

PALAEOANTHROPOLOGY

Homo floresiensis from head to toe

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Fossils of tiny ancient humans, found on the island of Flores, have provoked much debate and speculation. Evidence that they are a real species comes from analyses of the foot and also — more surprisingly — of dwarf hippos.

Good science requires a healthy dose of tempered scepticism — at its heart, the process involves trying to reject proposed hypotheses. So it was understandable that the announcement^{1,2} in 2004 of the discovery of a species of dwarfed hominin, *Homo floresiensis*, from the island of Flores, Indonesia, stimulated a range of opinions, many of them sceptical, that the fossils constituted a new species and were not the consequence of some pathological condition.

Two papers in this issue, by Jungers and colleagues³ and by Weston and Lister⁴, together with contributions to a special online issue of the *Journal of Human Evolution*, will go a long way towards addressing the sceptics' concerns. The studies provide considerable evidence — literally from head to toe — that *H. floresiensis* is a true species of hominin (that is, a species more closely related to humans than to chimpanzees and other apes). More importantly, the analyses prompt hypotheses about the human family tree that will require more fossil evidence to test.

So far, remains of *H. floresiensis* have been excavated from just a single cave, Liang Bua (Fig. 1). The fossils include a partial skeleton (LB1) plus fragments of at least half a dozen more individuals now dated to between 95,000 and 17,000 years ago^{5,6}. These were small people, about a metre tall. Most remarkably, LB1's skull has a chimp-size brain of 417 cm³ in an approximately 30-kg body. Some palaeoanthropologists hypothesized that *H. floresiensis* evolved from a non-modern species of hominin, possibly *H. erectus*, through a process called insular dwarfing that is common to islands such as Flores, in which large species undergo intense selection to become small. Archaeological data showed that *H. floresiensis* made stone tools, and hunted dwarfed elephants (*Stegodon*) and giant varanid lizards (Komodo dragons) that were also present on the island.

Such a minuscule brain in a species so recent that also made stone tools has strained credibility. Several scholars argued that the bones come from a pathological population of human pygmies suffering from some developmental syndrome that includes microcephaly^{7–9}. All such diagnoses have proved problematic, because none accounts for the entire suite of



Figure 1 | Fossil site — Liang Bua cave on the island of Flores.

features evident in *H. floresiensis*, including the size and shape of the brain and cranium^{10–12}, and the anatomy of the shoulder¹³ and wrist¹⁴.

The most serious criticism, however, has been that LB1's brain is too small to be explained by known scaling relationships between brain and body size. Across species, brain mass typically scales to body mass to the power of 0.75, but among closely related species the scaling exponent is usually 0.2–0.4, and within species it is 0.25 or less¹⁵. Accordingly, if LB1 were a dwarfed human of 30 kg, then its predicted brain volume would be about 1,100 cm³; if it were a dwarfed *H. erectus* then its brain volume would be expected to be about 500–650 cm³. All in all, many scientists (myself included) have sat on the fence, waiting for more evidence about the nature and form of *H. floresiensis*.

And now we have some. One remarkable line of thinking (page 81) comes from Jungers and colleagues' description³ of the species' fascinating foot. In some respects the foot is very human-like: the big toe is aligned with the

other toes; the middle of the foot apparently had a locking mechanism to help stiffen the arch after the heel lifted off the ground; and the metatarsals are typically human in several respects, including upwardly oriented joints at their ends that enable the toes to extend at the end of stance (the part of the stride when the foot is on the ground). But otherwise this is no human foot. Its approximate length, 20 cm, is much longer than one would find in any person of that stature, and instead has the proportionate length of a chimpanzee or an australopith (a genus of early hominin). Additional primitive features include long, curved and robust lateral toes; a short big toe; and a weight-bearing process on a crucial bone, the navicular, which acts like the keystone at the top of the inside of the human arch.

Together, these features suggest that the foot of *H. floresiensis* was capable of effective walking, because the middle of the foot could be stiffened when the calf muscles raised the heel off the ground. This mechanism permits the

