The geometry of hobbits: *Homo floresiensis* and human evolution

Until quite recently modern humans shared the earth with now extinct relatives—Neanderthals and others—in Europe and Asia. *Homo floresiensis*—dubbed the "hobbits" in the popular press—is the most recent, and the most surprising, addition to the human family tree. Were the tiny hobbit people of Flores dwarfed descendents of known species, modern humans suffering from a skull-shrinking genetic disease or a new species entirely? **William Jungers** and **Karen Baab** look at the time, the space and the body-shape of the astonishing hobbits.

A recent full-body reconstruction of LB1, the 'little lady of Flores', by the Parisian palaeoartist Elisabeth Daynès. (©2009, S. Plailly/E. Daynès—Reconstruction Atelier Daynès Paris)

The latest twig on the human evolutionary tree was lost in space and time until its discovery and diagnosis in 2003 by a team of Australian and Indonesian scientists[1,2]. Recovered deep in Late Pleistocene sediments (from around 95 000–15 000 years ago) within a remote limestone cave on the isolated island of Flores in the Indonesian archipelago, the barely fossilised remains of several individuals served as the basis for recognising the newest species of our own genus—*Homo floresiensis*. This was the unexpected "black swan" among fossil hominins. The huge cave, Liang

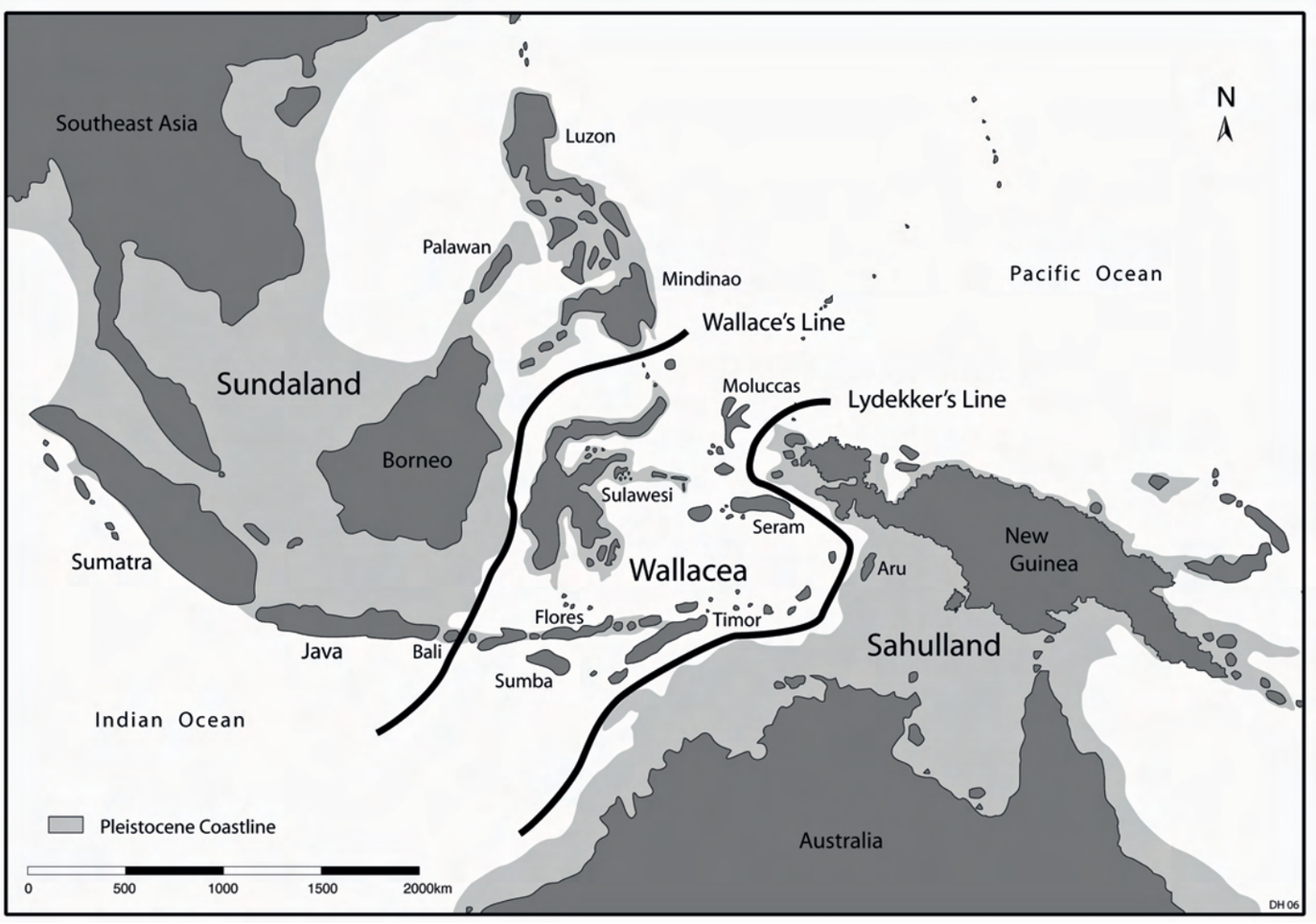

Figure 1. Wallacea today and in the Pleistocene, showing that Flores has always been an island. The ancestors of *Homo floresiensis* must have arrived by sea. The cave of Liang Bua is on western Flores. Stone tools dating to almost 1 million years ago have been found further east on Flores (courtesy of Mike Morwood)

Bua (translated as "cool cave"), was known to an earlier generation of archaeologists, but no one before had the imagination or determination to dig really deep into the sediments.

The small-bodied, small-brained, human-like ("hominin") fossils were found in association with stone artefacts and other extinct mammals and birds, including the smallish elephant-like *Stegodon*. These discoveries and the scientific announcement of "a new human"[3] literally shook the intellectual foundations of palaeoanthropology. Who were the ancestors of *Homo floresiensis*? How and when did they get to Flores? The answers to these and related questions have required the rewriting of textbooks on human evolution.

