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By Katherine Harmon

PUZZLE PIECES:
Fragmented skeleton of Aridpithecus ramidus has upended ideas about the earliest humans.

ANCESTRY
our most ancient progenitors

By Katherine Harmon
FROM A DISTANCE, YOU PROBABLY WOULD have assumed her to be human. Although she stood only about a meter tall, with long arms and a small head, she walked, if perhaps slightly inelegantly, upright on two legs, as we, alone among living mammals, do. This familiar yet strange individual is Lucy, a member of the species Australopithecus afarensis, who lived some 3.2 million years ago. She is one of the oldest creatures presumed to have strode on the evolutionary path leading to our species, Homo sapiens.

When Lucy was uncovered in 1974, evidence of bipedal locomotion virtually guaranteed her kind a spot in the human family tree. And although scientists had an inkling that other branches of humans coexisted more recently alongside our own, early human evolution appeared to be a simple affair, with Lucy and the other ancient bipeds that eventually came to light belonging to the same lone lineage. Thus, the discoveries seemed to uphold the notion of human evolution as a unilinear “march of progress” from a knuckle-walking chimplike ape to our striding, upright form—a schema that has dominated paleoanthropology for the past century. Yet as researchers dig back further in time, our origins are turning out to be a lot more complicated than that iconic image would suggest.

Two recent discoveries are shattering what scientists thought they knew about the rise of humans: one a stunningly complete skeleton from 4.4 million years ago and the other a very fragmentary foot from 3.4 million years ago. The freshly described fossils indicate that we probably came from a convoluted tree of humans—and that the ostensibly human hallmark of upright walking may have developed more than once—and in more than one fashion—including in creatures that were not our direct ancestors. Because of these finds, researchers are now reconsidering what traits mark a species as a direct human ancestor, what the pace has been for human evolution and whether it will ever be possible to confidently identify our last common ancestor with chimps.

“The more fossils we get, the more we’re realizing that the evolutionary tree is actually quite bushy,” says Carol V. Ward of the University of Missouri School of Medicine. The remains are also revealing that the human line is not the only one to have undergone astounding adaptations in the past several million years. The chimpanzee lineage, too, has surely changed considerably over that same period, becoming highly specialized for life in the trees—a revelation that may finally lay to rest the abiding notion that living chimpanzees are a good model for our ancient ancestors. This shift “gives us a whole different perspective on our origins,” Ward says.

SMALL HOMININ, BIG SHIFT

Nothing threw as large a wrench into the hunched-ape-to-Homo scenario as the petite creature known as Ardi. The description of this remarkably complete 4.4-million-year-old skeleton of Ardipithecus ramidus in a ream of papers in 2009 sent paleoanthropology into a tailspin. Uncovered at a site called Aramis in Ethiopia’s Afar region, Ardi looks little like researchers would have expected of a hominin from that time period (hominins are primates more closely related to us than are chimps—our closest living relatives). Many paleoanthropologists anticipated that a hominin dating to that era would have many traits of humans, of which our species is the sole survivor. Recent fossil discoveries have upended that scenario, however, providing intriguing evidence that the last common ancestor of humans and chimpanzees may not have looked particularly chimplike and that our early forebears were not alone in Africa. The findings are forcing researchers to reconsider what traits indicate that a species belongs on the line leading to us—and to question whether it will ever be possible to identify our last common ancestor.
seen in chimps and other modern African apes, including large canine teeth for aggression-based social systems, very long arms and fingers for climbing in trees, and wrist adaptations for knuckle walking, among other features.

Instead the slight *A. ramidus* is what Tim D. White of the University of California, Berkeley, who led the team that discovered Ardi, has described as a “mosaic organism” that possesses characteristics of later hominins and ancient apes—but not so much of chimpanzees. Like humans, Ardi has reduced canine teeth, which researchers think might signify a transition away from a male-dominated social system toward a more cooperative system revolving around pairs who form long-term bonds. Also unlike modern African apes, Ardi’s high degree of wrist extension suggests that when she walked on all fours, she supported her weight on her palms rather than her knuckles. Meanwhile Ardi’s fingers were relatively long and curved—helpful for climbing trees—but her wrists and hands might have prevented her from swinging between branches as capably as chimpanzees do.