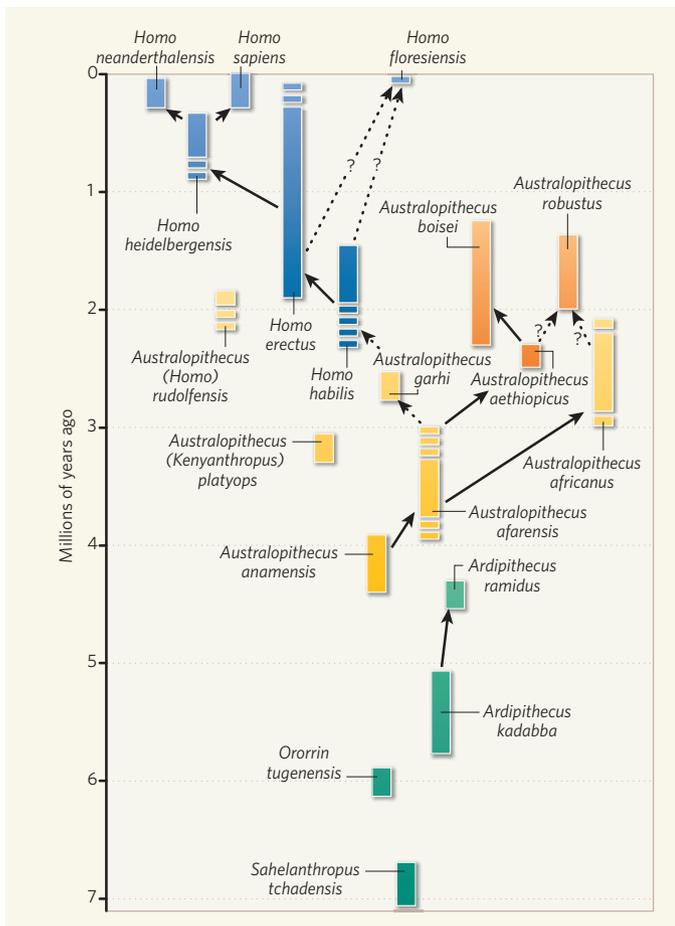


Figure 2 | The human family tree. *Homo floresiensis* might be most closely related to early *H. erectus*, but also shows potential affinities with *H. habilis*. In either case, recognizing *H. floresiensis* as a species will require us to re-examine how we define species of the genus *Homo* and how they were related to each other. Reasonably well-known relationships are indicated by solid arrows; less secure relationships are indicated by dotted arrows. Broken vertical bars indicate uncertainties about when species evolved or went extinct.

toe flexors to push the body up and forwards at the end of stance. But the inside of LB1's arch was either weak or flat, and apparently lacked the spring-like mechanism that humans use to store and release energy during running¹⁶. In addition, the long, slightly curved toes probably posed no hindrance to walking, but would have created problematically high torques around the toe joints during running¹⁷.

It is often assumed that a human-like foot with short toes and a high arch evolved for walking. But the primitive foot of *H. floresiensis* provides a tantalizing model for a non-modern hominin foot that had evolved for effective walking before selection for endurance running occurred in human evolution¹⁶. Recently discovered footprints from Kenya indicate that a modern foot had evolved by 1.5 million years ago, presumably in *H. erectus*¹⁸. Unless the Flores fossils re-evolved a primitive foot, they must have branched off the human line before this time.

The papers in the special issue of the *Journal of Human Evolution* bolster previously published evidence that the mosaic of primitive and derived features evident in the *H. floresiensis* foot can be seen elsewhere in the skeleton. Many aspects of the anatomy, such as the scapula, are quite human-like in spite of being tiny. But there are also numerous primitive features that resemble those of either australopiths or early *Homo*. Primitive features in the upper limbs include a relatively short, very curved

clavicle; a straight humerus that lacked the normal degree of twisting between the shoulder and the elbow; and an ape-like wrist^{13,14,19}. Primitive features in the hip and lower limbs include flared iliac blades, relatively small joints and relatively short leg bones^{1,20}.

These features suggest that *H. floresiensis* evolved from a species that was anatomically more primitive than classic *H. erectus* from Asia. One possibility (Fig. 2) is that *H. floresiensis* evolved from *H. habilis*, whose skeleton is poorly known but is australopith-like in many respects. Another is that *H. floresiensis* descended from an earlier type of *H. erectus*, whose body may have been much less modern than we currently credit, and which perhaps deserves a separate species designation (*H. ergaster*).

But what about the head of *H. floresiensis*? LB1 has a vertical face, no snout, and most of its teeth generally resemble those of *H. erectus*. A state-of-the-art shape analysis²¹ indicates that the LB1 skull conforms to what one predicts from a scaled-down *H. erectus* or possibly a *H. habilis*. Yet one also needs to explain how the species got such a small brain.

Here hippos come to the rescue. Weston and Lister (page 85)⁴ analysed several species of fossil hippo that underwent insular dwarfing in Madagascar. In these species, brain mass scales to body mass to the power of 0.35 after growth has slowed in infancy, and to 0.47 when growth from birth is considered. Further, in some dwarfed species, natural selection

evidently shrank brains to volumes well below the sizes predicted by these relationships. The extra reduction presumably occurs because brain tissue is so metabolically costly that animals with relatively smaller brains can save energy when resources are scarce.

Such dwarfing is enough to account for LB1's 417-cm³ brain and 30-kg body if *H. floresiensis* were a dwarfed version of the small early *H. erectus* females from Dmanisi, Georgia, that were 40 kg and had brain volumes in the range 600–650 cm³ (ref. 22). Alternatively, *H. floresiensis* might be descended from *H. habilis*, whose body size was possibly just as small, about 30 kg in females. But this hypothesis, too, requires some significant brain shrinking, about 25%, because the smallest known *H. habilis* cranium (KNM-ER 1813) has a 509-cm³ brain.

Overall, *H. floresiensis* presents a fascinating conundrum, and prompts some tantalizing predictions that will continue to strain credulity without more fossil evidence. First, if the species evolved from early *H. erectus*, possibly like the fossils found at Dmanisi, then this species (or group of species) was more diverse and anatomically more primitive in many respects (hands and feet for example) than previously recognized. A more audacious hypothesis is that *H. floresiensis* evolved from an even more primitive species, perhaps *H. habilis*. If so, then this species also migrated out of Africa but left no trace yet found, except on Flores. My wager is on the first possibility. But the only way to test these and other hypotheses is to find more fossils, especially in Asia. Get out your shovels!

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