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Ardipithecus ramidus

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See also related video, Science Podcast at www.sciencemag.org/ardipithecus/
Charles Darwin’s seminal work *On the Origin of Species*, published 150 years ago next month, contains just one understated sentence on the implications of his theory for human evolution: “Light will be thrown on the origin of man and his history.” As Darwin implied in his introduction to *The Descent of Man*, he felt that those implications were obvious; he appreciated, as events quickly showed, that it would be only natural to look at evolution foremost from our human perspective and contemplate what makes us unique among other primates—our large brains and ability to communicate, to create, and to understand and investigate our history and nature; our culture, society, and religion; the ability to run fast on two legs and manipulate tools; and more innovations that separate us from our primate relatives.

Tracing our evolution and how we came to acquire these skills and traits, however, has been difficult. Genetic data now confirm that our closest living primate relative is the chimpanzee. We shared and evolved from a common ancestor some 6 million or more years ago. But identifying our unique genes and other genetic differences between us and our primate cousins does not reveal the nature of that ancestor, nor what factors led to the genetic changes that underlie our divergent evolutionary paths. That requires a fossil record and enough parts of past species to assess key anatomical details. It also requires knowing the habitat of early humans well, to determine their diet and evaluate what factors may have influenced their evolution through time. Many early human fossils have been found, but with a few exceptions, these are all less than 4 million years old. The key first several million years of human evolution have been poorly sampled or revealed.

This issue presents 11 papers authored by a diverse international team (see following pages) describing an early hominin species, *Ardipithecus ramidus*, and its environment. The hominid fossils are 4.4 million years old, within this critical early part of human evolution, and represent 36 or more individuals, including much of the skull, pelvis, lower arms, and feet from one female. The papers represent three broad themes. Five focus on different parts of the anatomy that are revealing for human evolution. These show that *Ardipithecus* was at home both moving along trees on its palms and walking upright on the ground. Three characterize *Ardipithecus*’s habitat in detail, through analysis of the hosting rocks and thousands of fossils of small and large animals and plants. These show that *Ardipithecus* lived and ate in woodlands, not grasslands. The first paper presents an overview, and it and the last two papers trace early human evolution and synthesize a new view of our last common ancestor with chimps. One conclusion is that chimps have specialized greatly since then and thus are poor models for that ancestor and for understanding human innovations such as our ability to walk.

These papers synthesize an enormous amount of data collected and analyzed over decades by the authors. Because of the scope of these papers and the special broad interest in the topic of human evolution, we have expanded our usual format for papers and coverage. The papers include larger figures, tables, and discussions, and the overview and two concluding papers provide extended introductions and analyses.

In addition, to aid understanding and introduce the main results of each paper, the authors provide a one-page summary of each paper, with an explanatory figure aimed at the general reader. Our News Focus section, written by Ann Gibbons, provides further analysis and coverage, and it includes maps and a portrait of the meticulous and at times grueling field research behind the discoveries. Available online are a video interview and a podcast with further explanations.

To accommodate this material and allow the full papers, this print issue presents an Editorial, News coverage, the authors’ summaries, and four papers in full: the overview paper and one key paper from each thematic group above. The other research papers, and of course all content, are fully available online. In addition, a special online page (www.sciencemag.org/Ardipithecus/) links to several print and download packages of this material for AAAS members, researchers, educators, and other readers.

This collection, essentially an extra issue of *Science* in length, reflects efforts by many behind the scenes. Every expert reviewer evaluated, and improved, multiple papers, and several commented on all 11 of them. The authors provided the summaries on top of an already large writing and revision effort. Paula Kiberstis helped in their editing. The figures and art were drafted and improved by J. H. Matternes, Henry Gilbert, Kyle Brudvik, and Josh Carlson, as well as Holly Bishop, Nathalie Cary, and Yael Kats at *Science*. Numerous other *Science* copyediting, proofreading, and production staff processed this content on top of their regular loads. Finally, special thanks go to the people of Ethiopia for supporting and facilitating this and other research into human origins over many years, and for curating *Ardipithecus ramidus* for future research and for all of us to admire.

*Ardipithecus ramidus* thus helps us bridge the better-known, more recent part of human evolution, which has a better fossil record, with the scarcer early human fossils and older ape fossils that precede our last common ancestor. *Ardipithecus ramidus* is a reminder of Darwin’s conclusion of *The Origin*:

> There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

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Understanding Human Origins

RESPONDING TO A QUESTION ABOUT HIS SOON-TO-BE-PUBLISHED ON THE ORIGIN OF SPECIES, Charles Darwin wrote in 1857 to Alfred Russel Wallace, “You ask whether I shall discuss ‘man’; I think I shall avoid the whole subject, as so surrounded with prejudices, though I freely admit that it is the highest and most interesting problem for the naturalist.” Only some 14 years later, in The Descent of Man, did Darwin address this “highest problem” head-on: “There, he presciently remarked in his introduction that “It has often and confidently been asserted, that man’s origin can never be known: but . . . it is those who know little, and not those who know much, who so positively assert that this or that problem will never be solved by science.”

Darwin was certainly right. The intervening years provide conclusive evidence that it is very unwise to predict limits for what can be discovered through science. In fact, it now seems likely that, through synergistic advances in many disciplines, scientists will eventually decipher a substantial portion of the detailed evolutionary history of our own species at both the morphological and molecular levels.

First, what can we expect from paleoanthropology? In this 200th anniversary year of Darwin’s birth, Science is pleased to publish the results of many years of scientific research that suggest an unexpected form for our last common ancestor with chimpanzees. This issue contains 11 Research Articles involving more than 40 authors, plus News articles that describe the life and times of Ardipithecus ramidus, a hominid species that lived 4.4 million years ago in the Afar Rift region of northeastern Ethiopia. This region exposes a total depth of 300 meters of sediments that were deposited in rivers, lakes, and floodplains between about 5.5 and 3.8 million years ago. Even considering only this one site (there are many others), it is staggering to reflect on the huge number of hominin remains that can in principle be discovered, given sufficient time and effort. Moreover, the history of science assures us that powerful new techniques will be developed in the coming years to accelerate such research, as they have been in the past. We can thus be certain that scientists will eventually obtain a rather detailed record showing how the anatomy of the human body evolved over many millions of years.

What can we expect from a combination of genetics, genomics, biochemistry, and comparative organissal biology? We will want to interpret the history of the morphological transformations in the humanoid skeleton and musculature in terms of the molecular changes in the DNA that caused them. Genes and their regulatory regions control the morphology of animals through very complex biochemical processes that affect cell behavior during embryonic development. Nevertheless, experimental studies of model organisms such as fruit flies, worms, fish, and mice are advancing our understanding of the molecular mechanisms involved. New inexpensive methods for deciphering the complete genome sequence of any organism will soon accelerate this process, allowing scientists to analyze the recurring evolutionary morphological transformations that have been identified by organismal biologists, so as to determine the specific DNA changes involved. And the DNA sequences that have changed most rapidly during recent human evolution are being cataloged, providing a new tool for finding important molecular differences that distinguish us from chimpanzees.

The majesty of the discoveries already made represents a major triumph of the human intellect. And, as emphasized here, there will be many more discoveries to come. Darwin’s summary of his own efforts to understand human evolution is thus still relevant today: “Man may be excused for feeling some pride at having risen, though not through his own exertions, to the very summit of the organic scale; and the fact of his having thus risen, instead of having been aboriginally placed there, may give him hope for a still higher destiny in the distant future.”

— Bruce Alberts

Every day, scientists add new pages to the story of human evolution by deciphering clues to our past in everything from the DNA in our genes to the bones and artifacts of thousands of our ancestors. But perhaps once each generation, a spectacular fossil reveals a whole chapter of our prehistory all at once. In 1974, it was the famous 3.2-million-year-old skeleton “Lucy,” who proved in one stroke that our ancestors walked upright before they evolved big brains.

Ever since Lucy’s discovery, researchers have wondered what came before her. Did the earliest members of the human family walk upright like Lucy or on their knuckles like chimpanzees and gorillas? Did they swing through the trees or venture into open grasslands? Researchers have had only partial, fleeting glimpses of Lucy’s own ancestors—the earliest hominins, members of the group that includes humans and our ancestors (and are sometimes called hominids).

Now, in a special section beginning on page 60 and online, a multidisciplinary international team presents the oldest known skeleton of a potential human ancestor, 4.4-million-year-old *Ardipithecus ramidus* from Aramis, Ethiopia.

This remarkably rare skeleton is not the oldest putative hominin, but it is by far the most complete of the earliest specimens. It includes most of the skull and teeth, as well as the pelvis, hands, and feet—parts that the authors say reveal an “intermediate” form of upright walking, consid-
ed a hallmark of hominins. “We thought Lucy was the find of the century, but, in retrospect, it isn’t,” says paleoanthropologist Andrew Hill of Yale University. “It’s worth the wait.”

To some researchers’ surprise, the female skeleton doesn’t look much like a chimpanzee, gorilla, or any of our closest living primate relatives. Even though this species probably lived soon after the dawn of humankind, it was not transitional between African apes and humans. “We have seen the ancestor, and it is not a chimpanzee,” says paleoanthropologist Tim White of the University of California, Berkeley, co-director of the Middle Awash research group, which discovered and analyzed the fossils.

Instead, the skeleton and pieces of at least 35 additional individuals *Ar. ramidus* reveal a new type of early hominin that was neither chimpanzee nor human. Although the team suspects that *Ar. ramidus* may have given rise to Lucy’s genus, *Australopithecus*, the fossils how for the first time that there is some new evolutionary grade of smid that is not *Australopithecus*, that is not *Homo*,” says paleontologist Michel Brunet of the College de France in Paris.

In 11 papers published in this issue and online, the team of 47 researchers describes how *Ar. ramidus* looked and moved. The skeleton, nicknamed “Ardi,” is from a female who lived in a woodland clearing near the village of Aramis. It was the polished surface of a tooth root, and he immediately knew it was a hominin molar. Over the next few days, the team scoured the area on hands and knees, as they do whenever an important piece of hominin is found (see story, p. 41), and collected the lower jaw of a child with the milk molar still attached. The molar was so primitive that the team knew they had found a hominin both older and more primitive than Lucy. Yet the jaw also had derived traits—novel evolutionary characters—shared with Lucy’s species, *Au. afarensis*, such as an upper canine shaped like a diamond in side view.

The team reported 15 years ago in *Nature* that the fragmentary fossils belonged to the “long-sought potential root species for the Hominidae.” (They first called it *Au. ramidus*, then, after finding parts of the skeleton, changed it to *Ar. ramidus*—for the Afar words for “root” and “ground.”) In response to comments that he needed leg bones to prove *Ar. ramidus* was an upright hominin, White joked that he would be delighted with more parts, specifically a thigh and an intact skull, as though placing an order.

Within 2 months, the team delivered. In November 1994, as the fossil hunters crawled up an embankment, Berkeley graduate student Yohannes Haile-Selassie of Ethiopia, now a paleoanthropologist at the Cleveland Museum of Natural History in Ohio, spotted two pieces of a bone from the palm of a hand. That was soon followed by pieces of a pelvis; leg, ankle, and foot bones; many of the bones of the hand and arm; a lower jaw with teeth—and a cranium. By January 1995, it was apparent that they had made the rarest of rare finds, a partial skeleton.

“The authors … are framing the debate that will inevitably follow,” because the description and interpretation of the finds are entwined, says Pilbeam. “My first reaction is to be skeptical about some of the conclusions,” including that human ancestors never went through a chimpanzee-like phase. Other researchers are focusing intently on the lower skeleton, where some of the anatomy is so primitive that they are beginning to argue over just what it means to be “bipedal.”

The pelvis, for example, offers only “circumstantial” evidence for upright walking, says Walker. But however the debate about Ardi’s locomotion and identity evolves, she provides the first hard evidence that will inform and constrain future ideas about the ancient hominin bauplan.
It is one of only a half-dozen such skeletons known from more than 1 million years ago, and the only published one older than Lucy.

It was the find of a lifetime. But the team’s excitement was tempered by the skeleton’s terrible condition. The bones literally crumbled when touched. White called it road kill. And parts of the skeleton had been trampled and scattered into more than 100 fragments; the skull was crushed to 4 centimeters in height. The researchers decided to remove entire blocks of sediment, covering the blocks in plaster and moving them to the National Museum of Ethiopia in Addis Ababa to finish excavating the fossils.

It took three field seasons to uncover and extract the skeleton, repeatedly crawling the site to gather 100% of the fossils present. At last count, the team had cataloged more than 110 specimens of *Ar. ramidus*, not to mention 150,000 specimens of fossil plants and animals. “This team seems to suck fossils out of the earth,” says anatomist C. Owen Lovejoy of Kent State University in Ohio, who analyzed the postcranial bones but didn’t work in the field. In the lab, he gently unvels a cast of a tiny, pea-sized sesamoid bone for effect. “Their obsessiveness gives you—this!”

White himself spent years removing the silty clay from the fragile fossils at the National Museum in Addis Ababa, using brushes, syringes, and dental tools, usually under a microscope. Museum technician Alemu Ademassu made a precise cast of each piece, and the team assembled them into a skeleton.

