

BREAKTHROUGH OF THE YEAR

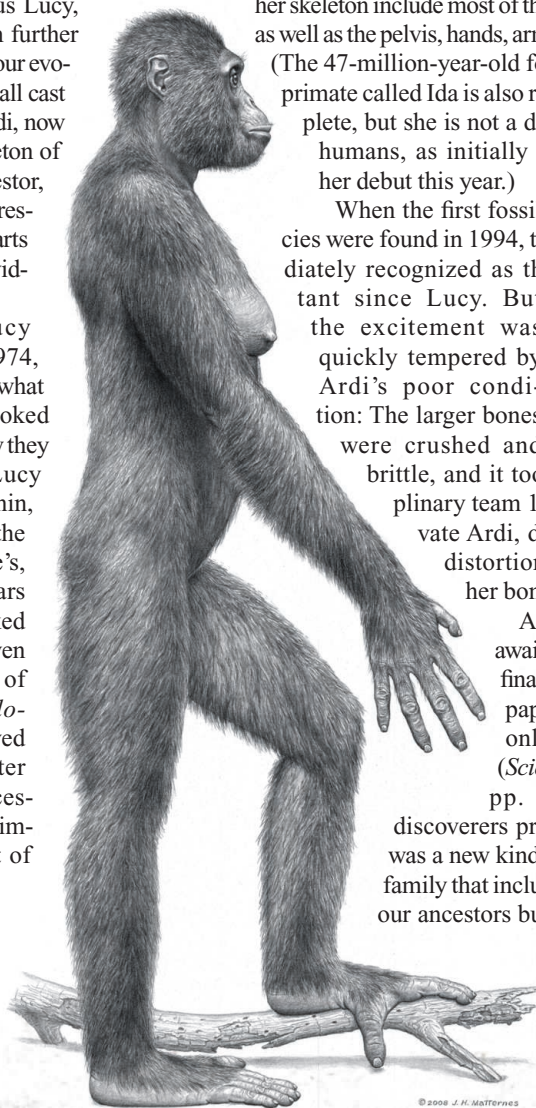
Ardipithecus ramidus

A rare skeleton draws back the curtain of time to reveal the surprising body plan and ecology of our earliest ancestors

ONLY A HANDFUL OF INDIVIDUAL FOSSILS HAVE become known as central characters in the story of human evolution. They include the first ancient human skeleton ever found, a Neanderthal from Germany's Neander Valley; the Taung child from South Africa, which in 1924 showed for the first time that human ancestors lived in Africa; and the famous Lucy, whose partial skeleton further revealed a key stage in our evolution. In 2009, this small cast got a new member: Ardi, now the oldest known skeleton of a putative human ancestor, found in the Afar Depression of Ethiopia with parts of at least 35 other individuals of her species.

Ever since Lucy was discovered in 1974, researchers wondered what her own ancestors looked like and where and how they might have lived. Lucy was a primitive hominin, with a brain roughly the size of a chimpanzee's, but at 3.2 million years old, she already walked upright like we do. Even the earliest members of her species, *Australopithecus afarensis*, lived millions of years after the last common ancestor we shared with chimpanzees. The first act of the human story was still missing.

Now comes Ardi, a 4.4-million-year-old female who shines bright new light on an obscure time in our past.



Her discoverers named her species *Ardipithecus ramidus*, from the Afar words for "root" and "ground," to describe a ground-living ape near the root of the human family tree. Although some hominins are even older, Ardi is by far the most complete specimen of such antiquity. The 125 pieces of her skeleton include most of the skull and teeth, as well as the pelvis, hands, arms, legs, and feet. (The 47-million-year-old fossil of the early primate called Ida is also remarkably complete, but she is not a direct ancestor to humans, as initially claimed during her debut this year.)

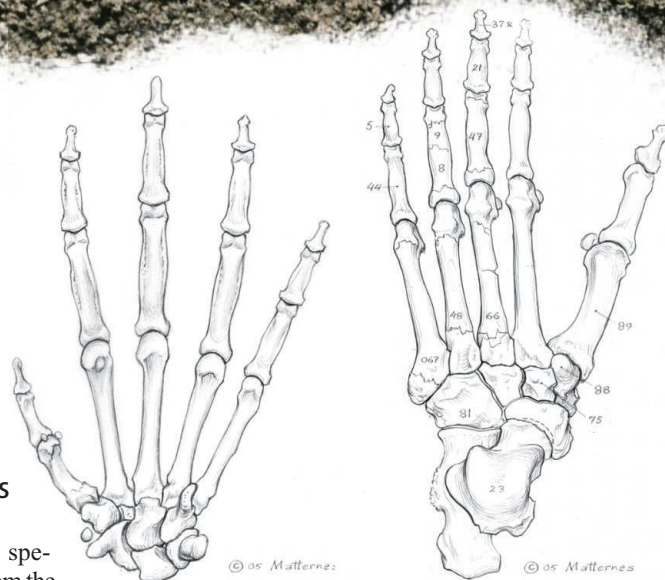
When the first fossils of Ardi's species were found in 1994, they were immediately recognized as the most important since Lucy. But

