MWP-1A has commonly been viewed as a short-lived acceleration within the long-term decline of North America's Laurentide Ice Sheet[2]. At the end of the Last Glacial Maximum, the Laurentide is estimated[1,6] to have contained enough water to raise global sea level by about 70 m; by roughly 7,000 years ago it had almost all disappeared[7]. Although it is natural to interpret MWP-1A as a manifestation of that decline, several problems have led many researchers to challenge the hypothesis of a primarily Laurentide source, and suggest instead a major Antarctic contribution[8].

With multiple well-dated records, it should be possible to 'fingerprint' the meltwater sources[9] (Fig. 1). When an ice sheet melts, a sizeable amount of water is redistributed from a fairly concentrated source (the ice sheet) to a distributed one (the ocean). This mass redistribution reshapes Earth's gravitational field, lessens the flexure of the lithosphere (Earth's rigid outermost layer) in the vicinity of the ice sheet and alters the rate and orientation of Earth's rotation. The net effect is an initial sea-level fall near a melting ice sheet and enhanced sea-level rise far from the ice sheet. Thus, Laurentide melt would have caused about 40% less sea-level rise in Barbados than in Tahiti, whereas Antarctic melt would have caused similar amounts of sea-level rise at both localities[9]. The similarity of sea-level rise at Barbados and Tahiti is most consistent with a predominantly Antarctic source, and is difficult to reconcile with a purely Laurentide one.

Deschamps and colleagues' Tahiti chronology and the most recent Barbados chronology[5] of MWP-1A indicate that the meltwater pulse started at around the same time as a period of warming in the Northern Hemisphere known as the Bølling, an episode of cooling in the Southern Hemisphere called the Antarctic cold reversal, and an associated strengthening of the Atlantic meridional overturning circulation (AMOC)[10]. Through the AMOC (the 'conveyer belt' that carries warm, upper Atlantic Ocean water to high northern latitudes and returns cold, deep waters to the south), Antarctic melt and the northern Bølling warming could have acted as feedbacks on one another. The introduction of fresh water into the Southern Ocean would have strengthened the AMOC, leading to an attendant northern warming and southern cooling[11]. Conversely, a warmer Northern Hemisphere would have promoted Northern Hemisphere ice-sheet melting, causing a sea-level rise that would have destabilized marine-based parts of the Antarctic ice sheet.

The evidence from sea-level fingerprints for a primarily Antarctic source of MWP-1A is unlikely to be the last word. Although geochemical records are consistent with less than about 5 m of melt sourced from the Laurentide[12], geologists working in both East and West Antarctica have had difficulty finding evidence for an ice-sheet retreat of the necessary scale and as early as required to explain MWP-1A[13,14]. But for the moment, the geographical patterns seen in the sea-level records of MWP-1A argue that the event was caused predominantly by rapid Antarctic melting. This evidence for Antarctic instability emphasizes that, although a negative local sea-level feedback may reduce the instability of marine-based ice sheets[15], this feedback cannot be regarded as a guarantee against the collapse of the marine-based sectors of the Antarctic ice-sheet in the face of a warmer and rising sea. There is enough marine-based ice remaining in the West Antarctic Ice Sheet today to raise global sea level by about 3.3 m (ref. 16). The example of MWP-1A serves as a reminder of the risk the ice sheet poses to the world's coasts. ■

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HUMAN EVOLUTION

Those feet in ancient times

A fossil foot found in Ethiopia suggests that human ancestors that walked on two feet and also ably climbed trees existed until 3.4 million years ago, adding evidence for locomotor diversity during early human evolution. **SEE ARTICLE P.565**

DANIEL E. LIEBERMAN

The limitations of the fossil record leave ample room for debate about human origins. But most palaeoanthropologists agree that selection for bipedalism was instrumental in setting the human lineage on its separate evolutionary path from the chimpanzee lineage. And, as with any journey, it was probably sensible for our ancestors to put their best foot forward when starting out. The big question is, what kind of foot? On page 565 of this issue, Haile-Selassie and colleagues[1] present findings from a partial foot fossil which suggest that the feet of early hominins (species more closely related to humans than to chimpanzees), and hence their locomotor behaviour, were more diverse than was previously thought, and that the diversity lasted for much longer than was thought.