Ardi’s lower limbs exhibit a similar combination of humanlike and ancient apelike characteristics. Whereas her relatively flat feet and divergent big toe (or hallux) would have aided arboreal locomotion, the stiffness of her foot and her minor toes’ ability to flex backward would have facilitated bipedal walking. Her pelvis was badly crushed, leaving some details about her leg motion unknown. But William Jungers of Stony Brook University says that from what he can tell, the short distance between Ardi’s hip bone and sacrum (the triangular bone at the base of the spine) is similar to that found in modern humans and other hominins known to have walked upright. Additionally, the foramen magnum, the opening at the base of the skull through which the spinal cord exits, is located quite far forward in Ardi—a trait that many scientists read as an indication of a vertical stance (and possible bipedalism) when she was on the ground. Some researchers, however, wonder whether she was instead only likely to stand upright intermittently, for example, if she needed to hold something in her hands.

With her startling mélange of anatomical features, Ardi has challenged scientists to reconsider how they define a hominin. The term has traditionally implied obligate upright walking. Yet Ardi shows that potential bipedalism does not exclude decent climbing capabilities. Even modern humans have some locomotor flexibility. “I think people forget [what] good climbers modern people are,” Jungers says. We might not be as well suited to swinging from branch to branch as chimps and other apes are, but in many indigenous human cultures, tree climbing is still an important method of gathering food. Moreover,
This ancient ape had several features indicative of upright posture, including short hips and a forward-located foramen magnum (the hole in the base of the skull through which the spinal cord passes). Like modern gibbons, however, it might only have used this posture in the trees.

This species is known only from skull fossil evidence, so little can be determined about how it got around. But the forward location of its foramen magnum hints at upright posture—at least in the branches.

The “Ardi” specimen’s pelvis is badly damaged, leaving some details of her locomotion unknown. But rigid feet and domed metatarsal heads suggest that she at least could get around bipedally while on the ground. Her upper body, in contrast, still features assets of an agile tree climber, including fairly long fingers and arms.

Hip and knee mechanics reveal that Lucy’s species strode upright though it retained some adaptations in its upper limbs for climbing. Most researchers agree that A. afarensis is a strong candidate for a direct human ancestor.

This species shows changes in its pelvis and feet that signal bipedal locomotion, although details of the ankle and midfoot suggest it walked quite differently than others in its genus. A. sediba still possessed long arms that could have been used for climbing, however.

Chimpanzees are highly specialized tree climbers, possessing long fingers and arms and grasping big toes to help them get around in the branches. Although scientists once thought chimpanzees were a good model for the last common ancestor of chimps and humans, discoveries of fossils such as Ardi—which does not look particularly chimplike—suggest that chimps have instead undergone just as much evolution as humans have since our lineages parted ways.
Our Tangled Family Tree

The evolution of *Homo sapiens* has long been viewed as a simple, stepwise trajectory that proceeded from a primitive chimpanzee ape, through a series of intermediary protohumans, and finally to upright and elegant humans. With each station, the features morphed in a single direction: fingers shortened, big toes came into forward alignment, and the head shifted to rest atop a vertical back. New discoveries, however, have shown this “march of progress” picture to be flawed. Fingers have come in all different lengths, diverged big toes (for climbing in trees) have persisted alongside forward-aligned big toes (adapted for upright walking), and even ancient apes show adaptations for walking upright.

This jumble of fossil features emphasizes that evolution is a messy business and hints that early human evolution involved multiple parallel lineages (orange and blue paths) just as later human evolution did. Thus, figuring out which species fossils belong to, along with sorting ancestral lines from dead-end branches, will be harder than was once thought. The illustration on these pages shows how the distribution of some key features related to locomotion in modern and extinct apes and human relatives is complicating the story of our origins.

*Orrorin tugenensis*

Only scattered fossils paint the picture of this animal. But some bones, such as the femur, suggest that this species might have been at least partially adapted for upright walking. Yet its strong arm muscle attachment and curved finger bone seem good for tree climbing.

*Burtele species*

Although only eight bones from this animal have been described, researchers are confident that it represents a new hominin species—one that was still prominently arboreal despite living at the same time as the bipedal *Australopithecus afarensis*, a probable direct ancestor of ours.