the excitement was quickly tempered by Ardi's poor condition: The larger bones were crushed and

brittle, and it took a multidisciplinary team 15 years to excavate Ardi, digitally remove distortions, and analyze her bones.

Ardi's long-awaited skeleton was finally unveiled in 11 papers in print and online in October (*Science*, 2 October, pp. 60–106). Her

discoverers proposed that she was a new kind of hominin, the family that includes humans and our ancestors but not the ancestors of other living apes. They say that



By hand or by foot? Ardi's foot (right) has an opposable toe for grasping branches.

Ardi's unusual anatomy was unlike that of living apes or later hominins, such as Lucy. Instead, Ardi reveals the ancient anatomical changes that laid the foundation for upright walking.

Not all paleoanthropologists are convinced that *Ar. ramidus* was our ancestor or even a hominin. But no one disputes the importance of the new evidence. Only a half-dozen partial skeletons of hominins older than 1 million years have ever been published. And having a skeleton rather than bits and pieces from

BREAKTHROUGH ONLINE

For an expanded version of this section, with references, links, and multimedia, see www.sciencemag.org/btoy2009 and sciencecareers.org.

different individuals not only provides a good look at the whole animal but also serves as a Rosetta stone to help decipher more fragmentary fossils. As the expected

debate over Ardi's anatomy and relations to other primates begins, researchers agree that she and the other specimens of her species provide a wealth of new and surprising data on some of the most fundamental questions of human evolution: How can we identify the earliest members of the human family? How did upright walking evolve? What did our last common ancestor with chimpanzees look like? From now on, researchers asking those questions will refer to Ardi.

Body of evidence

Ardi's biggest surprise is that she was not transitional between *Australopithecus* and a common ancestor that looked like living chimpanzees and gorillas. Standing 120 centimeters tall, Ardi had a body and brain only slightly larger than a chimpanzee's, and she was far more

Ancient upstart. Ardi may have moved upright on branches and on the ground, a key step in the evolution of upright walking.

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primitive than Lucy. But she did not look like an African ape, or even much like the known fragments of more ancient apes.

When researchers studied her face and teeth, they found derived features that tie *Ardipithecus* to all later hominins, including Lucy's species and us. For example, Ardi's muzzle juts out less than a chimpanzee's does. Even males of her species lacked the large, sharp, daggerlike upper canines seen in chimpanzees. The base of her skull is short from front to back, as in upright walkers, rather than elongated, as in quadrupedal apes.

In addition, Ardi's pelvis convinced her discoverers that she did indeed walk upright—long the defining trait for being a member of the human family. The upper blades of Ardi's pelvis are shorter and broader than in living apes, lowering her center of gravity so she could balance on one leg at a time while walking, for example. But she didn't walk as well as humans or Lucy. Her pelvis was useful for both climbing and upright walking, making her a "facultative" biped, according to her discoverers.

Ardi's remarkably complete hand and foot bones add to this picture. Her wrist joints were not as stiff as those of African apes, and the bones of her palm were short, indicating that she did not knuckle-walk like chimpanzees or swing beneath tree branches, the discoverers say. Yet Ardi's foot was more rigid than a chimpanzee's, suggesting that it was an odd mosaic used for both upright walking on the ground and careful climbing and walking atop branches in the trees. Indeed, Ardi's long curving fingers and opposable big toe suggest she grasped tree branches.

If so, our ancestors began walking upright while still living primarily in a woodland rather than in more open, grassy terrain, as once believed. The international discovery team went to great lengths to reconstruct the scene where Ardi took her first steps, collecting 150,000 specimens of fossil plants and animals from Aramis and nearby. After using radiometric methods to tightly date the fossil-bearing sediments to 4.4 million years ago, the team concluded that Ardi lived on an ancient floodplain covered in sylvan woodlands, climbing among hackberry, fig, and palm trees, and coexisting with monkeys, kudu antelopes, and peafowl.