Human feet are remarkably different from those of apes[2] (Fig. 1). We have long, hefty big toes whose orientation does not diverge from that of the other toes, which are shorter and straighter than in other primates. Our feet also have a large, stable heel, for striking the ground when we walk, and a well-developed arch that stiffens the middle of the foot and transfers the body's weight inward towards the base of the big toe, helping to push the body forward and upward at the end of stance.

Many of these distinctive features are also present in foot bones belonging to species of *Australopithecus*, a diverse genus of hominin that lived in Africa from about 4.4 million to 1.3 million years ago[3]. An absence of fossil feet older than those of *Australopithecus* led palaeoanthropologists to believe that human-like feet helped guide the way in human evolution, by enabling early hominins to walk effectively as bipeds, even while they retained some features that helped them to climb trees. In addition, the origin of the genus *Homo*, to which modern humans belong, was thought to have involved only minor modifications to foot anatomy, perhaps to improve our ancestors' ability to run long distances, although at the expense of climbing[4].

Recent discoveries have made that simple narrative more complex. Most importantly, a fossil foot from *Ardipithecus ramidus*[5], a 4.4-million-year-old species of hominin,

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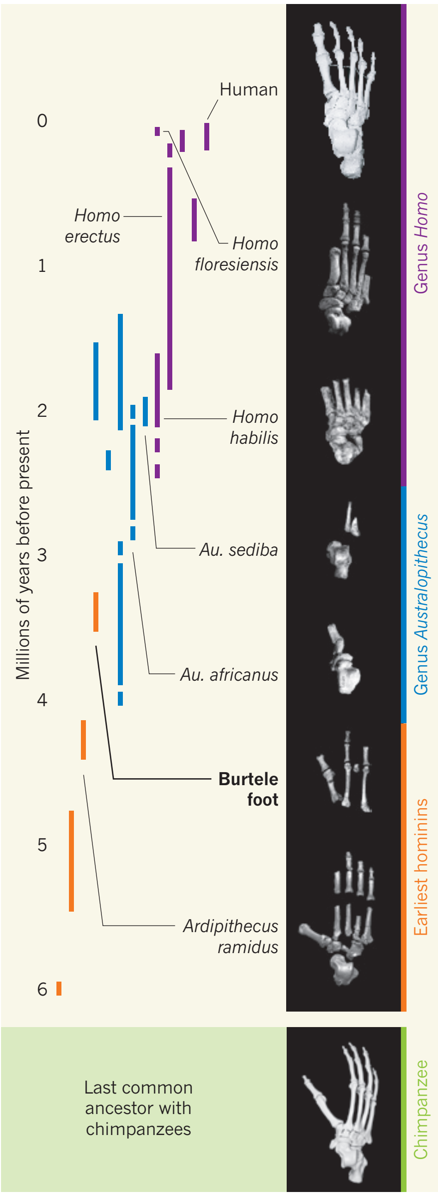

AR. RAMIDUS: G. SUWA, UNIV. MUSEUM, UNIV. TOKYO, FROM REF. 5; BURTELE FOOT: Y. HEILE-SELASSIE; *AU. AFRICANUS*: REF. 11; *AU. SEDIBA*: J. DESILVA; *H. FLORESIENSIS*: W. JUNGERS

Figure 1 | Walking along the evolutionary tree. Hominins have evolved many diverse forms of feet since diverging from their last common ancestor with chimpanzees about 6 million years ago. The early hominin species *Ardipithecus ramidus* was adapted for both walking and climbing trees[5], but, like a chimpanzee, had a highly divergent big toe and probably used its feet more like a chimpanzee than like a modern human when it walked. Foot fossils from more recent hominin species, such as *Australopithecus sediba, Australopithecus africanus, Homo habilis* and *Homo floresiensis*, have a more complete arch than *Ar. ramidus* and a non-divergent big toe, but they were not entirely modern, retaining some adaptations for life in trees. It was probably not until *Homo erectus* that very human-like feet evolved, with a completely developed arch and a large big toe aligned with the other toes. Haile-Selassie *et al.*[1] describe bones of a fossil foot from Burtele, Ethiopia, dated to around 3.4 million years ago, which is similar to the foot of *Ar. ramidus*. This finding indicates that feet adapted to both bipedal locomotion and tree-climbing persisted for a long time in human evolution. (Foot images not to scale; some have been reflected to make them all right feet.)

