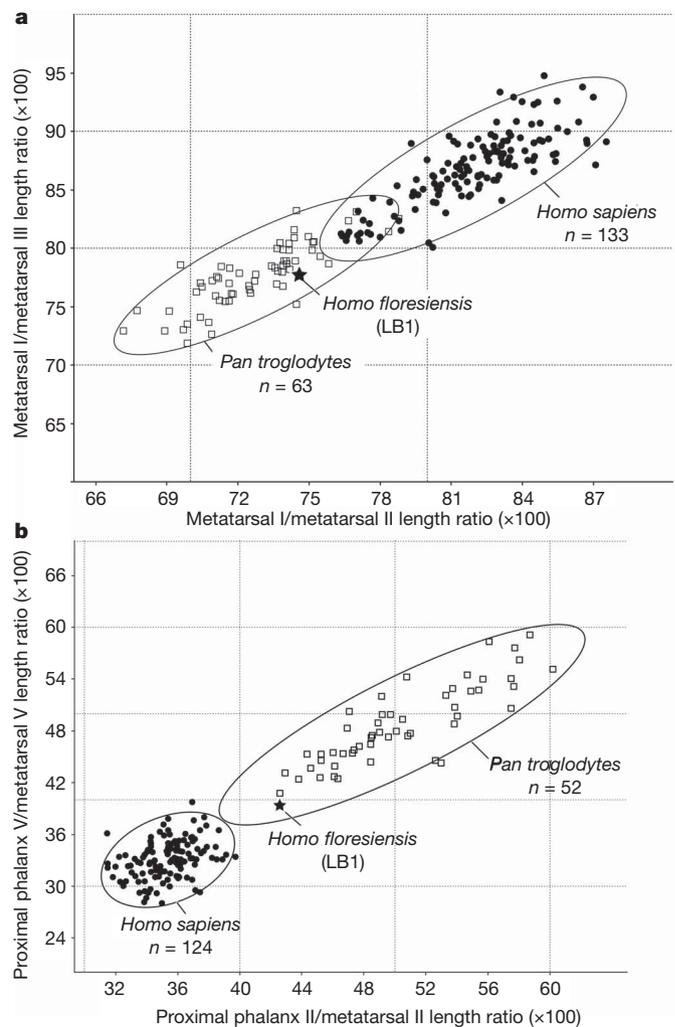


Figure 2 | Intrinsic foot proportions in *H. floresiensis*. **a**, Length of the hallux metatarsal relative to lengths of metatarsals II and III in humans, chimpanzees and LB1 (95% correlation ellipses are indicated for humans and chimpanzees). The human sample includes 124 individuals from the Indian subcontinent, five African pygmies and sex-specific means for Europeans and Japanese. *n*, sample size. **b**, Proximal phalangeal length relative to metatarsal length for digits II and V. The more complete right metatarsal V is substituted here for the fragmentary left one. Following a human template, the longest proximal phalanx (LB1/38) was assigned to metatarsal II, and the shortest (LB1/34) to metatarsal V (ref. 3).

The cuboids of LB1 appear less trapezoidal in shape than many modern humans, but both bear an incipient calcaneal process or asymmetrical 'beak' (Fig. 4), which is usually regarded as evidence of a stable lateral longitudinal column²¹. However, expression of this feature is variable in both modern humans²¹ and *H. floresiensis*; this surface is nearly flat in a newly discovered right cuboid (LB16) of another individual. In contrast, OH 8 exhibits a very pronounced calcaneal process^{17,22}.

The bony pelvis, lower-limb bones and feet of *H. floresiensis* combine to reveal an unequivocal adaptation to bipedalism^{1–3}, yet they also depart in functionally significant ways from the skeletal design of modern humans, with important biomechanical and evolutionary implications. For instance, because the foot lacks a well-defined medial longitudinal arch, recovery of stored elastic energy would have been limited in comparison with modern humans, especially during running, when mass-spring mechanics replace the pendular mechanics of walking¹⁵. With a short hallux, relatively long lateral rays and a weight-bearing navicular tuberosity, pressure transfer through the foot in support phase and at toe-off also probably differed from modern humans. Kinematic differences related to clearance of the foot