Splendid isolation in Indonesia

Flores Island is part of an unusual biogeographical region of Southeast Asia known as "Wallacea" (Figure 1). Wallace's Line is a boundary that signals a natural, severe filter that hinders non-flying species from dispersing farther to the east. The native fauna of Wallacea's islands differ markedly from that of their neighbours.

Even at the lowest sea levels, Flores was never connected to islands to the west (such as Java) or the north (Sulawesi and its group). This implies that the ancestors of *Homo floresiensis* had to cross open water to reach the island; they must have done so by some currently unknown, and probably one-off or only very occasional, chance mechanism, such as rafting—whether accidental or deliberate we may never know. (Palaeontologists refer to the crossing of such difficult barriers as a "sweepstake" mechanism on the grounds that chance must play a large part in assisting the few species that do manage to cross the barrier.) Once there they evolved in isolation until their recent extinction just before the Holocene, more than 10 000 but less than 15 000 years ago. This of course makes them by far the most recently-surviving of the non-modern humans who shared the earth with us: they survived long past the Neanderthals (*Homo neanderthalensis*), who became extinct about 24 000 years ago.

One clue to their origin are stone tools (but no fossilised hominin bones), which were recovered earlier on Flores to the east of Liang Bua within the Soa Basin and dated to almost 1 million years ago. It seems very likely that these were made by the first colonisers of Flores and the direct ancestors of *Homo floresiensis*.

What do the astonishing hobbits tell us about the career of the human species on earth?

Fossils attributed to the extinct species *Homo erectus* are well-known from Java and elsewhere in Asia from this earlier time period, so it seemed logical at first to interpret the hobbits as descendants of this ancient, cosmopolitan species, who had become dwarfed through isolation on their island. With additional fos-

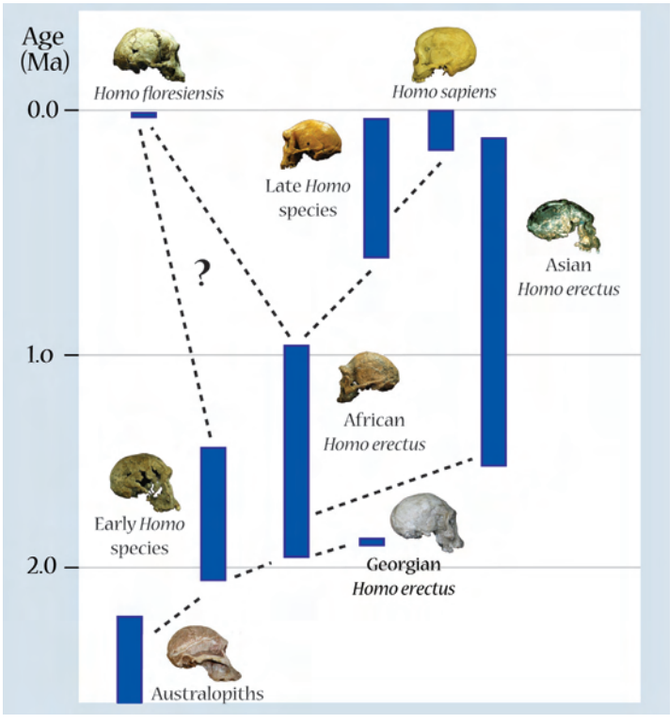

Figure 2. Possible ancestors of *Homo floresiensis*: is he a diseased *Homo sapiens*, a dwarfed *Homo erectus* or descended from an unknown still-earlier species? Ma = million years ago. (Skull photos courtesy of Mike Morwood, Karen Baab, Peter Brown and the Kenya National Museums)