*Homo sapiens*

Modern humans have many adaptations for walking upright, including arched feet and aligned big toes. We have retained some ability to climb trees, but we cannot swing through the branches like chimpanzees can, nor can we navigate the arboreal realm as adeptly as our early human relatives could.

*Homo heidelbergensis*

Evidence of adaptations for living in trees

- Strong
- Moderate

Evidence of adaptations for walking upright

- Strong
- Moderate
“What we’re glimpsing in the fossil record is but a flicker of the ancient diversity.”

—Carol V. Ward, University of Missouri School of Medicine

Lucy's species—*A. afarensis*—for all its bipedal ability, retained relatively long arms, suggesting that it might still have occasionally ascended into the trees. A recent analysis of fossils from a young *A. afarensis* found in 2000 in Dikika, Ethiopia, indicates that the species had rather apelike shoulders, which presumably rendered it a proficient climber. So perhaps Lucy, like Ardi and other species that came before and after, had “the best of both possible worlds,” Jungers says.

White and his colleagues have placed *A. ramidus* as a possible ancestor to *A. afarensis*—and therefore as a potential direct forebear to *H. sapiens*. Given Ardi’s age and other details of her anatomy, however, plenty of researchers suspect she might not be in our direct line. “Ardi may be an early hominin that went off in its own direction,” says David Begun of the University of Toronto. Ardi lived just 200,000 years before a more solidly bipedal species called *Australopithecus anamensis*, which many experts believe to be ancestral to *A. afarensis*. A rapid evolution from *A. ramidus* to *A. anamensis* (eventually leading to *A. afarensis*) might have been possible, but many researchers, including Begun, agree that the more likely explanation is that these species belong not to a single tidy lineage but to two or more different lines. “I think [*A. ramidus*] probably is an evolutionary side branch,” Begun says. Not even Lucy’s place as a direct human ancestor has been settled; the paucity of hominin fossils between the end of the Miocene and the emergence of early *Homo* has kept this question open, notes Yohannes Haile-Selassie of the Cleveland Museum of Natural History, who worked on the 2009 Ardi papers.

Although Ardi’s curious mix of traits—those palm-walking wrists, backward-flexing toes and small canine teeth, for instance—has caused considerable consternation over her place in the family tree, her remains have yielded important insights into human origins precisely because she neither resembles a chimp nor fits the traditional conception of a hominin. If she is an early hominin in the line leading to us, then our last common ancestor probably did not look much like a chimpanzee. And if Ardi represents a hominin lineage distinct from our own or perhaps is an extinct ape, then she shows that upright walking is not the defining trait of our line alone. Either way, scientists’ understanding of human evolution gets a shake-up.

**COMPANY FOR LUCY**

While many researchers were still reeling from the implications of Ardi, a new anatomical mystery emerged from a site called Burtele, also in Ethiopia’s central Afar region. Described in 2012, this find consists of just eight small foot bones—too few to warrant a new species name but enough for scientists to confidently assert that this specimen is unlike anything seen before. The foot hammers home the idea that hominin evolution was a lot more complex than even Ardi would suggest.

Despite having few bones to tell us about the Burtele speci-
Scientists are also slowly learning that these findings should not be as unexpected as they have been. Ward suggests that “when you find something like the Burtele foot, which is clearly different than *A. afarensis*, in some ways we should say, ‘Of course!’” In the Miocene epoch, between 23 million and five million years ago, hundreds of great ape species lived all over the world. To think that somehow that diversity suddenly disappeared is crazy, Ward says. “What we’re glimpsing in the fossil record is but a flicker of the ancient diversity,” she adds. Unfortunately, however, the variety makes it harder to identify our early direct ancestors and the last common ancestor of humans and chimpanzees. Further complicating matters, chimpanzees and other African apes currently have a poor fossil record.