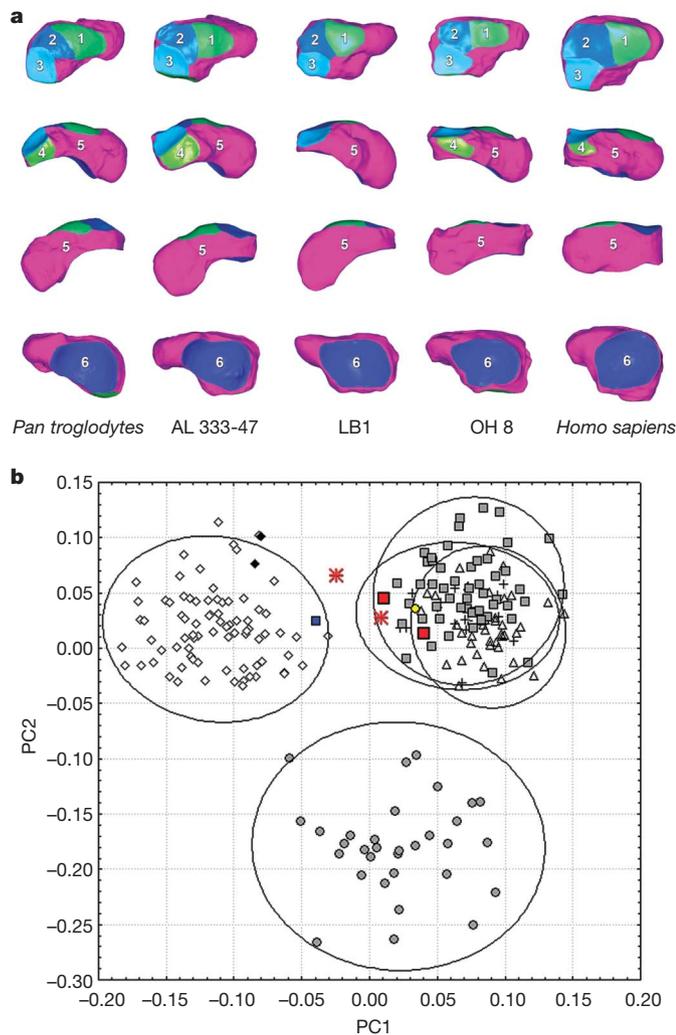


Figure 3 | The comparative anatomy and morphometrics of the navicular bone in *H. floresiensis*. **a**, Laser scans of naviculars from *P. troglodytes*, *A. afarensis* (AL 333-47), *H. floresiensis* (LB1), OH 8 and *H. sapiens* (scaled to approximately similar size and shown as from the right side). From top to bottom, the rows show distal, plantar, dorsal and proximal views. Articular facets are indicated: entocuneiform (green, 1), mesocuneiform (blue, 2), ectocuneiform (light blue, 3), cuboid (light green, 4) and talus (purple, 6); non-articular surface (magenta, 5). **b**, First two principal components of a generalized Procrustes analysis of three-dimensional coordinates (see Supplementary Fig. 4), with 95% confidence ellipses. PC1 accounts for 24.6% of the variance, and PC2 for 19% (*H. sapiens*, open diamonds; *P. troglodytes*, open triangles; *P. paniscus*, crosses; *Gorilla*, grey squares; *Pongo*, grey circles; human pituitary dwarf, black diamonds; OH 8, blue square; *A. afarensis*, red asterisks; South African *Australopithecus*, yellow circle; *H. floresiensis* (left and right sides), red squares). Sample sizes, composition and statistical software are documented in Supplementary Table 3.

in swing phase would have been evident during both walking and running. The foot of *H. floresiensis* was not well-designed for either high-speed or efficient endurance running^{15,16}.

Concerning phylogeny, the foot of *H. floresiensis* exhibits a broad array of primitive features that are not seen in modern humans of any body size. Primitive traits are also seen in the LB1 cranium, mandible, brain, shoulder, wrist, pelvis, limb bones and body proportions^{1–3,23–26}. It is conceivable that a few of these plesiomorphic traits could have evolved through reversals during ~800 kyr of insular isolation on Flores^{1,27,28}, but it is improbable that all of them from head to toe were simply a consequence of 'island dwarfing'. Some modern humans (pygmies) have reduced greatly in body size repeatedly and independently throughout the world, without any evidence of evolutionary reversals to such primitive morphologies and body

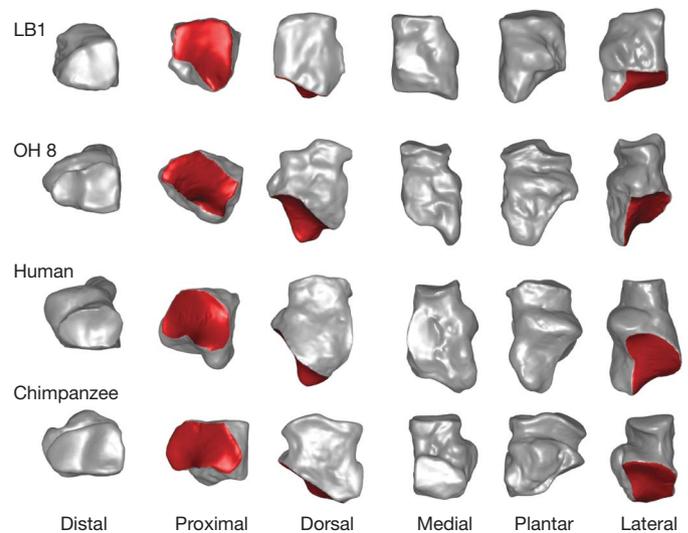


Figure 4 | The comparative anatomy of the cuboid bone in *H. floresiensis*. High-resolution laser scans of the left cuboid in LB1, OH 8, a human and a chimpanzee (scaled to approximately similar size). The calcaneal facet is highlighted in red. The calcaneal beak is present but weakly expressed in LB1; it is especially pronounced in OH 8.

proportions²⁹. Re-evolving short hindlimbs, long lateral toes, a short hallux and a flat foot would impair locomotor performance, and no known human skeletal pathology fully recapitulates this ancient body design. The comparative and functional anatomical evidence of the foot (and much of the rest of the skeleton) suggests that *H. floresiensis* possesses many characteristics that may be primitive for the genus *Homo*. It follows that if these features are primitive retentions, then *H. floresiensis* could be a descendant of a primitive hominin that established a presence in Asia either alongside or at a different time than *H. erectus sensu stricto*³⁰.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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