Figure 3. Reassembled skeleton of LB1, the type specimen of *Homo floresiensis*. In life she would have stood 106 cm (3 ft 6 in) tall (photo: W. Jungers)

sils from Liang Bua and more detailed analyses, however, this evolutionary scenario now seems increasingly unlikely. Here we discuss some of the evidence that leads us to believe that the hobbits are probably derived instead from an even more primitive hominin species. Figure 2 shows a simplified evolutionary history of humanity, and the uncertain place of *Homo floresiensis* in this scheme.

Although there are several individuals in the sample of *Homo floresiensis* from Liang Bua, it is the type specimen (LB1) that is truly extraordinary for its degree of completeness (Figure 3). Found almost 6 m down in the cave sediments, these skeletal remains of a female are not only well-preserved but are also associated and even partially articulated. She has been nicknamed "Little Lady of Flores" or "Flo". It is a very rare opportunity to be able to study skulls and postcrania (limb bones, bony girdles, etc.) from the same individual in the fossil record, and we now possess a wealth of integrated information on the cranium, brain, jaw, arms, legs, hands and feet of the hobbits. What these bones reveal is simply astonishing.

Heads of hobbits

The small brain of LB1 was a bone of contention from the moment it was first described. With a cranial capacity of just over 400 cm^3, it is remarkably small compared with living humans, including modern "pygmies", and other extinct species of *Homo*; it is much more similar in size to the brains of chimpanzees and more ancient hominins like the australopithecines (bipedal "ape-men" of East and South Africa). Some have concluded that a head so abnormal could only have been caused by pathological disease. Despite its small absolute size, however, multivariate statistical analysis reveals absolutely no resemblance to the brain shape of modern human microcephalics (those born with abnormally small heads). The endocast—the impression of the inside of the skull showing the shape of the brain—also appears to be globally reorganised in comparison with the brain shape of apes[4]. This implies that brain architecture and some aspects of function are not tightly constrained by absolute size; if we go by brain size alone we may severely underestimate the cognitive capabilities of the hobbit. Their core-and-flake stone tool technology shows that they were far from unintelligent.

If *Homo floresiensis* was a dwarfed descendant of *Homo erectus*, as some have suggested, this implies that substantial brain size reduction must have occurred. However, if the ancestors of the hobbits were not *Homo erectus* but a different species, with already-small bodies and smaller brains when they arrived on Flores, then perhaps relatively little reduction occurred in either body or brain after they reached the island. The relatively poorly known earliest African *Homo* species (e.g., *Homo habilis*) then emerge as alternative ancestral candidates (Figure 2). Brains are known to be expensive organs in terms of their energy requirements, so it is also plausible that ecological constraints on a small island like Flores might have favoured somewhat smaller brains and bodies. Mammals stranded on islands tend to undergo evolutionary shrinkage: foxes no bigger than housecats on islands off California and extinct pygmy elephants from Crete are but two examples.

The shape of the bony brain case can be summarised efficiently by the first two principal components of three-dimensional ("procrustes") shape variables derived from 13 landmarks (yielding 39 size-adjusted *x-y-z* coordinates) in a sample of modern humans, LB1 and other fossil hominins in the genus *Homo* (Figure 4). Three major groups can be identified in this reduced ordination space: modern humans, all fossil humans including LB1 and a subset of pathological, microcephalic humans. Modern humans and some putative microcephalics are separated from the fossils and other microcephalics along the first principal axis of shape by virtue of higher, more globular cranial vaults in the former. The second axis of vault shape serves to separate the various fossils from the remaining microcephalics, and LB1 is most similar overall to the subadult specimen (D2700) from Dmanisi (Republic of Georgia), dated to around 1.8 million years ago and thought by some to be a very early *Homo erectus* (but regarded as a separate species by others). It is intriguing and noteworthy that in aspects of shape related to a small neurocranium, some human microcephalic skulls do in fact resemble fossil hominins (and not just LB1) to a limited degree.