shows substantial differences from the feet of *Australopithecus*. The *Ardipithecus* foot (Fig. 1) has several features suggestive of bipedalism, including evidence for a stiffened midfoot and toe joints capable of bending upward at the end of stance. But it has a very divergent and relatively short big toe, similar to that of African great apes. The foot bones also indicate that this animal placed its weight more along the lateral side of the foot when it walked, much like a chimpanzee does. The fossil's discoverers proposed[5] that these features indicate that *Ardipithecus* was both a tree-climber and an occasional upright walker. Some researchers have argued[6] that *Ardipithecus* was actually an ape that had independently evolved adaptations for bipedalism, whereas others, myself included, consider *Ardipithecus* to have been a hominin whose foot partly resembled an African great ape's, but with some key adaptations for bipedalism.

The foot fossil reported by Haile-Selassie and colleagues[1] is a valuable addition to the fossil record, as it extends the evidence for the existence of *Ardipithecus*-like feet by a million years. The fossil, which was discovered in fossil-rich deposits dated to 3.4 million years ago in a locality named Burtele, in the Afar region of Ethiopia, comprises eight bones, all from the front half of a single right foot (Fig. 1). In many ways, the foot is ape-like, especially resembling that of a gorilla. The big toe is short, very divergent, and apparently capable of grasping against the second toe. In addition, the toe bones are generally long and slightly curved, placing them between those of apes and hominins, although the fourth metatarsal bone is curiously long, like a monkey's.

However, the foot bears several traces of adaptation for bipedalism. Most tellingly, the ends of its metatarsal bones (other than those in the big toe) are large and spherical, and the matching phalange bones, which form joints with the metatarsals, have upwardly canted ends. These features, which are typical of later hominins (but also variably present in chimps and gorillas[7]), suggest that the Burtele foot was able to hyperextend its toes to help push off at the end of stance. Although there is no indication that the foot has a longitudinal arch, as was the case in *Australopithecus*[3,8,9], the tall base of its first metatarsal bone hints at the presence of a transverse arch.

Haile-Selassie and colleagues have not yet assigned the Burtele foot to a particular species, as more fossils are needed to make a secure assessment. However, the resemblance of this fossil, from 3.4 million years ago, to the 4.4-million-year-old foot of *Ar. ramidus* suggests that ardipith hominins were both climbing trees and walking in eastern Africa at the same time that *Australopithecus afarensis* was walking around in that region — sometimes leaving footprints that strongly suggest a human-like gait[10]. In other words, if *Ardipithecus* was a hominin (as I think it was), then it seems that there was more diversity in hominin locomotion than was previously thought, and not all of it took place on the ground. Additional evidence for this diversity comes from foot bones of the recently discovered *Australopithecus sediba*, which lived approximately 2 million years ago in South Africa[9]. This species' fascinating foot (Fig. 1) has many adaptations for bipedalism, including an arch, but its ape-like heel and other features in its ankle suggest that it walked on an inwardly angled foot (like an ape), while retaining other adaptations for climbing trees.

Taking the next step to understanding the implications of this limb diversity for human evolution will require researchers to continue getting their feet dirty in the field and the lab. We need more fossils to determine what sorts of bodies went with these feet, and to resolve which features evolved just once and which evolved multiple times. We also need to have a better understanding of how the anatomical variations we see in hominin feet affected the different species' ability to climb, walk and run. For example, how much did a divergent big toe and keeping weight on the outside of the foot affect early hominins' ability to walk effectively? And to what extent did the more human-like foot of *Australopithecus* compromise its ability to climb trees? Whatever the answers, it is evident that hominin feet, like heads, were adaptively diverse, and that tree-climbing remained an important part of the hominin locomotive repertoire for several million years.

Human evolution is often portrayed as a triumph of bipedalism, but who among us has not occasionally regretted our species' comparative clumsiness in trees? I, for one, am pleased to know that some hominins retained feet well adapted for arboreality millions of years after we started to walk on two feet. ■

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