Meanwhile in Tokyo and Ohio, Suwa and Lovejoy made virtual reconstructions of the crushed skull and pelvis. Certain fossils were taken briefly to Tokyo and scanned with a custom micro–computed tomography (CT) scanner that could reveal what was hidden inside the bones and teeth. Suwa spent 9 years mastering the technology to reassemble the fragments of the cranium into a virtual skull. “I used 65 pieces of the cranium,” says Suwa, who estimates he spent 1000 hours on the task. “You go piece by piece.”

Once he had reassembled the pieces in a digital reconstruction, he and paleoanthropologist Berhane Asfaw of the Rift Valley Research Service in Addis Ababa compared the skull with those of ancient and living primates in museums worldwide. By March of this year, Suwa was satisfied with his 10th reconstruction. Meanwhile in Ohio, Lovejoy made physical models of the pelvic pieces based on the original fossil and the CT scans, working closely with Suwa. He is also satisfied that the 14th version of the pelvis is accurate. “There was an *Ardipithecus* that looked just like that,” he says, holding up the final model in his lab.

**Putting their heads together**

As they examined Ardi’s skull, Suwa and Asfaw noted a number of characteristics. Her lower face had a muzzle that juts out less than a chimpanzee’s. The cranial base is rather than to the front of the spine, indicating that her head balanced atop the spine as in later upright walkers, rather than to the front of the spine, as in quadrupedal apes. Her face is in a more vertical position than in chimpanzees. And her teeth, like those of all other hominins, lack the daggerlike sharpened upper canines seen in chimpanzees. The team realized that this combination of traits matches those of an even older skull, 6-million to 7-million-year-old *Sahelanthropus tchadensis*, found by Brunet’s team in Chad. They conclude that both represent an early stage of human evolution, distinct from both *Australopithecus* and chimpanzees. “Similarities with *Sahelanthropus* are striking, in that it also represents a first-grade homind,” agrees Zollikofer, who did a three-dimensional reconstruction of that skull.

Another, earlier species of *Ardipithecus*—*Ar. kadabba*, dated from 5.5 million to 5.8 million years ago but known only from teeth and bits and pieces of skeletal bones—is part of that grade, too. And *Ar. kadabba’s* canines and other teeth seem to match those of a third very ancient specimen, 6-million-year-old *Orrorin tugenensis* from...
Kenya, which also has a thighbone that appears to have been used for upright walking (Science, 21 March 2008, p. 1599). So, “this raises the intriguing possibility that we’re looking at the same genus” for specimens now put in three genera, says Pilbeam. But the discoverers of O. tugenensis aren’t so sure. “As for Ardi and Orrorin being the same genus, no, I don’t think this is possible, unless one really wants to accept an unusual amount of variability” within a taxon, says geologist Martin Pickford of the College de France, who found Orrorin with Brigitte Senut of the National Museum of Natural History in Paris.

Whatever the taxonomy of Ardipithecus and the other very ancient hominins, they represent “an enormous jump to Australopithecus,” the next hominin in line (see timeline, p. 38), says australopithecine expert William Kimbel of Arizona State University, Tempe. For example, although Lucy’s brain is only a little larger than that of Ardipithecus, Lucy’s species, Au. afarensis, was an adept biped. It walked upright like humans, venturing increasingly into more diverse habitats, including grassy savannas. And it had lost its opposable big toe, as seen in 3.7-million-year-old footprints at Laetoli, Tanzania, reflecting an irreversible commitment to life on the ground.

Lucy’s direct ancestor is widely considered to be Au. anamensis, a hominin whose skeleton is poorly known, although its shibone suggests it walked upright 3.9 million to 4.2 million years ago in Kenya and Ethiopia. Ardipithecus is the current leading candidate for Au. anamensis’s ancestor, if only because it’s the only putative hominid in evidence between 5.8 million and 4.4 million years ago. Indeed, Au. anamensis fossils appear in the Middle Awash region just 200,000 years after Ardi.

Making strides

But the team is not connecting the dots between Au. anamensis and Ar. ramidus just yet, awaiting more fossils. For now they are focusing on the anatomy of Ardi and how she moved through the world. Her foot is primitive, with an opposable big toe like that used by living apes to grasp branches. But the bases of the other toe bones were oriented so that they reinforced the forefoot into a more rigid lever as she pushed off. In contrast, the toes of a chimpanzee curve as flexibly as those in their hands, say Lovejoy and co-author Bruce Latimer of Case Western Reserve University in Cleveland. Ar. ramidus “developed a pretty good bipedal foot while at the same time keeping an opposable first toe,” says Lovejoy.

The upper blades of Ardi’s pelvis are shorter and broader than in apes. They would have lowered the trunk’s center of mass, so she could balance on one leg at a time while walking, says Lovejoy. He also infers from the pelvis that her spine was long and curved like a human’s rather than short and stiff like a chimpanzee’s. These changes suggest to him that Ar. ramidus “has been bipedal for a very long time.”

Yet the lower pelvis is still quite large and primitive, similar to African apes rather than hominins. Taken with the opposable big toe, and primitive traits in the hand and foot, this indicates that Ar. ramidus didn’t walk like Lucy and was still spending a lot of time in the trees. But it wasn’t suspending its body beneath branches like African apes or climbing vertically, says Lovejoy. Instead, it was a slow, careful climber that probably moved on flat hands and feet on top of branches in the midcanopy, a type of locomotion known as palmigrady. For example, four bones in the wrist of Ar. ramidus gave it a more flexible hand that could be bent backward at the wrist. This is in contrast to the hands of knuckle-walking chimpanzees and gorillas, which have stiff wrists that absorb forces on their knuckles.

However, several researchers aren’t so sure about these inferences. Some are skeptical that the crushed pelvis really shows the anatomical details needed to demonstrate bipedality. The pelvis is “suggestive” of bipedality but not conclusive, says paleoanthropologist Carol Ward of the University of Missouri, Columbia. Also, Ar. ramidus “does not appear to have had its knee placed over the ankle, which means that when walking bipedally, it would have had to shift its weight to the side,” she says. Paleoanthropologist William Jungers of Stony Brook University in New York state is also not sure that the skeleton was bipedal. “Believe me, it’s a unique form of bipedalism,” he says. “The postcranium alone would not unequivocally signal hominin status, in my opinion.” Paleoanthropologist Bernard Wood of George Washington University in Washington, D.C., agrees. Looking at the skeleton as a whole, he says, “I think the head is consistent with it being a hominin. … but the rest of the body is much more questionable.”

All this underscores how difficult it may be to recognize and define bipedality in the earliest hominins as they began to shift from trees to ground. One thing does seem clear, though: The absence of many specialized traits found in African apes suggests that our ancestors never knuckle-walked.

That throws a monkey wrench into a hypothesis about the last common ancestor of living apes and humans. Ever since Darwin...
Habitat for Humanity

ARAMIS, ETHIOPIA—A long cairn of black stones marks the spot where a skeleton of *Ardipithecus ramidus* was found, its bones broken and scattered on a barren hillside. Erected as a monument to an ancient ancestor in the style of an Afar tribesman’s grave, the cairn is a solitary marker in an almost sterile zone, devoid of life except for a few spindly acacia trees and piles of sifted sediment.

That’s because the Middle Awash research team sucked up everything in sight at this spot, hunting for every bit of fossil bone as well as clues to the landscape 4.4 million years ago, when *Ardipithecus* died here. “Literally, we crawled every square inch of this locality,” recalls team co-leader Tim White of the University of California, Berkeley. “You crawl on your hands and knees, collecting every piece of bone, every piece of wood, every seed, every snail, every scrap. It was 100% collection.” The heaps of sediment are all that’s left behind from that fossil-mining operation, which yielded one of the most important fossils in human evolution (see main text, p. 36), as well as thousands of clues to its ecology and environment.

The team collected more than 150,000 specimens of fossilized plants and animals from nearby localities of the same age, from elephants to songbirds to millipedes, including fossilized wood, pollen, snails, and larvae. “We have crates of bone splinters,” says White.

A team of interdisciplinary researchers then used these fossils and thousands of geological and isotope samples to reconstruct *Ardipithecus*’s Pliocene world, as described in companion papers in this issue (see p. 56 and 87). From these specimens, they conclude that Ardhi lived in a woodland, climbing among hackberry, fig, and palm trees and coexisting with monkeys, kudu antelopes, and peafowl. Doves and parrots flew overhead. All these creatures prefer woodlands, not the open, grassy terrain often conjured for our ancestors.

The team suggests that *Ardipithecus* was “more omnivorous” than chimpanzees, based on the size, shape, and enamel distribution of its teeth. It probably supplemented woodland plants such as fruits, nuts, and tubers with the occasional insects, small mammals, or bird eggs. Carbon-isotope studies of teeth from five individuals show that *Ardipithecus* ate mostly woodland, rather than grassland, plants. Although *Ardipithecus* probably ate figs and other fruit when ripe, it didn’t consume as much fruit as chimpanzees do today.

This new evidence overwhelmingly refutes the once-favored but now moribund hypothesis that upright-walking hominins arose in open grasslands. “There’s so much good data here that people aren’t going to be able to question whether early hominins were living in woodlands,” says paleoanthropologist Andrew Hill of Yale University. “Savannas had nothing to do with upright walking.”

Geological studies indicate that most of the fossils were buried within a relatively short window of time, a few thousand to, at most, 100,000 years ago, says geologist and team co-leader Giday WoldeGabriel of the Los Alamos National Laboratory in New Mexico. During that sliver of time, Aramis was not a dense tropical rainforest with a thick canopy but a humid, cooler woodland. The best modern analog is the Kibwezi Forest in Kenya, kept wet by groundwater, according to isotope expert Stanley Ambrose of the University of Illinois, Urbana-Champaign. These woods have open stands of trees, some 20 meters high, that let the sun reach shrubs and grasses on the ground.

Judging from the remains of at least 36 *Ardipithecus* individuals found so far at Aramis, this was prime feeding ground for a generalized early biped. “It was the habitat they preferred,” says White. —A.G.
MIDDLE AWASH VALLEY, THE AFAR DEPRESSION, ETHIOPIA—It’s about 10 a.m. on a hot morning in December, and Tim White is watching a 30-year-old farmer inch his way up a slippery hill on his knees, picking through mouse-colored rubble for a bit of gray bone. The sun is already bleaching the scrubby badlands, making it difficult to distinguish a fragment of bone in the washed-out beige and gray terrain. The only shade in this parched gully is from a small, thorny acacia tree, so the fossil hunters have draped their heads with kerchiefs that hang out from under their “Cal” and “Obama for President” baseball caps, making them look like a strange tribe of Berkeley Bedouins. If there are fossils here, White is confident that the slender farmer, Kampiro Kayrento, will find them. “Kampiro is the best person in the world for finding little pieces of fossilized human bone,” says White, 59, a paleoanthropologist at the University of California, Berkeley, who has collected fossils in this region since 1981.

Watching Kayrento is a sort of spectator sport, because he scores so often. Just minutes earlier, he had walked over the crest of a small hill, singing softly to himself, and had spotted the fossilized core of a horn from an ancient bovid, or antelope. Then he picked up a flat piece of gray bone nearby and showed the fossil to Ethiopian paleoanthropologist Berhane Asfaw, asking, “Bovid?” Asfaw, 55, who hired Kayrento when he was a boy hanging out at fossil sites in southern Ethiopia, looked over the slightly curved piece of bone the size of a silver dollar and suggested, “Monkey?” as he handed it to White. White turned it over gently in his hands, then said: “Check that, Berhane. We just found a hominin cranium. Niiice.”

As word spreads that Kayrento found a hominin, or a member of the taxon that includes humans and our ancestors, the other fossil hunters tease him: “Homo bovid! Homo bovid! Niiice.”

The Middle Awash project, which includes 70 scientists from 18 nations, is best known for its discovery of the 4.4-million-year-old partial skeleton of *Ardipithecus ramidus* at Aramis, about 34 kilometers north of here. That skeleton is now dramatically revising ideas of how upright walking evolved and how our earliest ancestors differed from chimpanzees (see overview, p. 60, and main Focus text, p. 36). But Aramis is just one of 300 localities in the Middle Awash, which is the only place in the world to yield fossils that span the entire saga of hominin evolution. At last count, this team had gathered 19,000 vertebrate fossils over the past 19 years. These include about 300 specimens from seven species of hominins, from some of the first members of the human family, such as 5.8-million-year-old *Ar. ramidus kadabba*, to the earliest members of our own species, *Homo sapiens*, which lived here about 160,000 years ago.

As they work in different places in the valley, the team members travel back and forth in time. Today, this core group is working in the western foothills near the Burka catchment, where an ancient river laid down sediments 3 million to 2 million years ago and where the team has found specimens of *Australopithecus garhi*, a species they suspect may have given rise to the first members of our genus, *Homo*.

This season, after a rough start, the 25 scientists, students, cooks, and Ethiopian and Afar officials and guards in camp are working well together. Their tented camp is hours from any town, graded road, or fresh water. (They dig their own well to get water.) “The 1st week, it’s like an engine that’s running but not running smoothly,” says White, who, with Asfaw, runs a well-organized camp where every tool, map, and shower bag has its proper place. “By the 3rd week, people know their jobs.”