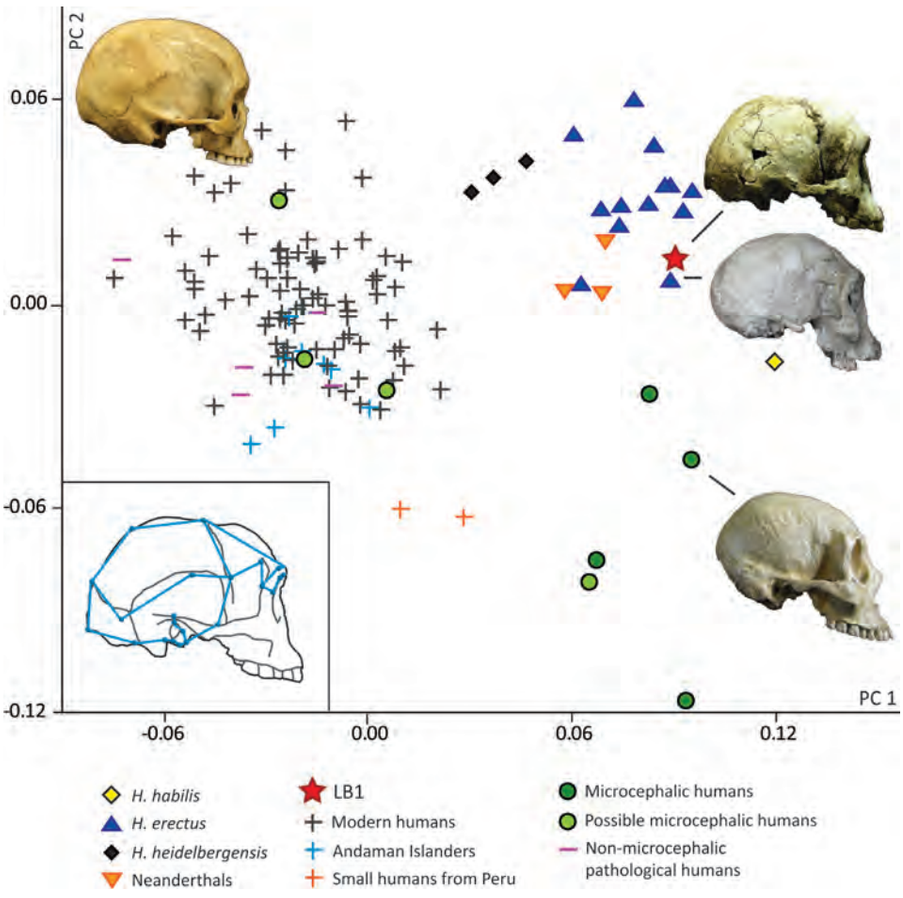

Figure 4. Scatterplot of the first two principal components of 3D landmarks that capture cranial vault (neurocranial) shape in modern humans, microcephalic humans, LB1 and other crania of fossil *Homo*. LB1 (photo courtesy of P. Brown) is most similar in overall shape to fossil skulls of early *Homo*, especially one from Dmanisi in the Republic of Georgia, and is distinct from both modern humans and microcephalics (photos: K. Baab)

The relatively tiny brain of LB1 is housed in a small cranium that looks unlike any normal modern human of which we are aware. The bones of the skull are very thick and highly pneumatised—that is, honeycombed by air spaces. The forehead slopes backwards and the eye sockets are topped by prominent brow ridges. There are paired pillars of bone in the lower face associated with large canine tooth roots. The anatomy of some teeth (especially the lower premolars) is strikingly primitive in both crown shape and root structure. The thick lower jaw lacks a true chin, and is buttressed by bony bars internally that are not normally seen in people but which recall the standard condition seen in ancient australopithecines. These features are also found in a second hobbit jaw referred to as LB6. All published multivariate statistical analyses of LB1's cranial shape consistently depict it as remarkably primitive in overall aspect; it resembles extinct members of the genus *Homo*—but, notably, it shares no special affinities with Asian *Homo erectus*[5,6,7]. Geometric morphometric analysis of 3D landmark data corroborates this characterisation and indicates that the overall shape of the LB1 cranium is predicted well by extrapolating size–shape trajectories of early *Homo* species down to very small skull sizes[8]. In other words, arrange early hominid skulls by size, carry the trend on downward, and you end up with not only the size but also the shape of the hobbit skull.