Human relations

At face value, Ardi is a hominin—if you define hominin on the basis of traits in the face, skull, and teeth. Many researchers who have read the descriptions of *Ardipithecus* or seen casts of the fossils agree on this. But since Lucy's discovery, the gold standard for identifying a hominin has been walking upright. Among primates, only humans and our closest relatives were habitual bipeds. On this point, Ardi stands on shakier ground.

The pelvis, which provides the pivotal evidence for upright walking, is fragmentary

or was less able to climb and swing beneath branches. The next steps will be to further compare Ardi's bones with those of more ancient apes and to see how her unique anatomical features affected how she moved.

Many researchers also challenge the papers' forceful argument that Ardi reveals the basic body plan of the common ancestor of humans and chimpanzees. They point out that Ardi lived perhaps 1 million to 3 million years after that ancestor—plenty of time for evolutionary change. Some also question the social implications of *Ardipithecus* males' reduced canines, which the discovery team interprets as implying less male-male aggression than is seen in chimps.

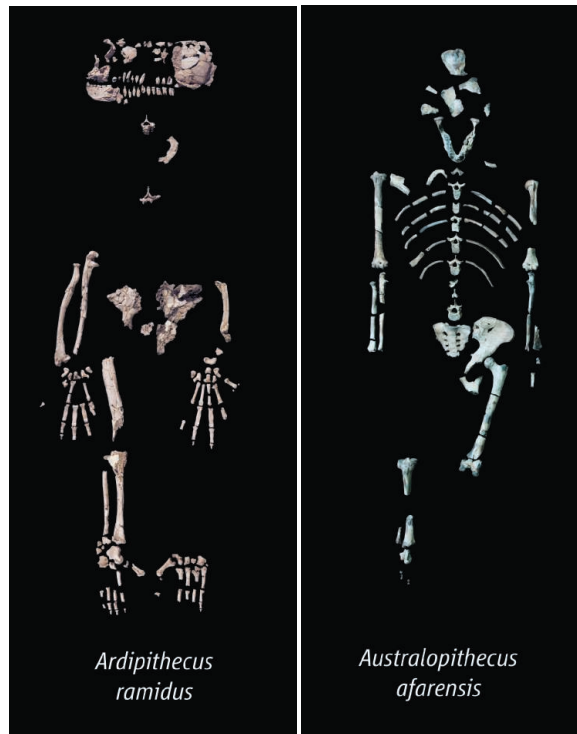
The debate reveals how hard it is to identify upright walking in such an early hominin. Must Ardi walk upright like an australopithecine to be admitted to the human family? Or is it enough that she walked upright in an intermediate manner, if her face, skull, and canines align her with later protohumans? Ardi is already prompting some to ask whether habitual upright walking is essential to being a hominin. Perhaps some ancient apes became hominins head first.

There's precedent for new hominin fossils provoking controversy and redefining what it means to be a member of the human family. Many thought a big brain and tool use emerged in concert with upright walking—until Lucy, with her chimp-sized brain, proved that upright walking came first.

As researchers ponder the definition of a hominin, they also wonder exactly where Ardi fits in our family tree. The discovery team suggested as one hypothesis that *Ardipithecus* gave rise to Lucy's genus *Australopithecus*, which is generally thought to have led to our own genus, *Homo*. But they also noted that Ardi could have been a side branch, an extinct lineage that was a sister species to our direct ancestors. As the study of Ardi widens to include new collaborators, the team is granting requests to view the casts and will return to Aramis to search for more fossils.

In the year of the bicentennial of Darwin's birth, it seems fitting that researchers finally broke through the 4-million-year barrier to understanding our origins. Models for our earliest ancestors can now be informed by plenty of fresh data and at least one body of hard evidence.

—ANN GIBBONS



Lucy, meet Ardi. Ardi (left) this year joined Lucy as one of the rare fossil hominin skeletons that shape our understanding of human evolution.

and crushed—parts of it have been called "Irish stew"—and outside researchers want to review its reconstruction. The discoverers note, however, that the interpretation of upright walking rests on traits in the foot and on the best-preserved portions of the original pelvis, not the reconstruction.

A few outside researchers who have already seen the cast of the pelvis agree that it shares some key traits with later hominins, such as the shape and size of a large opening known as the sciatic notch. Yet Ardi's hands and feet are so primitive that some researchers strongly question whether she really walked upright more often than other apes