The 1st week, White and a paleontologist were sick, and White is still fighting a harsh cough that keeps him awake at night. The 2nd week, some aggressive Alisera tribesmen who live near the *Ar. ramidus* site threatened to kill White and Asfaw, making it difficult to return there. (That’s one reason the team travels with six Afar policemen armed with AK-47s and Obama caps, dubbed “The Obama Police.”) The day before, a student had awakened with a high fever and abdominal pain and had to be driven 4 hours to the nearest clinic, where he was diagnosed with a urinary tract infection, probably from drinking too little water in

**The View From Afar**

How do you find priceless hominin fossils in a hostile desert? Build a strong team and obsess over the details.
The best laid plans change every day,” says White, who has dealt with poisonous snakes, scorpions, malarial mosquitoes, lions, hyenas, flash floods, dust tornadoes, warring tribesmen, and contaminated food and water over the years. “Nothing in the field comes easy.”

Calling the “A” team

Nothing in the Afar, for that matter, comes easy. We are reminded of that as we drive across the dusty Saragata plain to the target fossil site at 8 a.m., making giant circles in the dust with the Toyota Land Cruiser so we can find our tracks home at the end of the day. Men clad in plaid wraps, with AK-47s slung over their shoulders, flag us down seeking help. They bring over a woman who looks to be in her 70s but is probably much younger. Her finger is bleeding, and the men tell White and Asfaw, in Afar, that a puff adder bit her the night before while she was gathering wood. A quick-thinking boy had sliced her finger with a knife, releasing the venom and probably saving her life. White gets out a first-aid kit, removes a crude poultice, and cleans and bandages the wound, putting on an antibiotic cream. “It’s good she survived the night,” he says as we drive off. “The danger now is infection.”

After inching down the sandy bank of a dry river, we reach the so-called Chairman’s site. This is one of dozens of fossil localities discovered in the Burka area since 2005: exposed hillsides that were spotted in satellite and aerial photos, then laboriously explored on foot. The plan was to search for animal fossils to help date a hominid jawbone discovered last year. But in the 1st hour, with Kayrento’s discovery, they’re already on the trail of another individual instead.

As soon as White identifies the bit of skull bone, he swings into action. With his wiry frame and deep voice, he is a commanding presence, and it soon becomes clear how he earned his nickname, “The General.” In his field uniform—a suede Australian army hat with a rattlesnake band, blue jeans, and driving gloves without fingers—he uses a fossil pick to delineate the zones in the sandstone that it comes from a larger piece of skull that broke after it was exposed not while it was buried. As Kayrento and the others find other bits bone, they place yellow pin-flags at those spots. “This process establishes the distributional cone,” White explains. The top flag marks the highest point on the surface where the skull came out of the ground; the bottom boundary marks the farthest point where a fragment might finally have come to rest, following the fall line down the slope.

This discovery also illustrates one reason why the team comes to the field right after the rainy season. If they’re lucky, rain and flood will cut into the ancient sediments, exposing fossils. But they have to get there before the fossils disintegrate as they are exposed to the elements or are trampled by the Afar’s goats, sheep, and cattle. Tilling everything, and this season they’re a bit late. “The ideal situation is find a fossil just as it is eroding out of the bank,” says White.

As they crawl the entire length of the gully, they turn over even rock, mud clod, and piece of carbonate rubble to make sure it doesn’t contain a fossil fragment. “Not good,” says Kayrento. “This is yucky,” agrees Asfaw, co-director of the team and the first Ethiopian scientist to join it, in 1979 when he was invited to earn his Ph.D. at Berkeley (Science, 29 August 2003, p. 1178).

After 2 hours, the team has collected a few more pieces of skull around the temple, forehead, and ear. “It’s getting bigger by the minute,” White says. “If we’re lucky, we’ll find it buried right in here.”

The team has to wait until the next day to find out just how lucky they are. At 9:45 a.m. Thursday, they return with reinforcements: Asfaw hired two Afar men to help with the heavy lifting of buckets of dirt with a button-down Oxford cloth shirt and a pistol stuck in the waist of his khakis, Asfaw commands respect, and he is the best negotiating with the Afar. In this case, he settles an argument by letting clan leaders select which men, among a large group, will get jobs.

At the site, White sets up a perimeter of blue pin-flags that look like a mini slalom course, outlining the gully that he calls the “H Zone” where fossil pieces are most likely to be buried. The plan is to excavate all the rock and dirt around those flags, down to the original layers of sediment. White explains that the ancient landscape would have been flatter and more verdant before tectonic movements of Earth’s crust cracked and tilted the sediment layers. But the original soil is still there, a red-brown layer of clay beneath a gray veneer of sandstone. “Throw every piece of stone out of the channel,” he orders. “If you see a hominid, I need to know right away!”

White and Kayrento literally sweep off the gray lag with a push broom and then scrape back the layers of time with a trowel to the ancient surface underneath. “Once we brush out the slopes, we’ll
sure no fossil is left in place,” says White. In case they miss a fragment, the loose sediment is carried to giant sieves where the crew sifts it for bits of bone or teeth. The sifted rubble is taken to a circle of workers who then empty it into small aluminum pans, in which they examine every single, tiny piece—a job that gives new meaning to the word tedium. “Sieving 101,” observes Asfaw, who supervises sieving and picking today.

By 11:10 a.m., the pace of discovery has slowed. When the A team tells White it’s “not good,” he tries to infuse them with some of his energy, reminding everyone to stay focused, to keep going, to not step on fossils. But by midday, White is grumbling, too, because they’ve scour ed the Hot Zone and it’s clear the skull is not there. “We’ve eliminated every hope of finding it in situ.”

Time travel
It’s a good time to take a walk with the four geologists, who are combing the terrain, hoping to find sediments with volcanic minerals to help them date the locality and its fossils precisely. While fossil hunters move slowly, stooped at the waist and focused on the ground, the geologists move fast, heads up, scanning the next horizon for a rock face with a layer cake of sediments, like those exposed in road cuts. The 6-million-year record of Middle Awash sediments is not stacked neatly in one place, with oldest rocks on the bottom and youngest on top. (If it were, the stack would be 1 kilometer thick.) Instead, the rocks are faulted and tilted into different ridges. By tracing a once-horizontal layer from ridge to ridge, sometimes for kilometers, the geologists can link the layers and place different snapshots of time into a sequence.

Today, Ethiopian geologist Giday WoldeGabriel of the Los Alamos National Laboratory in New Mexico, also a co-leader of the team (he joined in 1992), is searching for a familiar-looking motif—a distinct layer of volcanic tuff called the SHT (Sidiha Koma Tuff), previously dated to 3.4 million years ago by radiometric methods.

So far, the team has found just one species of hominin—*Au. garhi*—that lived at this time in the Middle Awash (Science, 23 April 1999, p. 629), although a more robust species, *Au. aethiopicus*, appears 2.6 million years ago in southern Ethiopia and Kenya. That’s also when the earliest stone tools appear in Gona, Ethiopia, 100 kilometers north of here. The earliest fossils of our genus *Homo* come a bit later—at 2.3 million years ago at Hadar, near Gona, also with stone tools. That’s why it is important to date *Au. garhi* precisely: Was it the maker of the stone tools left in the Afar? The team thinks *Au. garhi* is the direct descendant of the more primitive *Au. afarensis*, best known as the species that includes the famous 3.2-million-year-old skeleton of Lucy, also from Hadar. But did *Au. garhi* then evolve into early *Homo*? They need better dates—and more fossils—to find out.

“Now that we have the SHT as a reference point here, we have to try to trace it to where the new fossils are,” says WoldeGabriel. The only problem is that the SHT is several ridges and basins over from the excavation; linking the two will be difficult if not impossible. The team will also use other methods to date the new fossils.

By the end of 3 days, the team of 20 will have collected a dozen pieces of one skull, an average yield for this region. Taken together, says White, those pieces show that *Au. garhi* gave rise to *Au. afarensis*—and so perhaps in *Au. garhi*, too.

For now, White and Asfaw are pleased with the new snapshot they’re getting of *Au. garhi*. On our way back to camp, White stops so we can take a photo of the moon rising over Yardi Lake in front of us, the sun setting behind us. The landscape has changed since the australopithecines were here. But one thing’s been constant in the Middle Awash, he notes: “Hominids have been right here looking at the moon rising over water for millions of years.”

—ANN GIBBONS
Charles Darwin and Thomas Huxley were forced to ponder human origins and evolution without a relevant fossil record. With only a few Neanderthal fossils available to supplement their limited knowledge of living apes, they speculated about how quintessentially human features such as upright walking, small canines, dexterous hands, and our special intelligence had evolved through natural selection to provide us with our complex way of life. Today we know of early Homo from >2.0 million years ago (Ma) and have a record of stone tools and animal butchery that reaches back to 2.6 Ma. These demonstrate just how deeply technology is embedded in our natural history.

Australopithecus, a predecessor of Homo that lived about 1 to 4 Ma (see figure), was discovered in South Africa in 1924. Although slow to gain acceptance as a human ancestor, it is now recognized to represent an ancestral group from which Homo evolved. Even after the discoveries of the partial skeleton (“Lucy”) and fossilized footprints (Laetoli) of Au. afarensis, and other fossils that extended the antiquity of Australopithecus to ~3.7 Ma, the hominid fossil record before Australopithecus was blank. What connected the small-brained, small-canined, upright-walking Australopithecus to the last common ancestor that we shared with chimpanzees some time earlier than 6 Ma?

The 11 papers in this issue, representing the work of a large international team with diverse areas of expertise, describe Arhipithecus ramidus, a hominid species dated to 4.4 Ma, and the habitat in which it lived in the Afar Rift region of northeastern Ethiopia. This species, substantially more primitive than Australopithecus, resolves many uncertainties about early human evolution, including the nature of the last common ancestor that we shared with the line leading to modern human. Ar. ramidus remains were recovered from a sedimentary horizon representing a short span of time (within 100 to 10,000 years). This has enabled us to assess available and preferred habitats for the early hominids by systematic and repeated sampling of the hominin-bearing strata.

By collecting and classifying thousands of vertebrate, invertebrate, and plant fossils, and characterizing the isotopic composition of soil samples and teeth, we have learned that Ar. ramidus was a denizen of woodland with small patches of forest. We have also learned that it probably was more omnivorous than chimpanzees (ripe fruit specialists) and likely fed both in trees and on the ground. It apparently consumed only small amounts of open-environment resources, arguing against the idea that an inhabitation of grasslands was the driving force in the origin of upright walking.

Ar. ramidus, first described in 1994 from teeth and jaw fragments, is now represented by 110 specimens, including a partial female skeleton rescued from erosional degradation. This individual weighed about 50 kg and stood about 120 cm tall. In the context of the many other recovered individuals of this species, this suggests little body size difference between males and females. Brain size was as small as in living chimpanzees. The numerous recovered teeth and a largely complete skull show that Ar. ramidus had a small face and a reduced canine/premolar complex, indicative of minimal social aggression. Its hands, arms, feet, pelvis, and legs collectively reveal that it moved capably in the trees, supported on its feet and palms (palmigrade clambering), but lacked any characteristics typical of the suspension, vertical climbing, or knuckle-walking of modern gorillas and chimps. Terrestrially, it engaged in a form of bipedality more primitive than that of Australopithecus, and it lacked adaptation to “heavy” chewing related to open environments (seen in later Australopithecus). Ar. ramidus thus indicates that the last common ancestor of humans and African apes was not chimpanzee-like and that both hominids and extant African apes are each highly specialized, but through very different evolutionary pathways.
The Geological, Isotopic, Botanical, Invertebrate, and Lower Vertebrate Surroundings of *Ardipithecus ramidus*

Giday WoldeGabriel, Stanley H. Ambrose, Doris Barboni, Raymonde Bonnefille, Laurent Bremond, Brian Currie, David DeGusta, William K. Hart, Alison M. Murray, Paul R. Renne, M. C. Jolly-Saad, Kathlyn M. Stewart, Tim D. White

*Ardipithecus ramidus* was found in exposed sediments flanking the Awash River, Ethiopia. The local geology and associated fossils provide critical information about its age and habitat.

Most of Africa’s surface is non depositional and/or covered by forests. This explains why so many discoveries related to early hominid evolution have been made within eastern Africa’s relatively dry, narrow, active rift system. Here the Arabian and African tectonic plates have been pulling apart for millions of years, and lakes and rivers have accumulated variably fossil-rich sediments in the Afar Triangle, which lies at the intersection of the Red Sea, Gulf of Aden, and Main Ethiopian Rifts (see map). Some of these deposits were subsequently uplifted by the rift tectonics and are now eroding. In addition, volcanoes associated with this rifting have left many widespread deposits that we can use to determine the age of these fossils using modern radioisotopic methods.

Several of the most important hominid fossils have been found near the Afar’s western margin, north and west of the Awash River (star on map), including Hadar (the “Lucy” site), Gona [known for the world’s oldest stone tools at 2.6 million years ago (Ma)], and the Middle Awash (including Aramis). Cumulatively, these and nearby study areas in Ethiopia have provided an unparalleled record of hominid evolution.

Fossil-bearing rocks in the Middle Awash are intermittently exposed and measure more than 1 km in thickness. Volcanic rocks near the base of this regional succession are dated to more than 6 Ma. Its uppermost sediments document the appearance of anatomically near-modern humans 155,000 years ago. As is the case for many river and lake deposits, fossil accumulation rates here have been highly variable, and the distribution and preservation of the fossils are uneven. Alterations of the fossils caused by erosion and other factors further complicate interpretation of past environments. To meet this challenge, beginning in 1981, our research team of more than 70 scientists has collected 2000 geological samples, thousands of lithic artifacts (e.g., stone tools), and tens of thousands of plant and animal fossils. The emergent picture developed from the many Middle Awash rock units and their contents represents a series of snapshots taken through time, rather than a continuous record of deposition.