Statistical analyses of skull shapes find modern humans in one grouping, microcephalic humans in another and the hobbit, together with ancient hominins, in a third (see box and Figure 4).

Hobbit size and shape

Because it is so complete, we can reconstruct the body size and overall shape of LB1 quite reliably and these reconstructions reveal a body design decidedly unlike that of any modern human. The femur (thigh bone) and tibia (shin bone) of LB1 are much shorter than any modern humans that we have studied in skeletal collections around the world. In fact, they are shorter than the corresponding bones in the shortest living people on earth, including Central African pygmies, South African Khoe-San (formerly known as "bushmen") and "negrito" pygmies from the Andaman Islands and the Philippines of Southeast Asia. The arms, however, are by no means so drastically shortened. The humerus (arm bone) of LB1 does actually fall (though only just) within the distribution of humeral lengths in samples of modern small-bodied people. This extremely high ratio (around 87%) is never found in modern humans[9]; this index is closely matched, however, in the partial skeleton of "Lucy", a famous fossil of *Australopithecus afarensis* from Ethiopia dated to more than 3 million years ago! *Homo erectus*, in contrast, is known to have possessed long hind limbs and essentially modern human proportions by almost 2 million years ago.

In other words, *Homo floresiensis* had very, very short legs, both absolutely and relatively. This must represent either an ancient retention or an evolutionary reversal that makes little biomechanical sense. It makes little sense because relatively long hind limbs serve to improve the economy of bipedal walking and running. It is hard to see how any evolutionary pressure would lead to less economical movement.

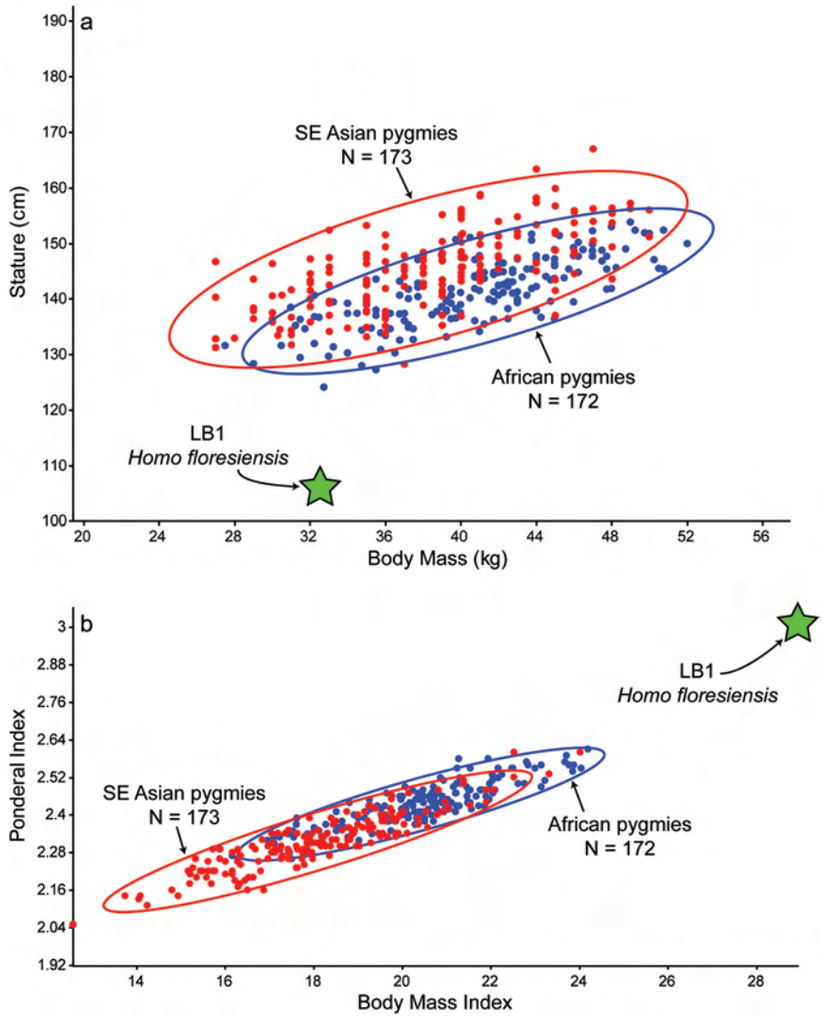

Figure 5. Scatterplots of stature on mass (a) and the ponderal index on the body mass index (BMI) (b). Human pygmies are relatively common at the estimated body mass of LB1 but none are ever as short. This produces very high values for indices that capture mass per unit stature in LB1, values never observed in modern human pygmies from either Asia or Africa