Will it ever be possible to infer evolutionary relationships precisely enough to construct our family tree with confidence? Possibly not—at least not anytime soon. In a 2011 paper in *Nature*, two anthropologists said the quest may be doomed by homoplasy, in which different species develop similar traits independently. (*Scientific American* is part of Nature Publishing Group.) Independent development means that the presence of a trait, such as walking upright—even in species separated by millions of years—does not guarantee that one species is directly descended from the other. “Shared features can only take you so far in determining evolutionary relationships,” notes biological anthropologist Terry Harrison of the Center for the Study of Human Origins at New York University, co-author of the *Nature* paper with Bernard Wood of George Washington University.

For instance, the extinct ape *Oreopithecus bambolii*, which lived in what is now Italy nine million to seven million years ago, had small canine teeth relative to other Miocene apes, a short face, a forwardly placed foramen magnum, and short, broad hips—all features associated with hominins. Yet it is nonetheless assumed to be a primitive great ape rather than an early hominin, partly because of its different style of upright locomotion (which may have been confined to trees—similar to extant gibbons), along with characteristics of its feet, fingers and arms, which appear to have been well adapted to climbing in, and swinging among, tree branches.

The Burtele foot adds evidence for homoplasy in the case of upright walking. “Just like you have multiple forms of climbing and multiple ways of walking on four legs in the primate world, why not a couple of different versions of being bipedal?” DeSilva asks. “Evolution’s pretty clever and comes up with solutions to problems over and over again.” He admits to having been a critic of theories arguing for different types of upright walking in creatures, such as the recently discovered *Australopithecus sediba*, a nearly two-million-year-old species from South Africa, which had unique heel, ankle, midfoot and knee anatomy. He initially had assumed that the anatomical variations evident in this species might not result in much more locomotor difference than the variation seen in how various modern humans walk. But the Burtele bones helped to change his mind. “No one’s bones look like that,” he says. “You’re forced to come to the conclusion that there were different strategies—different ways of getting around.”

But this realization is not always comfortable. “Everybody wants to think that humans are special,” Latimer says. But if Ardipithecus and other early hominins possess so many nonchimpanzee traits and chimps themselves are so highly derived, then our last common ancestor was probably not chimplike. Indeed, it may have looked more homininlike. Latimer points out that the last common ancestor probably had shorter fingers, like those of *A. ramidus* and *A. afarensis*. It probably also had a brain smaller than a chimp’s. As Jungers notes, chimpanzees appear to have bigger brains than some early hominins.

The challenge of figuring out what the last common ancestor might have looked like and how it moved seems bound to intensify. If the past decade has taught paleoanthropologists anything, it is that the branches of human ancestors most likely will continue to get even more convoluted—especially going back further in time. “It’ll get messy back there,” Latimer says.

**ANCESTRAL QUAGMIRE**

To make matters more confusing, the last common ancestor is not going to be a single individual, as DeSilva points out. It is going to be a population—and that population will have cousins, and they will have cousins. “Knowing whether you have the common ancestor without DNA is going to be difficult.”

Advances in genetic analysis of living humans and apes have helped scientists estimate when our last common ancestor with chimps lived. But the window—of six million to 10 million years—is still a large one, and sequencing alone cannot yet reveal what the creature might have looked like. Still, current research is starting to refine estimates of mutation rates, which will narrow the target and help paleoanthropologists home in on geologic deposits of the right age that could potentially yield fossils of the ancestor. And pairing fossil evidence with genetic analysis can move the science forward by fleshing out what changes in the genome separated our line from that of chimpanzees as we first began to diverge.

Yet without the genomes of these ancient hominins, it is difficult to place them on any kind of a family tree—or Bramble bush. This endeavor is especially tricky “because these things are more closely related to you and me than anything else living on the planet today,” DeSilva explains. So, for example, trying to figure out what the smallest changes in the shape of a foot bone over time say about the evolutionary relationships of the creatures represented in the fossil record has been, unsurprisingly, quite difficult and often contentious.

Although many researchers suspect they might not ever be able to put together a complete picture of hominin ancestry, that worry is unlikely to stop them from trying. But this ever shifting field will need to brace for more Ardis and many more Burteles that shake the established tree. “Be prepared to be shown that you’re wrong,” DeSilva says. “Embrace it—because it shows that things are much more interesting and surprising.”

**Katherine Harmon is an associate editor at Scientific American. Her book about octopuses will be published this fall by Penguin’s Current imprint. Sharon Begley provided additional reporting for this article.**