*Ardipithecus ramidus* was recovered from one such geological unit, 3 to 6 m thick, centered within the study area. Here, the Aramis and adjacent drainage basins expose a total thickness of 300 m of sediments largely deposited in rivers and lakes, and on floodplains, between ~5.5 and 3.8 Ma. Within this succession, the *Ardipithecus*–bearing rock unit comprises silt and clay beds deposited on a floodplain. It is bracketed between two key volcanic markers, each dated to 4.4 Ma. Their similar ages and sedimentology imply that the fossils themselves date to 4.4 Ma and were all deposited within a relatively narrow time interval lasting anywhere from 100 to 10,000 years. Today the unit is exposed across a 9-km arc that represents a fortuitous transect through the ancient landscape. The western exposure, in particular, preserves a rich assemblage of plant and animal fossils and ancient soils.

Fossilized wood, seeds, and phytoliths (hard silica parts from plants) confirm the presence of hackberry, fig, and palm trees. There is no evidence of a humid closed-canopy tropical rainforest, nor of the subdesertic vegetation that characterizes the area today. Invertebrate fossils are abundant and include insect larvae, brood-balls and nests of dung beetles, diverse gastropods, and millipedes. The terrestrial gastropods best match those seen in modern groundwater forests such as the Kibwezi in Kenya. Aquatic lower vertebrates are relatively rare and probably arrived episodically during flooding of a river distal to the Aramis area. The most abundant fish is catfish, probably introduced during overbank flooding and/or by predatory birds roosting in local trees.

Our combined evidence indicates that *Ardipithecus* did not live in the open savanna that was once envisioned to be the predominant habitat of the earliest hominids, but rather in an environment that was humid and cooler than it is today, containing habitats ranging from woodland to forest patches.
Taphonomic, Avian, and Small-Vertebrate Indicators of *Ardipithecus ramidus* Habitat

Antoine Louchart, Henry Wesselman, Robert J. Blumenschine, Leslea J. Hlusko, Jackson K. Njau, Michael T. Black, Mesfin Asnake, Tim D. White

The stratigraphic unit containing *Ardipithecus ramidus* was probably deposited rapidly, thus providing a transect through a 4.4-million-year-old landscape. To help reconstruct and understand its biological setting as thoroughly as possible, we recovered an assemblage of >150,000 plant and animal fossils. More than 6000 vertebrate specimens were identified at the family level or below. These specimens represent animals ranging in size from shrews to elephants and include abundant birds and small mammals that are usually rare in hominid-bearing assemblages. Many of these birds and small mammals are highly sensitive to environmental conditions and thus are particularly helpful in reconstructing the environment.

Accurate interpretation of fossil assemblages can be challenging. Even fossils from one layer can represent artificial amalgamations that might have originated thousands of years apart. Moreover, the remains of animals living in different habitats can be artificially mixed by flowing water or by shifting lake and river margins. Ecological fidelity can be further biased by unsystematic recovery if, for example, only the more complete, identifiable, or rare specimens are collected. Thus, interpreting the *Ardipithecus*-bearing sediments requires that we deduce the physical and biological conditions under which the fossils accumulated and the degree to which these biases operated at the time of deposition—a practice called “taphonomy.”

Both the large- and small-mammal assemblages at Aramis lack the damage that would result from transport and sorting by water, a finding consistent with the fine-grained sediments in which the bones were originally embedded. Many of the limb bone fragments of large mammals show traces of rodent gnawing and carnivore chewing at a time when the bones were still fresh. These bones were most probably damaged by hyenas, which in modern times are known to destroy most of the limb bones and consume their marrow. The actions of hyenas and other carnivores that actively competed for these remains largely explain why the fossil assemblage at Aramis contains an overrepresentation of teeth, jaws, and limb bone shaft splinters (versus skulls or limb bone ends).

As a result of this bone destruction, whole skeletons are extremely rare at Aramis, with one fortunate exception: the partial skeleton of *Ar. ramidus* excavated at ARA-VP-6/500. The relative abundance and damage patterns of the fossils representing small mammals and birds suggest that they are derived from undigested material regurgitated by owls (owl pellets). Because of their fragility and size, bird bones have been rare or absent at most other eastern African fossil assemblages that included early hominids. However, we cataloged 370 avian fossils; these represent 29 species, several new to science. Most of the birds are terrestrial rather than aquatic, and small species such as doves, lovebirds, mousebirds, passerines, and swifts are abundant. Open-country species are rare. Eagles and hawks/kites are present, but the assemblage is dominated by parrots and the peafowl *Pavo*, an ecological indicator of wooded conditions.

The small-mammal assemblage includes up to 20 new species, including shrews, bats, rodents, hares, and carnivores. Extant counterparts live in a variety of habitats, but their relative abundance in the fossil assemblage indicates that *Ardipithecus* lived in a wooded area. Avian predators most probably procured the much rarer squirrels and gerbils from drier scrub or arid settings at a distance. Most of the bat, shrew, porcupine, and other rodent specimens are compatible with a relatively moist environmental setting, as are the abundant fossils of monkeys and spiral-horned antelopes.

The combination of geological and taphonomic evidence, the assemblage of small-mammal and avian fossils, and the taxonomic and isotopic compositions of remains from larger mammals indicate that Aramis was predominantly a woodland habitat during *Ar. ramidus* times. The anatomical and isotopic evidence of *Ar. ramidus* itself also suggests that the species was adapted to such a habitat.

See pages 5–6 for authors’ affiliations.

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Macrovertebrate Paleontology and the Pliocene Habitat of Ardipithecus ramidus


Ever since Darwin, scholars have speculated about the role that environment may have played in human origins, evolution, and adaptation. Given that all living great apes live and feed in trees, it has been assumed that the last common ancestor we shared with these forms was also a forest dweller. In 1925, Raymond Dart described the first Australopithecus, a child’s skull, at Taung, South Africa. Its occurrence among other fossils indicative of a grassland environment prompted speculation that the open grasslands of Africa were exploited by early hominins and were therefore somehow integrally involved with the origins of upright walking.

The Ardipithecus-bearing sediments at Aramis now provide fresh evidence that Ar. ramidus lived in a predominately woodland setting. This and corroborative evidence from fossil assemblages of avian and small mammals imply that a grassland environment was not a major force driving evolution of the earliest hominids. A diverse assemblage of large mammals (>5 kg body weight) collected alongside Ardipithecus provides further support for this conclusion. Carbon isotopes from tooth enamel yield dietary information because different isotope signatures reflect different photosynthetic pathways of plants consumed during enamel development. Therefore, animals that feed on tropical open-environment grasses (or on grass-eating animals) have different isotopic compositions from those feeding on browse, seeds, or fruit from shrubs or trees. Moreover, oxygen isotopes help deduce relative humidity and evaporation in the environment.

The larger-mammal assemblage associated with Ar. ramidus is the spiral-horned antelope, Tragelaphus (the kudu, green circle). Today, these antelopes are browsers (eating mostly leaves), and they prefer bushy to wooded habitats. The dental morphology, wear, and enamel isotopic composition of the Aramis kudu species are all consistent with such placement. In contrast, grazing antelopes (which eat mostly grass) are rare in the Aramis assemblage.

The large-mammal assemblage shows a preponderance of browsers and fruit eaters. This evidence is consistent with indications from birds, small mammals, soil isotopes, plants, and invertebrate remains. The emergent picture of the Aramis landscape during Ar. ramidus times is one of a woodland setting with small forest patches. This woodland graded into nearby habitats that were more open (red crosses in figure) account for nearly a third of the entire large mammal collection. Leaf-eating colobines today exhibit strong preferences for arboreal habitats, and the carbon isotope compositions of the fossil teeth are consistent with dense to open forest arboreal feeding (see figure).

The other dominant large mammal associated with Ar. ramidus is the spiral-horned antelope, Tragelaphus (the kudu, green circle). Today, these antelopes are browsers (eating mostly leaves), and they prefer bushy to wooded habitats. The dental morphology, wear, and enamel isotopic composition of the Aramis kudu species are all consistent with such placement. In contrast, grazing antelopes (which eat mostly grass) are rare in the Aramis assemblage.

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Carbon and oxygen isotope analyses of teeth from the Ar. ramidus localities. Species are listed in order of abundance, and isotopic data separate species by what they ate and their environment.

See pages 5–6 for authors’ affiliations.

When citing, please refer to the full paper, available at DOI 10.1126/science.1175822.
The Ardipithecus ramidus Skull and Its Implications for Hominid Origins

Gen Suwa, Berhane Asfaw, Reiko T. Kono, Daisuke Kubo, C. Owen Lovejoy, Tim D. White

The key feature that distinguishes Homo sapiens from other primates is our unusually large brain, which allows us to communicate, make tools, plan, and modify our environment. Understanding how and when our cognitive ability evolved has been a special focus in anthropology and, more recently, genetics. Fossil hominid skulls provide direct evidence of skull evolution and information about diet, appearance, and behavior. Skulls feature prominently in the characterization of species, in taxonomy, and in phylogenetic analyses of both extinct and living primates.

Unfortunately, hominid skulls are relatively rare in the fossil record. A number of partial skulls and crania (skulls without a lower jaw) of early Homo and its predecessor, Australopithecus (which lived ~1 to 4 million years ago), have been recovered, but relatively few are complete enough for extensive comparisons. One surprisingly complete but distorted cranium from 6 to 7 million years ago was discovered in central Africa (Chad). This fossil, *Sahelanthropus tchadensis* (a.k.a. “Toumai”), is thought by many to represent the earliest known hominid, although some have argued that it is a female ape.

The Ardipithecus ramidus skull is of particular interest because it predates known *Australopithecus* and thereby illuminates the early evolution of the hominid skull, brain, and face. The *Ar. ramidus* skull was badly crushed, and many of its bones were scattered over a wide area. Because the bones were so fragile and damaged, we imaged them with micro–computed tomography, making more than 5,000 slices. We assembled the fragments into more than 60 key virtual pieces of the braincase, face, and teeth, enough to allow us to digitally reconstruct a largely complete cranium.

The fossil skulls of *Australopithecus* indicate that its brain was ~400 to 550 cm³ in size, slightly larger than the brains of modern apes of similar body size and about a third of those of typical *Homo sapiens*. Its specialized craniofacial architecture facilitated the production of strong chewing forces along the entire row of teeth located behind its canines. These postcanine teeth were enlarged and had thick enamel, consistent with a hard/tough and abrasive diet. Some species exhibited extreme manifestations of this specialized chewing apparatus and are known as “robust” *Australopithecus*.

*Ar. ramidus* had a small brain (300 to 350 cm³), similar to that of bonobos and female chimpanzees and smaller than that of *Australopithecus*. The *Ar. ramidus* face is also small and lacks the large cheeks of “heavy chewing” *Australopithecus*. It has a projecting muzzle as in *Sahelanthropus*, which gives it a decidedly ape-like gestalt. Yet the *Ar. ramidus* skull is not particularly chimpanzee-like. For example, the ridge above the eye socket is unlike that of a chimpanzee, and its lower face does not project forward as much as a chimpanzee’s face. Chimps primarily eat ripe fruits and have large incisors set in a projecting lower face. *Ar. ramidus* instead was probably more omnivorous and fed both in trees and on the ground. Additionally, in chimpanzees, forward placement of the entire lower face is exaggerated, perhaps linked with their large tuskslike canines (especially in males) and elevated levels of aggression. This is not seen in *Ar. ramidus*, implying that it was less socially aggressive.

Like *Ar. ramidus*, *S. tchadensis* had a brain that was less than 400 cm³ in size. It also resembled *Ar. ramidus* in having small non–sharpened canines. Details of the bottom of the skull show that both *Ar. ramidus* and *Sahelanthropus* had a short cranial base, a feature also shared with *Australopithecus*. Furthermore, we infer that the rear of the *Ar. ramidus* skull was downturned like that suggested for *Sahelanthropus*. These similarities confirm that *Sahelanthropus* was indeed a hominid, not an extinct ape.

These and an additional feature of the skull hint that, despite its small size, the brain of *Ar. ramidus* may have already begun to develop some aspects of later hominin-like form and function. The steep orientation of the bone on which the brain stem rests suggests that the base of the *Ar. ramidus* brain might have been more flexed than in apes. In *Australopithecus*, a flexed cranial base occurs together with expansion of the posterior parietal cortex, a part of the modern human brain involved in aspects of visual and spatial perception.

See pages 5–6 for authors’ affiliations.

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Paleobiological Implications of the 
Ardipithecus ramidus Dentition

Gen Suwa, Reiko T. Kono, Scott W. Simpson, Berhane Asfaw, C. Owen Lovejoy, Tim D. White

Teeth are highly resilient to degradation and therefore are the most abundant specimens in the primate fossil record. The size, shape, enamel thickness, and isotopic composition of teeth provide a wealth of information about phylogeny, diet, and social behavior. *Ardipithecus ramidus* was originally defined in 1994 primarily on the basis of recovered teeth, but the sample size was small, limiting comparison to other primate fossils. We now have over 145 teeth, including canines from up to 21 individuals. The expanded sample now provides new information regarding *Ar. ramidus* and, using comparisons with teeth of other hominids, extant apes, and monkeys, new perspectives on early hominid evolution as well.