The short hind limb also implies that the hobbits themselves were surprisingly short. Based on regression equations, which predict body height from femur length, developed by one of us (WJ) from data on human pygmies, the initial species diagnosis[1] included a reconstructed stature of around 106 cm for the female type specimen LB1—or 3 ft 6 in for those who prefer to think of human height in that format. (As a comparison, anthropologists define modern pygmies as any group whose adult males grow to less than 150 cm—4 ft 11 in—in average height.) We can also estimate her body mass from dimensions of the weight-supporting joints of the hind limb[10]. Our best estimate is 32.5 kg, with a range of roughly 30–35 kg. When mass and stature are plotted together for LB1 and large samples of African (Efe) and Southeast Asian (Semang and Aeta) human pygmies, it is clear that the body mass of *Homo floresiensis* can be matched easily among small-bodied living people but that its stature cannot (Figure 5a). This suggests a very non-human body shape for our hobbit, in the sense that a relatively large mass is being distributed over a relatively small skeletal frame. Our hobbit is far stockier than any modern human.

This observation is driven home by the scatterplot (Figure 5b) of two widely used biomedical and anthropometric indices that combine mass and stature: the body mass index (BMI), which is mass divided by the square of the height, and the ponderal index, which is the cube root of mass divided by height. LB1 plots far outside and well above the 95% correlation ellipses for African and southeast Asian pygmies. If we were to plot similar estimates for Lucy and known values for living chimpanzees, their mass-per-unit-stature values would fall in the same bivariate space as LB1 and far away from modern humans (and *Homo erectus*). Simply put, the hobbits display a very different body shape than modern human pygmies at similar body masses. The new sculpture of LB1 by the Parisian paleoartist Elisabeth Daynès, shown on page 158, nicely captures the distinctive and stocky body design of *Homo floresiensis*.

Will the real ancestor of *Homo floresiensis* please stand up?

It is now evident that there is no systemic human pathology that reduces a modern human to the size and shape of a hobbit and simultaneously transforms one into an ancient, ancestral phenotype. Attempts to dismiss the hobbits as pathological people have failed repeatedly because the differential medical diagnoses of various dwarfing syndromes and microcephaly bear no resemblance to the unique anatomy of *Homo floresiensis*. There are no known sick humans that look like *Homo floresiensis* because no known illness reverses the evolutionary changes of a species. The hobbits therefore cannot be a diseased sub-population of healthy humans.

There are, however, at least two viable and competing scientific hypotheses that can account for the existence of *Homo floresiensis*. "Island dwarfing" is a well-known evolutionary process, but it appears to happen most frequently among ungulates, carnivores and rodents. With Javanese *Homo erectus* as a starting point, could the hobbits represent a rare insular dwarfing event? Perhaps, but in addition to a decrease in both body size and brain size, this scenario would require numerous evolutionary reversals in many details of body design from brain to toes. It is also relevant to point out that modern humans have, in fact, "dwarfed" to the same body mass as the hobbits repeatedly and independently around the world, but no known human pygmy manifests anything resembling evolutionary reversals or any meaningful convergence on *Homo floresiensis*.

Could the hobbits instead represent evidence for an "out-of-Africa" event that predated the emergence and dispersal of *Homo erectus*? Could *Homo habilis* or some as yet unknown ancient species have made the long trek and left no trace save for the hobbits themselves? Recall that there is no special resemblance between Asian *Homo erectus* and *Homo floresiensis* in skull shape or body proportions. Wrist bones of the hobbits are also exceedingly primitive and resemble apes,

australopithecines and *Homo habilis*[11]. The hobbits also share a primitive shoulder configuration with various ancient hominins[12], and their relatively long feet simply do not match the footprints left by *Homo erectus*[13,14] (Figure 6).

We have then two competing scenarios: island dwarfing of *Homo erectus* or migration from Africa of a still more ancient and unknown species. They can be affirmed, falsified or modified by discovering which hominins made those million-year-old stone tools from Flores[3]. As the palaeoanthropolgy mantra goes, we need more fossils. Happily, we now know several places to look for them. Along the way, we also hope to learn whether modern people and the hobbits ever met on Flores and what eventually caused the demise of the smallest human of them all.

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Figure 6. The nearly complete left foot of LB1 next to the right tibia (shin bone, which is ~235 mm long). The foot is relatively very long and has unusual intrinsic proportions; its footprint matches no other species (photo: W. Jungers)