In apes and monkeys, the male's upper canine tooth usually bears a projecting, daggerlike crown that is continuously sharpened (honed) by wear against a specialized lower premolar tooth (together these form the C/P3 complex). The canine tooth is used as a slicing weapon in intra- and intergroup social conflicts. Modern humans have small, stublike canines which function more like incisors.

All known modern and fossil apes have (or had) a honing C/P3 complex. In most species, this is more developed in males than females (in a few species, females have male-like large canines, either for territorial defense or for specialized feeding). The relatively large number of *Ar. ramidus* teeth, in combination with Ethiopian *Ar. kadabba*, Kenyan *Orrorin*, and Chadian *Sahelanthropus* [currently the earliest known hominids at about 6 million years ago (Ma)], provide insight into the ancestral ape C/P3 complex and its evolution in early hominids.

In basal dimensions, the canines of *Ar. ramidus* are roughly as large as those of female chimpanzees and male bonobos, but their crown heights are shorter (see figure). The *Ar. ramidus* sample is now large enough to assure us that males are represented. This means that male and female canines were not only similar in size, but that the male canine had been dramatically “feminized” in shape. The crown of the upper canine in *Ar. ramidus* was altered from the pointed shape seen in apes to a less-threatening diamond shape in both males and females. There is no evidence of honing. The lower canines of *Ar. ramidus* are less modified from the inferred female ape condition than the uppers. The hominid canines from about 6 Ma are similar in size to those of *Ar. ramidus*, but (especially) the older upper canines appear slightly more primitive. This suggests that male canine size and prominence were dramatically reduced by ~6 to 4.4 Ma from an ancestral ape with a honing C/P3 complex and a moderate degree of male and female canine size difference.

Dentitions from human (left), *Ar. ramidus* (middle), and chimpanzee (right), all males. Below are corresponding samples of the maxillary first molar in each. Red, thicker enamel (~2 mm); blue, thinner enamel (~0.5 mm). Contour lines map the topography of the crown and chewing surfaces.

In modern monkeys and apes, the upper canine is important in male agonistic behavior, so its subdued shape in early hominids and *Ar. ramidus* suggests that sexual selection played a primary role in canine reduction. Thus, fundamental reproductive and social behavioral changes probably occurred in hominids long before they had enlarged brains and began to use stone tools.

Thick enamel suggests that an animal’s food intake was abrasive; for example, from terrestrial feeding. Thin enamel is consistent with a diet of softer and less abrasive foods, such as arboreal ripe fruits. We measured the enamel properties of more than 30 *Ar. ramidus* teeth. Its molar enamel is intermediate in thickness between that of chimpanzees and Australopithecus or Homo. Chimpanzees have thin enamel at the chewing surface of their molars, whereas a broad concave basin flanked by spiky cusps facilitates crushing fruits and shredding leaves. *Ar. ramidus* does not share this pattern, implying a diet different from that of chimpanzees. Lack of thick enamel indicates that *Ar. ramidus* was not as adapted to heavy chewing and/or eating abrasive foods as were later Australopithecus or even Homo. The combined evidence from the isotopic content of the enamel, dental wear, and molar structure indicates that the earliest hominid diet was one of generalized omnivory and frugivory and therefore differed from that of Australopithecus and living African apes.

See pages 5–6 for authors' affiliations.

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Agrasping hand and highly mobile forelimb are defining characteristics of primates. The special ability to pick things up and manipulate them has probably been a central selective force in making primates so unusually intelligent. It’s something that porpoises can’t do at all and crows can’t do very well. It may also be one reason why humans alone eventually evolved cognition.

The hands of African apes are specialized in a number of ways that make them dramatically different from our own. Apes must support their large body mass during climbing to feed and nest, especially in the middle and higher parts of the tree canopy. Their hands must therefore withstand very high forces, and this is facilitated by their elongated palms and fingers. Our palms are much shorter and our wrists more mobile. This allows us to grasp objects and compress them with great dexterity and force—something often called a “power grip.” The differences between ape and human forelimbs become less pronounced going to the shoulder. Ape and human elbow joints, for example, diverge only moderately in their manner of load transmission.

The high loads that apes bear during locomotion have required them to greatly stiffen the joints between their fingers and palms. Because their thumb has not been elongated in the same way as their palms and fingers have, thumb-to-palm and thumb-to-finger oppositions are more awkward for them. We are therefore much more adept at making and using tools. All of these forelimb characteristics in apes have led them to adopt an unusual form of terrestrial quadrupedality, in which they support themselves on their knuckles rather than on their palms. Only African apes exhibit this “knuckle-walking.” Other primates, such as monkeys, still support themselves on their palms.

It has long been assumed that our hands must have evolved from hands like those of African apes. When they are knuckle-walking, their long forelimbs angle their trunks upward. This posture has therefore long been viewed by some as “preadapting” our ancestors to holding their trunks upright.

Until now, this argument was unsettled, because we lacked an adequate fossil record. Even Lucy, the most complete *Australopithecus* skeleton yet found, had only two hand bones—far short of the number needed to interpret the structure and evolution of the hand. The *Ardipithecus* skeleton reported here changes that. Not only is it more than 1 million years older than Lucy (4.4 million versus 3.2 million years old), its hands are virtually complete and intact. They show that *Ardipithecus* did not knuckle-walk like African apes and that it lacked virtually all of the specializations that protect great ape hands from injury while they climb and feed in trees.

*Ardipithecus* hands were very different from those of African apes. Its wrist joints were not as stiff as those of apes, and the joints between their palms and fingers were much more flexible. Moreover, a large joint in the middle of the wrist (the midcarpal joint) was especially flexible, being even more mobile than our own. This would have allowed *Ardipithecus* to support nearly all of its body weight on its palms when moving along tree branches, so that it could move well forward of a supporting forelimb without first releasing its grip on a branch.

This discovery ends years of speculation about the course of human evolution. Our ancestors’ hands differed profoundly from those of living great apes, and therefore the two must have substantially differed in the ways they climbed, fed, and nested. It is African apes who have evolved so extensively since we shared our last common ancestor, not humans or our immediate hominid ancestors. Hands of the earliest hominids were less ape-like than ours and quite different from those of any living form.

*Ardipithecus* also shows that our ability to use and make tools did not require us to greatly modify our hands. Rather, human grasp and dexterity were long ago inherited almost directly from our last common ancestor with chimpanzees. We now know that our earliest ancestors only had to slightly enlarge their thumbs and shorten their fingers to greatly improve their dexterity for tool-using.

**See pages 5–6 for authors’ affiliations.**

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The Pelvis and Femur of *Ardipithecus ramidus*: The Emergence of Upright Walking

C. Owen Lovejoy, Gen Suwa, Linda Spurlock, Berhane Asfaw, Tim D. White

Virtually no other primate has a human-like pelvic girdle—not even our closest living relatives, the chimpanzee and bonobo. Such uniqueness evolved via substantial modifications of a pelvis more originally suited for life in trees. This arboreal primate heritage has left us rather ungracefully. Our legs are massive because they continue to house almost all of the muscles originally required for climbing. Our hamstrings, the large muscles in our posterior thighs, must decelerate the swinging limb with each step, and when we run, the limb’s inertia is sometimes too great and these muscles fail (not something one would want to happen on a savanna).

Furthermore, when each limb leaves the ground to be swung forward, it and the pelvis are unsupported and would slump toward the ground were it not for muscles acting on the opposite side of the body (the anterior gluteals). One early anthropologist described human locomotion as a process by which we alternately almost fall on our faces. Chimpanzees and other primates cannot prevent such slumping when walking upright because they cannot reposition these muscles effectively. Their spine is too inflexible and their ilia—the large pelvic bones to which the gluteals attach—are positioned and shaped differently than ours. Modifying a typical chimp or gorilla pelvis to facilitate upright walking would require extensive structural changes.

Until now, the fossil record has told us little about when and how the early hominid pelvis evolved. Even 3 to 4 million years ago (when our brains were still only slightly larger than those of chimpanzees), it had already undergone radical transformation. One of the oldest hominid pelvis, that of *Australopithecus afarensis* (*A.L. 288-1; "Lucy"), shows that her species had already evolved virtually all of the fundamental adaptations to bipedality. Even the kinetics of her hip joint were similar to ours. Although the human pelvis was later further reshaped, this was largely the result of our much enlarged birth canal.

*Ardipithecus ramidus* now unveils how our skeleton became progressively modified for bipedality. Although the foot anatomy of *Ar. ramidus* shows that it was still climbing trees, on the ground it walked upright. Its pelvis is a mosaic that, although far from being chimpanzee-like, is still much more primitive than that of *Australopithecus*

The gluteal muscles had been repositioned so that *Ar. ramidus* could walk without shifting its center of mass from side to side. This is made clear not only by the shape of its ilium, but by the appearance of a special growth site unique to hominids among all primates (the anterior inferior iliac spine). However, its lower pelvis was still almost entirely ape-like, presumably because it still had massive hindlimb muscles for active climbing.

Changes made in the upper pelvis rendered *Ar. ramidus* an effective upright walker. It could also run, but probably with less speed and efficiency than humans. Running would also have exposed it to injury because it lacked advanced mechanisms such as those that would allow it to decelerate its limbs or modulate collision forces at its heel. *Australopithecus*, which had given up its grasping foot and abandoned active climbing, had evolved a lower pelvis that allowed it to run and walk for considerable distances.

*Ar. ramidus* thus illuminates two critical adaptive transitions in human evolution. In the first, from the human-chimp last common ancestor to *Ardipithecus*, modifications produced a mosaic pelvis that was useful for both climbing and upright walking. In the second, from *Ardipithecus* to *Australopithecus*, modifications produced a pelvis and lower limb that facilitated more effective upright walking and running but that were no longer useful for climbing. Because climbing to feed, nest, and escape predators is vital to all nonhuman primates, both of these transitions would likely have been a response to intense natural selection.

See pages 5–6 for authors’ affiliations. When citing, please refer to the full paper, available at DOI 10.1126/science.1175831.
Combining Prehension and Propulsion: The Foot of *Ardipithecus ramidus*

C. Owen Lovejoy, Bruce Latimer, Gen Suwa, Berhane Asfaw, Tim D. White

The special foot adaptations that enable humans to walk upright and run are central to understanding our evolution. Until the discovery of *Ardipithecus ramidus*, it was generally thought that our foot evolved from one similar to that of modern African apes. Apes have feet that are modified to support their large bodies and to facilitate vertical climbing, thus allowing them to feed, nest, and seek safety in trees. Our foot differs from theirs in myriad ways, and its evolution from theirs would consequently have required an extensive series of structural changes. Some mid–20th-century comparative anatomists were so impressed with the profound differences between human and extant ape feet that they postulated a deep, pre-ape origin for hominids.

*Ar. ramidus* brings a new perspective to this old controversy. Its foot turns out to be unlike those of the African apes in many ways. The partial skeleton of *Ar. ramidus* preserves most of the foot and includes a special bone called the os peroneum that is critical for understanding foot evolution. This bone, which is embedded within a tendon, facilitates the mechanical action of the fibularis longus, the primary muscle that draws in the big toe when the foot is grasping. Until now, we knew little about this bone’s natural history, except that it is present in Old World monkeys and gibbons but generally not in our more recent ape relatives. Monkeys are very accomplished at leaping between trees. They must keep their feet fairly rigid during takeoff when they hurl themselves across gaps in the tree canopy; otherwise, much of the torque from their foot muscles would be dissipated within the foot rather than being transferred to the tree.

The African apes are too large to do much leaping. They have therefore given up the features that maintain a rigid foot and instead modified theirs for more effective grasping—almost to the point of making it difficult to distinguish their feet from their hands. Indeed, very early anatomists argued that the “quadrumanus” apes were not related to humans because of their hand-like feet. Extant apes lack the os peroneum, and their fibularis tendon, which draws the great toe closed during grasping, has been relocated more toward the front of the foot. This makes the tendon run more parallel to other joints that cross the midfoot, and allows apes to grasp with great power without stiffening these other, flexible joints. Apes can thus both powerfully grasp and mold their feet around objects at the same time. However, their feet have become less effective as levers, making them far less useful in terrestrial propulsion.

The foot of *Ar. ramidus* shows that none of these ape-like changes were present in the last common ancestor of African apes and humans. That ancestor, which until now has been thought to be chimpanzee-like, must have had a more monkey-like foot. Not only did it still have an os peroneum, it must also have had all of the other characteristics associated with it (subsequently abandoned in chimpanzees and gorillas). We infer this because humans still have these characteristics, so we must have retained them from our last common ancestor. The mid–20th-century anatomists were correct to worry about the human foot as they did: Ours turns out to have evolved in one direction, while those of African apes were evolving in quite another.

One of the great advantages of our more rigid foot is that it works much better as a lever during upright walking and running (as it also does in monkeys). However, *Ar. ramidus* still had an opposable big toe, unlike any later hominin. Its ability to walk upright was therefore comparatively primitive. Because it had substantially modified the other four toes for upright grasping, the *Ardipithecus* foot was an odd mosaic that worked for both upright walking and climbing in trees. If our last common ancestor with the chimpanzee had not retained such an unspecialized foot, perhaps upright walking might never have evolved in the first place.
Evolutionary biologists have long recognized that the living primates most similar to humans are the great apes, and comparative genomic sequence analyses confirm that we are most closely related to chimpanzees and bonobos (genus *Pan*). Because of our great genomic similarity (sometimes even cited as ~99%), the presumption that we evolved from a chimpanzee-like ancestor has become increasingly common wisdom. The widely held view that the hominid descendant of the last common ancestor we shared with chimpanzees is *Australopithecus afarensis* at 4.4 million years ago provides the first substantial body of fossil evidence that temporally and anatomically extends our knowledge of what the last common ancestor we shared with chimpanzees was like, and therefore allows a test of such presumptions.

Until now, *Australopithecus afarensis*, which lived 3 to 4 million years ago, represented the most primitive well-known stage of human evolution. It had a brain only slightly larger than that of chimpanzees, and a snout that projected more than in later hominids. Assuming some variant of a chimpanzee-like ape ancestry, the bipedality of *Au. afarensis* has been widely interpreted as being so primitive that it probably could not have extended either its hip or knee joints and was a clumsy upright walker. Some researchers have even postulated that *Au. afarensis* could walk but not run, or vice versa. Still others have suggested that *Au. afarensis* had a grasping ape-like foot. Similarly, it has been suggested that *Au. afarensis* had forelimbs that were ape-like, including long, curved fingers used to forage daily in the arboreal canopy, and that its immediate ancestors must have knuckle-walked. *Australopithecus* males were noticeably larger than females, and this has often been interpreted as signifying a single-male, polygynous, *Gorilla*-like mating system. Unlike gorillas, it has diminutive canines, but these were argued to be a consequence of its huge postcanine teeth. Early hominids have even been posited to have possibly interbred with chimpanzees until just before the appearance of *Australopithecus* in the fossil record.

The *Ar. ramidus* fossils and information on its habitat now reveal that many of these earlier hypotheses about our last common ancestor with chimpanzees are incorrect. The picture emerging from *Ar. ramidus* is that this last common ancestor had limb proportions more like those of monkeys than apes. Its feet functioned only partly like those of apes and much more like those of living monkeys and early apes such as *Proconsul* (which lived more than 15 million years ago). Its lower back was mobile and probably had six lumbar vertebrae rather than the three to four seen in the stiff backs of African apes. Its hand was unpredictably unique: Not only was its thumb musculature robust, unlike that of an ape, but its midcarpal joint (in the wrist) allowed the wrist to bend backward to a great degree, enhancing its ability to move along tree branches on its palms. None of the changes that apes have evolved to stiffen their hands for suspensorial use were present, so its locomotion did resemble that of any living ape.

The hominid descendant of the last common ancestor we shared with chimpanzees (the CLCA), *Ardipithecus*, became a biped by modifying its upper pelvis without abandoning its grasping big toe. It was therefore an unpredicted and odd mosaic. It appears, unlike *Au. afarensis*, to have occupied the basal adaptive plateau of hominin natural history. It is so rife with anatomical surprises that no one could have imagined it without direct fossil evidence.

![Cladogram adding Ar. ramidus to images of gorilla, chimpanzee, and human.](image)

See pages 5–6 for authors’ affiliations. When citing, please refer to the full paper, available at DOI 10.1126/science.1175833.
Chimpanzees, bonobos, and gorillas are our closest living relatives. The most popular reconstructions of human evolution during the past century rested on the presumption that the behaviors of the earliest hominids were related to (or even natural amplifications of) behaviors observed in these living great apes. One effect of chimpanzee-centric models of human evolution has been a tendency to view Australopithecus as transitional between an ape-like ancestor and early Homo.

Ardipithecus ramidus nullifies these presumptions, as it shows that the anatomy of living African apes is not primitive but instead has evolved specifically within extant ape lineages. The anatomy and behavior of early hominids are therefore unlikely to represent simple amplifications of those shared with modern apes. Instead, Ar. ramidus preserves some of the ancestral characteristics of the last common ancestor with much greater fidelity than do living African apes. Two obvious exceptions are its ability to walk upright and the absence of the large projecting canine tooth in males, derived features that Ardipithecus shares with all later hominids.

Ar. ramidus illuminates our own origins because it clarifies our relationship to Australopithecus. For example, the enlarged rear teeth of Australopithecus have long been viewed as adaptations to a rough, abrasive diet. This has led to speculation that canine teeth might have become smaller simply to accommodate the emergence of these other enlarged teeth, or that the importance of canine teeth in displays of male-to-male aggression waned with the development of weapons. Ar. ramidus negates such hypotheses because it demonstrates that small canines occurred in hominids long before any of the dental modifications of Australopithecus or the use of stone tools. The loss of large canine teeth in males must have occurred within the context of a generalized, non-specialized diet. Comparisons of the Ar. ramidus dentition with those of all other higher primates indicate that the species retained virtually no anatomical correlates of male-to-male conflict. Consistent with a diminished role of such agonism, the body size of Ar. ramidus males was only slightly larger than that of females.

The discovery of Ar. ramidus also requires rejection of theories that presume a chimpanzee- or gorilla-like ancestor to explain habitual upright walking. Ar. ramidus was fully capable of bipedality and had evolved a substantially modified pelvis and foot with which to walk upright. At the same time, it preserved the ability to maneuver in trees, because it maintained a grasping big toe and a powerful hip and thigh musculature. Because upright walking provided no energy advantage for Ar. ramidus (it lacked many of the adaptations evolved in later hominids such as Australopithecus), reproductive success must have been central to its evolution in early hominids.

Loss of the projecting canine raises other vexing questions because this tooth is so fundamental to reproductive success in higher primates. What could cause males to forfeit their ability to aggressively compete with other males? What changes paved the way for the later emergence of the energy-thirsty brain of Homo? Such questions can no longer be addressed by simply comparing humans to extant apes, because no ape exhibits an even remotely similar evolutionary trajectory to that revealed by Ardipithecus.

When the likely adaptations of early hominids are viewed generally rather than with specific reference to living chimpanzees, answers to such questions arise naturally. Many odd hominin characteristics become transformed from peculiar to commonplace. Combining our knowledge of mammalian reproductive physiology and the hominid fossil record suggests that a major shift in life-history strategy transformed the social structure of early hominids. That shift probably reduced male-to-male conflict and combined three previously unseen behaviors associated with their ability to exploit both trees and the land surface: (i) regular food-carrying, (ii) pair-bonding, and (iii) reproductive cryptis (in which females did not advertise ovulation, unlike the case in chimpanzees). Together, these behaviors would have substantially intensified male parental investment—a breakthrough adaptation with anatomical, behavioral, and physiological consequences for early hominids and for all of their descendants, including ourselves.

See pages 5–6 for authors’ affiliations.

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Hominid fossils predating the emergence of Australopithecus have been sparse and fragmentary. The evolution of our lineage after the last common ancestor we shared with chimpanzees has therefore remained unclear. *Ardipithecus ramidus*, recovered in ecologically and temporally resolved contexts in Ethiopia’s Afar Rift, now illuminates earlier hominid paleobiology and aspects of extant African ape evolution. More than 110 specimens recovered from 4.4-million-year-old sediments include a partial skeleton with much of the skull, hands, feet, limbs, and pelvis. This hominid combined arboreal palmigrade clambering and careful climbing with a form of terrestrial bipedality more primitive than that of *Australopithecus*. *A. ramidus* had a reduced canine/premolar complex and a little-derived cranial morphology and consumed a predominantly C3 plant–based diet (plants using the C3 photosynthetic pathway). Its ecological habitat appears to have been largely woodland-focused. *A. ramidus* lacks any characters typical of suspension, vertical climbing, or knuckle-walking. *A. ramidus* indicates that despite the genetic similarities of living humans and chimpanzees, the ancestor we last shared probably differed substantially from any extant African ape. Hominids and extant African apes have each become highly specialized through very different evolutionary pathways. This evidence also illuminates the origins of orthogamy, bipedality, ecology, diet, and social behavior in earliest Hominidae and helps to define the basal hominid adaptation, thereby accentuating the derived nature of *Australopithecus*.

In 1871, Charles Darwin concluded that Africa was humanity’s most probable birth continent [(1), chapter 7]. Anticipating a skeptical reception of his placement of *Homo sapiens* as a terminal twig on the organic tree, Darwin lamented the mostly missing fossil record of early hominids (2). Following T. H. Huxley, who had hoped that “the fossilized bones of an Ape more anthropoid, or a Man more pithecoid” might be found by “some unborn palæontologist” [(3), p. 50], Darwin observed, “Nor should it be forgotten that those regions which are the most likely to afford remains connecting man with some extinct ape-like creature, have not as yet been searched by geologists.” He warned that without fossil evidence, it was “useless to speculate on this subject” [(1), p. 199].

Darwin and his contemporaries nonetheless sketched a scenario of how an apelike ancestor might have evolved into humans. That scenario easily accommodated fossil evidence then restricted to European Neandertals and *Dryopithecus* (a Miocene fossil ape). Javanese *Homo erectus* was found in the 1890s, followed by African *Australopithecus* in the 1920s. By the 1960s, successive grades of human evolution were widely recognized. *Australopithecus* comprised several Plio-Pleistocene small-brained species with advanced bipedality. This grade (adaptive plateau) is now widely recognized as foundational to more derived *Homo*.

Molecular studies subsequently and independently confirmed Huxley’s anatomically based phylogeny linking African apes and living humans (4). They also challenged age estimates of a human/chimpanzee divergence, once commonly viewed as exceeding 14 million years ago (Ma). The latter estimates were mostly based on erroneous interpretations of dentognathic remains of the Miocene fossil ape *Ramapithecus*, combined with the presumption that extant chimpanzees are adequate proxies for the last common ancestor we shared with them (the CLCA).

The phylogenetic separation of the lineages leading to chimpanzees and humans is now widely thought to have been far more recent. During the 1970s, discovery and definition of *Australopithecus afarensis* at Laetoli and Hadar extended knowledge of hominid biology deep into the Pliocene [to 3.7 Ma (5, 6)]. The slightly earlier (3.9 to 4.2 Ma) chronospecies *Au. anamensis* was subsequently recognized as another small-brained biped with notably large postcanine teeth and postcranial derivations shared with its apparent daughter species (7, 8). Late Miocene hominid fossils have been recently recovered from Ethiopia, Kenya, and Chad. These have been placed in three genera [*Ardipithecus* (9–12), *Orrorin* (13), and *Sahelanthropus* (14)]. They may represent only one genus (12, 15), and they challenge both savanna- and chimpanzee-based models (16) of hominid origins.

Continuing to build on fossil-free expectations traceable to Darwinian roots, some hold that our last common ancestors with African apes were anatomically and behaviorally chimpanzee-like (17), that extant chimpanzees can be used as “time machines” (18), and/or that unique features of *Gorilla* are merely allometric modifications to accommodate its great body mass. Thus, early *Australopithecus* has routinely been interpreted as “transitional” and/or a “locomotor missing link” (19, 20) between extant humans and chimpanzees. Bipedality is widely suggested to have arisen as an opportunistic, or even necessary, response to a drier climate and the expansion of savannas. These views have been challenged on paleontological and theoretical grounds (9, 21). However, without additional fossil evidence, the evolutionary paths of the various great apes and humans have remained shrouded.

In related papers in this issue (22–27), we describe in detail newly discovered and/or analyzed specimens of *A. ramidus*, including two individuals with numerous postcranial elements. All are dated to 4.4 Ma and come from the Middle Awash area of the Ethiopian Afar rift. Local geology and many associated fossils are also described (28–30). These new data jointly establish *Ardipithecus* as a basal hominid adaptive plateau preceding the emergence of *Australopithecus* and its successor, *Homo*. Inferences based on *A. ramidus* also facilitate understanding its precursors (22, 23, 27, 31). Here, we provide an integrated view of these studies and summarize their implications.

The Middle Awash. The Middle Awash study area contains a combined thickness of >1 km of Neogene strata. To date, these deposits have yielded eight fossil hominid taxa spanning the Late Miocene to Pleistocene (~6.0 to ~0.08 Ma) (32, 33). Hominids make up only 284 of the 18,327 total cataloged vertebrate specimens. Spatially and chronologically centered in this successional, the Central Awash Complex (CAC) (28, 34) rises above the Afar floor as a domelike structure comprising >300 m of radioisotopically and paleomagnetically calibrated, sporadically fossiliferous strata dating between 5.55 and 3.85 Ma. Centered in its stratigraphic column are two prominent and widespread volcanic marker horizons that encapsulate the Lower Aramis Member of the Sagantole Formation (Fig. 1). These, the Gàala (‘camel’ in Afar language) Vitric Tuff Complex (GATC) and the superimposed Daam Aatu (‘baboon’ in Afar language) Basaltic Tuff (DABT), have indistinguishable laser fusion 39Ar/40Ar dates of 4.4 Ma. Sandwiched between

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**Ardipithecus ramidus and the Paleobiology of Early Hominids**

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the two tuffs are fossiliferous sediments averaging ~3 m in thickness and cropping out discontinuously over an arc-shaped, natural erosional transect of >9 km (28). The rich fossil and geologic data from these units provide a detailed characterization of the Pliocene African landscape inhabited by *Ardipithecus*.

We first surveyed the CAC during 1981 in attempts to understand the distribution of fossils within the region. We launched a systematic program of geological, geochronological, and paleontological investigation in 1992. Initial visits to the CAC’s northeastern flank documented abundant fossilized wood and seeds in the interval between the two tuffs. We collected and identified a highly fragmented sample of vertebrates, including abundant cercopithecid monkeys and trachelaphine bovids. The first hominid fossils were found at Aramis vertebrate paleontology locality 1 (ARA-VP-1) on 17 December 1992. Two initial seasons of stratigraphic and geochronological studies yielded 649 cataloged vertebrates, including a minimum number of 17 hominid individuals represented mostly by teeth (10).

Because of its content, the Lower Aramis Member became the focus of our paleontological efforts. Fourteen sublocalities within the original ARA-VP-1 locality were circumscribed and subjected to repeated collecting of all biological remains, based on multiple team crawls (35) across the eroding outcrops between 1995 and 2005. Analogous collections were made at adjacent localities (ARA-VP-6, -7, and -17), as well as at the eastern and western exposures of the *Ardipithecus*-bearing sedimentary units (KUS-VP-2 and SAG-VP-7) (KUS, Kuseralee Dora; SAG, Sagantole). The Lower Aramis Member vertebrate assemblage (table S1) now totals >6000 cataloged specimens, including 109 hominid specimens that represent a minimum of 36 individuals. An additional estimated 135,000 recovered fragments of bone and teeth from this stratigraphic interval are cataloged by locality and taxon as pooled “bulk” assemblages. Analogous samples were collected from the Lower Aramis Member on the eastern transect pole (SAG-VP-1, -3, and -6). Fossils from localities higher in the section in 1993 (10). However, on 5 November 1994, Y.H.S. collected two hominid metacarpal fragments (ARA-VP-6/500-001a and b) from the surface of an exposed silty clay ~3 m below the upper tuff (DABT), 54 m to the north of the point that had 10 months earlier yielded the *Ardipithecus* holotype dentition. Sieving produced additional hominid phalanges. The outcrop scrape exposed a hominid phalanx in situ, followed by a femur shaft and nearly complete tibia. Subsequent excavation during 1994
and the next field season (at a rate of ~20 vertical mm/day across ~3 m²) revealed >100 additional in situ hominid fragments, including sesamoids (Fig. 2 and table S2). Carnivore damage was absent.

The bony remains of this individual (ARA-VP-6/500) (Fig. 3) (37) are off-white in color and very poorly fossilized. Smaller elements (hand and foot bones and teeth) are mostly undistorted, but all larger limb bones are variably crushed. In the field, the fossils were so soft that they would crumble when touched. They were rescued as follows: Exposure by dental pick, bamboo, and porcupine quill probe was followed by in situ consolidation. We dampened the encasing sediment to prevent desiccation and further disintegration of the fossils during excavation. Each of the subspecimens required multiple coats of consolidant, followed by extraction in plaster and aluminum foil jackets, then additional consolidant before transport to Addis Ababa.

Pieces were assigned number suffixes based on recovery order. Back-dirt was weathered in place and resieved. The 1995 field season yielded facial fragments and a few other elements in northern and eastern extensions of the initial excavation. Further excavation in 1996 exposed no additional remains. Each fragment’s position, axial orientation, and dip were logged relative to a datum (strata here dip east at ~4° to 5°). A polygon representing the outer perimeter and vertical extent of the hominid fragment constellation (based on each bone’s center point) was demarcated by a carapace of limestone blocks cemented with concrete after excavation, then further protected by a superimposed pile of boulders, per local Afar custom.

Fig. 2. The ARA-VP-6/500 skeletal excavation. Successive zooms on the ARA-VP-6/500 partial skeleton discovery are shown. Insets show the application of consolidant to the tibia shaft and removal of the os coxae in a plaster jacket in 1994–1995. No skeletal parts were found articulated (the mandible excavation succession shows the close proximity of a proximal hand phalanx and trapezium). Only in situ specimens are shown on the plan and profile views. Note the tight vertical and wider horizontal distributions of the remains. Local strata dip ~5° to the east. The lower inside corner of each yellow pin flag marks the center point for each in situ specimen from the 1994–1995 excavation. The 1995–1996 excavation recovered additional, primarily craniodental remains between these flags and the vehicle. The boulder pile emplaced at the end of the 1996–1997 excavation marks the discovery site today.

Fig. 3. The ARA-VP-6/500 skeleton. This is a composite photograph to show the approximate placement of elements recovered. Some pieces found separately in the excavation are rejoined here. Intermediate and terminal phalanges are only provisionally allocated to position and side.
The skeleton was scattered in typical Lower Aramis Member sediment (Fig. 2): fine-grained, massive, unsilikened red-brown alluvial silty clay containing abundant decalcified root casts, fossil wood, and seeds. A 5- to 15-cm lens of poorly sorted sand and gravel lies immediately below the silty clay, and the spread of cranial parts to the north suggests that the bones of the carcass came to rest in a shallow swale on the floodplain.

There is no evidence of weathering or mammalian chewing on ARA-VP-6/500. Bony elements were completely disarticulated and lacked anatomical association. Many larger elements showed prefossilization fragmentation, orientation, and scatter suggestive of trampling. The skull was particularly affected, and the facial elements and teeth were widely scattered across the excavated area. Bioturbation tilted some phalanges and metacarpals at high dip angles (Fig. 2). A few postcrania of a large Aquila (eagle) and other birds were discovered during excavation, as were a few micromammals. No large mammal remains (except isolated cercopithecoid teeth and shaft splinters from a medium-to-large mammal limb bone) were associated. The cause of death is indeterminate. The specimen is judged to be female. The only pathology is a partially healed osteolytic lesion suggestive of local infection of the left proximal ray 5 pedal phalanx (ARA-VP-6/500-044).

Laboratory exposure and consolidation of the soft, crushed fossils were accomplished under binocular microscope. Acetone was applied with brushes and hypodermic needles to resolven and remove small patches of consolidant-hardened encasing matrix. Microsurgery at the interface between softened matrix and bone proceeded millimeter by millimeter, rehardening each cleaned surface with consolidant after exposure. This process took several years. The freed specimens remain fragile and soft, but radiographic accessibility is excellent. Most restoration and correction for distortion were accomplished with plaster replicas or micro-computed tomography digital data to preserve the original fossils in their discovery state.

Environmental context. The Lower Aramis Member lacks any evidence of the hydraulic mixing that afflicts many other hominid-bearing assemblages. The unwarranted inference that early hominids occupied “mosaic habitats” (38) is often based on such mixed assemblages, so the resolution and fidelity of the Aramis environmental data sets are valuable. We estimate that the interval of time represented by the strata between the two tuffs at Aramis is <105 years, and perhaps just a few hundred or thousand years (28, 39). The lithology, thickness, taphonomic evidence, and similar age of the constraining marker horizons imply that geologically, the evidence can be viewed as “habitat time-averaged” (40). Indeed, we do not see notably different environmental indicators in the fossils or geologic or chemical data sampled vertically throughout the interval. The wealth of data allows a high-fidelity representation [sensu (41)] of the ecological community and environment inhabited by Ar. ramidus 4.4 Ma.

A variety of data indicate that the wooded biotope varied laterally across the Pliocene landscape (28–30). The hominid-bearing localities (centered on the ARA-VP-1 sublocalities) are rich in fossilized wood fragments, seeds, and animal fossils. Here, isotopic paleosol compositions indicate mostly wooded conditions (28). There was obviously more water at Aramis then (4.4 Ma) — supporting a much richer flora and fauna — than there is today. The higher water budget is possibly due to higher elevation during deposition (42) or to paleoclimatic factors such as a more continuous Pliocene El Niño effect (43). An abrupt transition occurs southeast of the SAG-VP-7 locality, where sedimentary, faunal, taphonomic, and isotopic data imply a more open rift-axis setting depauperate in faunal remains and lacking in primates, micromammals, and macrobotanical remains (29, 30).

Along the northern slope of the CAC, all localities of the Lower Aramis Member yielded tragelaphine bovids, monkeys, and other data indicative of more wooded conditions. Carbon isotopes from the teeth of five Ardipithecus individuals found here imply that they fed largely on C3 plants in woodlands and/or among the small patches of forests in the vicinity. We interpret the combined contextual data to indicate that Ar. ramidus preferred a woodland-to-forest habitat (29, 30) rather than open grasslands. This finding is inconsistent with hypotheses positing hominid origins via climate-driven savanna expansion.

Variation and classification. Initial (1994) description of the limited hominid sample from Aramis placed these remains in a newly discovered Australopithecus species interpreted as the most primitive then known (10). Subsequent recovery of the ARA-VP-6/500 skeleton showed that, relative to body size, its dentition was small, unlike Australopithecus. Strict cladistic practice required a new genus name for this sister taxon of Australopithecus, so the material was renamed as the new genus Ardipithecus in 1995, with the lack of megadonty added to the species diagnosis even as the partial skeleton’s excavation was still under way (44). Subsequent discovery of the earlier probable chronospecies Ar. kadabba in 1997 (11, 12) was followed by recovery of Orrorin in 2000 (13) and Sahelanthropus in 2001 (14). These Late Miocene fossils provide additional outgroup material useful in assessing the phylogenetic position of Ar. ramidus.

Only two adjacent Ethiopian study areas (the Middle Awash and Gona) have yielded confirmed remains of Ar. ramidus to date (7, 36). Neither has produced any evidence to reject a single species lineage as the source of the combined hominid sample from these Pliocene sites. We thus interpret the Lower Aramis Member hominid assemblage as a single taxon (22). Penecontemporary (~4.3 to 4.7 Ma) hominid remains from elsewhere are sparse (45, 46), and these are broadly compatible with the now expanded range of variation in Ar. ramidus (22, 23). Thus, although continental sampling is still obviously inadequate, describing hominid species diversity in this time frame (47) as “very bushy” seems unwarranted (48).

The amount of variation within the known Afar Ar. ramidus sample appears to be lower than typical for species of Australopithecus. This is probably due to a lesser degree of sexual dimorphism in Ardipithecus, combined with the narrow time window represented by the interval between the two Aramis tuffs. Skeletal dimorphism is notably difficult to assess, except in rare instances of geologically isochronous samples of a species lineage (e.g., A.L. 333 “first family”) (49). For Ar. ramidus, the ARA-VP-6/500 skeleton (Figs. 3 and 4) provides a rare opportunity for guiding a probabilistic approach to sex attribution of conspecific fossils, relying on canines (22) and postcranially based estimates of body size (27). The implication is that there was broad overlap in body size between males and females of Ar. ramidus.

Cranial and dental anatomy. The Ar. ramidus skull (23) is very similar to the larger, more robust Sahelanthropus cranium (TM 266-01-60-1) from Chad, also interpreted as an early hominoid (14, 50). Some of the differences are probably partly sex-related. Ar. ramidus shares with Sahelanthropus a small cranial capacity (300 to 350 cc) and considerable midfacial projection but a maxillo-premaxillary complex that is less prognathic than that of modern African apes [not necessarily a derived trait shared with Homo, in contrast with (51)]. The Ardipithecus and Sahelanthropus crania each lack a distinct post-toral sulcus, and both exhibit an anteriorly positioned posterior cranial base.

Most aspects of the craniofacial structure of Sahelanthropus/Ardipithecus are probably close to the African ape and hominid ancestral state. Gorilla and chimpanzee cranial morphologies, as well as their specialized dentitions, are clearly divergently derived (22). In Gorilla, enhanced facial size and prognathism occur in relation to larger general size and an increasing adaptation to herbivory and folivory. In Pan (also with enhanced prognathism), derived cranial form (including anterior basioccipital lengthening) probably occurred as a part of enhanced terrestriality accompanied by elevated agonistic behavior and its anatomical correlates, such as tuskslike canines (22, 23). The bonobo cranial base and Ardipithecus craniofacial structure may be less derived, but even the bonobo seems to be derived in its relatively small face and global dental reduction (22). This was probably at least in part due to decreased intraspecific aggression in the bonobo lineage after separation from the common chimpanzee lineage.

The supero-inferiorly short but intermediately prognathic Ar. ramidus face lacks the
broadening and anterior migration of the zygomatic area seen to varying degrees in species of Australopithecus. The primitive craniofacial pattern shared between Sahelanthropus and Ardipithecus suggests that the genus Australopithecus would later evolve a craniofacial structure capable of increased postcanine mastication consequent to an ecological breakout from wooded habitats, expanding its foraging into more open environments (7, 10).

The Ardipithecus dentition suggests omnivory (22). It exhibits none of the specializations seen among modern apes; neither the large incisors of Pongo nor Pan nor the specialized molar morphology of Pongo, Pan, or Gorilla. Postcanine size relative to body size was slightly larger than in Pan but smaller than in Gorilla, Pongo, or (especially) Au. afarensis. Ar. ramidus molars overlap considerably with Pan in some measures of enamel thickness but differ in overall thickness and structure. Chimpanzee molars have a broad occlusal basin with locally thin enamel not seen in Ardipithecus. Pan molar morphology is probably an adaptation to crushing relatively soft and nonabrasive food items such as ripe fruits, while retaining some shearing capacities. The Ardipithecus dentition shows no strong signals of ripe-fruit frugivory, folivory-herbivory, or feeding on hard objects. Its macroscopic and microscopic wear patterns, as well as the low bunodont cusps with intermediate enamel thickness (22), suggest that its diet was not particularly abrasive but may have included some hard foods. It is consistent with a partially terrestrial, partially arboreal pattern of feeding in a predominantly wooded habitat.

Carbon isotopic evidence from the teeth of five Ar. ramidus individuals suggests that Ardipithecus and Australopithecus were distinct in dietary intake (30). “Robust” and “nonrobust” Australopithecus have enamel isotope values indicating a diet of more than 30% C4 plants, with variation ranging up to ~80% C4. In contrast, the known Ar. ramidus individuals vary only between ~10 and 25% C4, and thus also differ from Pan troglodytes, which prefers ripe fruit and is considered closer to a pure C3 feeder (30). Thus, Ardipithecus appears to have exploited a wider range of woodland resources than do chimpanzees, but without relying on the open biotope foods consumed by later Australopithecus.

Evolution of the canine/lower third premolar complex (C/P3) potentially illuminates social and reproductive behavior. The Ar. ramidus canine sample totals 21 Aramis individuals. Some are small fragments, but all show informative morphology and/or wear. All specimens are either morphologically similar to those from female apes or are further derived toward the later hominid condition (22). Morphological and metric variation in the sample is small. Functionally important sex-related size dimorphism is not apparent. There is no evidence of functional honing (planar facets on the mesiobuccal P3 or sharpened edges on the distolabial upper canine margin). The largest, presumably male, specimens are as morphologically derived as the smallest, showing that dimorphic canine morphology was virtually absent in these hominids by 4.4 Ma. Furthermore, a juvenile probable male lacks the delayed canine eruption seen in chimpanzees, approximating the Au. anamensis and Au. afarensis conditions and indicating that the canine was not an important component of adult sociocultural relationships.

The differential status of upper versus lower canine morphology is informative. In Ar. ramidus,
Ardipithecus ramidus

the lower canines retain modally more apelike morphology than do the uppers, and, in contra-
distinction to other anthropoids, the height of the
maxillary canine crown is lower than that of the
mandibular (22). This relationship is opposite that
seen in great apes and cercopithecids, whose
upper canine dominance is exaggerated, particu-
larly in males of dimorphic species. In these
primates, upper canine projection and prominence
function in both weaponry and display. The
Ar. ramidus canines are metrically and morpho-
logically derived in the direction of later homi-
nids, and we hypothesize that reduction and
alteration of upper canine size and shape in this
and earlier hominid species are related to changes
in social behaviors (22, 31).

The canines of Sahelanthropus, Orrorin, and
Ar. kadabba are broadly equivalent to those of
Ar. ramidus in size and function. However, the
upper canines of Late Miocene hominids exhibit
a subtle but distinctly more primitive morphol-
ogy than their Ar. ramidus homologs, potentially
including occasional residual (female ape-like)
honing as part of their variation (12, 15). This
suggests that upper canine prominance was
reduced through the Late Miocene and Early
Pliocene. In contrast, the C/P3 complex of the last
common ancestor of hominids and chimpanzees
probably had a moderate level of canine dimor-
phism combined with functional honing. This was
subsequently generally retained in P. paniscus
and enhanced in P. troglodytes.

Body size and dimorphism. The partial skeleton
ARA-VP-6/500 is identified as female based on
probability assessments of canine size
(its canines are among the smallest of those of 21
available individuals) (22). This interpretation is
corroborated by its small endo- and exocranial
size, as well as its superoinferiorly thin supra-
orbital torus (23). Bipedal standing body height
for the ARA-VP-6/500 individual is estimated at
approximately 120 cm, and body mass at ~50 kg
(27). Although actual body mass may vary con-
siderably in relation to skeletal size, this is a large
female body mass.

Of the Ar. ramidus postcrania! elements, the
humerus represents the largest minimum num-
ber of individuals (seven). ARA-VP-6/500 does
not preserve a humerus, but detailed comparisons
suggest that its forelimb was ~2 to 8% larger in
linear dimensions than the partial forelimb skele-
ton ARA-VP-7/2 (24, 27), which does include a
humerus. This would make ARA-VP-6/500 either
the second- or third-largest of eight individuals
within the Aramis hominid sample. The com-
bined evidence suggests that Ardipithecus skele-
tal body size was nearly monomorphic, and less
dimorphic than Australopithecus, as estimated from
template bootstrapping (49). Most likely,
Ardipithecus exhibited minimal skeletal body
size dimorphism, similar to Pan, consistent with
a male-bonded social system, most likely a primi-
tive retention from the CLCA condition (31).
With its subsequent commitment to terrestrial
bipedality, Australopithecus probably enhanced
female cooperation and group cohesion, thus
potentially reducing female body size, whereas
male size increased in response to predation
pressure, probably elevated by expanding niche
breadth.

Postcranial biology and locomotion. Regard-
less of whether the Afar Ar. ramidus popu-
lation represents a hominid relic or a lineal
ancestor, this taxon’s biology resolves funda-
mental evolutionary questions persisting since
Darwin. Its substantially primitive postcranial
anatomy appears to signal a grade-based differ-
ce from later Australopithecus. The challenge
of understanding its evolutionary and functional
implications required a nontraditional approach.
Without testable hypotheses of underlying gene-
based developmental mechanisms, many paleo-
anthropological analyses have been adaptationist
(52) and/or purely numerically discriminatory.
Therefore, wherever possible, in the accompany-
ng postcranial papers (24–27) we restrict
hypotheses to those that can be formulated
consistent with putative selection acting on
cascades of modular-based positional infor-
mation, especially when these can be potentially
grounded in known anabolic mechanisms. This
approach is summarized elsewhere (53, 54) and
in supporting online material text S1.

The upper pelvis of Ar. ramidus presents a
contrast to its primitive hand, foot, and limbs.
The ilia are abbreviated superoinferiorly and sagitally
oriented but broad mediolaterally, so much so that
the anterior inferior iliac spine has become a
separate growth site, as in all later hominids. The
pubic symphyseal face is quite short. A slight
sciatic notch is present, although ischial structure
– including occasional residual (female ape
characters as well as traits specialized for habitual
bipedality, such as the expanded second meta-
tarsal base that anchored plantarflexion during
heel- and toe-off. Many of the foot’s primary
adaptations to fulcrumation are probable reten-
tions from the gorilla/chimpanzee/human last
common ancestor (GLCA), but these have been
eliminated in apes, presumably for vertical
climbing.

The ARA-VP-6/500 radius/tibia ratio is 0.95,
as in generalized above-branch quadrupeds such as
maeques and Proconsul (an Early Miocene
ape) (27). Its intermembranar index (the ratio of
forelimb length to hindlimb length) is also similar
to those of above-branch quadrupeds. These facts
suggest that African apes experienced both
forelimb elongation and hindlimb reduction,
whereas hominid proportions remained largely
unchanged until the dramatic forearm shortening
and hindlimb elongation of Plio-Pleistocene
Homo.

These primitive proportions are consistent with
virtually all other aspects of the Ar. ramidus
skeleton. The inferred locomotor pattern com-
bined both terrestrial bipedality and arboreal
clambering in which much weight was supported
on the palms. The hand phalanges are elongate
relative to those of Proconsul, but metacarpals
(Mc) 2 to 5 remained primitively short and lacked
any corporeal modeling or adaptations typical of
knuckle-walking (24). Moreover, the virtually
complete wrist of ARA-VP-6/500 (lacking only
the pisiform) exhibits striking adaptations for
midcarpal dorsiflexion (backward deflection of
the dorsum of the hand), consistent with a highly
advanced form of arboreal palmigrady. In addi-
tion, substantial metacarpal-phalangeal dorsi-
flexion is indicated both by moderate dorsal
notching of the Mc2 to -5 heads and by marked
carpal displacement of the capitate head. Togeth-
er these must have permitted dorsiﬂexion of the
wrist and hand to a degree unparalleled in great
apes.

The Ar. ramidus elbow joint provided full
extension but lacks any characters diagnostic of
habitual suspension. Ulnar withdrawal was com-
plete and the thumb moderately robust, with
indications of a distinct and fully functional flex-
or pollicis longus tendon. The hamate’s hamulus
permitted substantial metacarpal motion for
opposition against the first ray. The central joint
complex (Mc2/Mc3/capitate/trapezoid) exhibits
none of the complex angular relationships and
marked syndesmotic reinforcement seen in extant
apes. Together, these retained primitive char-
acters, unlike their homologs in highly derived
African apes, imply that the dominant locomotor
pattern of the GLCA was arboreal palmigrady
rather than vertical climbing and/or suspension
(orthograpy). Another strong inference is that
hominids have never knuckle-walked (26).

The extraordinary forelimb of Ar. ramidus,
in combination with its limb proportions and
likely primitive early hominid lumbar column
(35), casts new light on the evolution of the
lower spine. The traditional interpretation has
between those species sprung, need in no respect be intermediate. This reinforces what Huxley appreciated in 1860:

In the supporting online material (226). The expanded Ar. ramidus sample allows more detailed consideration of early hominid phylogenetics. The placement of Ardipithecus relative to later hominids can be approached by using modern and Miocene apes as the outgroup. An earlier cladistic study of this kind concluded that Ar. ramidus was the sister taxon of all later hominids (71). A more recent assessment of Ar. ramidus dental characters came to the same conclusion (7). In these analyses, a suite of derived features and character complexes exclusively aligning Ar. ramidus with Australopithecus was identified, but these were based on comparatively limited anatomical elements. The Ar. ramidus characters reported here, combined with those from Gona (36), allow a more complete analysis that clarifies the relationships among early hominid taxa.

 Parsimony-based cladistic analyses are useful in deciphering relationships within the hominid family tree, despite their shortcomings (72, 73). The distribution of characters identified in Table 1 clearly shows that Ar. ramidus is derived relative to all known Late Miocene fossils attributed to the hominid clade. The earlier and more primitive probable chronospecies Ar. kadabba is found in 5.5- to 5.7-million-year-old deposits a mere 22 km west of Aramis, consistent with local (and perhaps regional) phylogenetic evolution. Its limited known elements are similar to those of other Late Miocene hominids in Kenya and Chad (12–14).

Table 1. (See pages 82 and 83.) The assembly of shared derived characters among early hominid taxa. Late Miocene and early Pliocene fossils now allow the strong inference of some character states (primitive, in blue) in the last common ancestor shared by chimpanzees and humans. Many other characters (not shown here) of extant apes were once considered primitive but are now shown to be derived and specific to those lineages. Late Miocene fossils from Ethiopia, Kenya, and Chad share some derived characters (in yellow) with all later hominids. The Ar. ramidus sample reported here shows a mixture of primitive and derived characters consistent with its phylogenetic and chronological placement. Phylogenetic implications are in Fig. 5. (An Excel version of this table is available in the supporting online material.)
### Table 1. The assembly of shared derived characters among early hominin taxa.

<table>
<thead>
<tr>
<th>Craniomandibular characters</th>
<th>Chimp/human LCA (INFERRED)</th>
<th><em>At. kadabba/Sa. tchadensis/ O. tugenensis</em></th>
<th><em>Ar. ramidus</em></th>
<th><em>Au. anamensis</em></th>
<th><em>Au. afarensis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>TM articulating eminence</td>
<td>flat</td>
<td>flat</td>
<td>flat</td>
<td>TM with defined eminence</td>
<td>TM with defined eminence</td>
</tr>
<tr>
<td>Mandible corpus breadth</td>
<td>indeterminate</td>
<td>mandibular corpus broad</td>
<td>mandibular corpus broad</td>
<td>mandibular corpus broad</td>
<td>mandibular corpus broad</td>
</tr>
<tr>
<td>Mental foramen</td>
<td>indeterminate</td>
<td>circum mid-corpus ht</td>
<td>circum mid-corpus ht</td>
<td>secondary lowered</td>
<td>secondarily lowered</td>
</tr>
<tr>
<td>Mandibular lateral prominence</td>
<td>weak</td>
<td>weak</td>
<td>weak</td>
<td>intermediate</td>
<td>lateral prominence developed</td>
</tr>
<tr>
<td>Ramus root/ extramolar sulcus</td>
<td>root posterior, sulcus narrow</td>
<td>root posterior, sulcus narrow</td>
<td>root posterior, sulcus narrow</td>
<td>intermediate</td>
<td>ramus root anterior and wide extramolar sulcus</td>
</tr>
<tr>
<td>Symphyseal inclination</td>
<td>strong</td>
<td>strong</td>
<td>strong</td>
<td>strong</td>
<td>bulbous (Laet.) to vertical (AL MAK)</td>
</tr>
<tr>
<td>Basion position</td>
<td>slightly posterior</td>
<td>anterior</td>
<td>indeterminate</td>
<td>anterior</td>
<td>anterior</td>
</tr>
<tr>
<td>Cranial base flexion</td>
<td>moderate mid-sagittal flexion, orbital kyphosis minimal</td>
<td>advanced?</td>
<td>advanced</td>
<td>indeterminate</td>
<td>advanced</td>
</tr>
<tr>
<td>Midfacial breadth</td>
<td>not extreme</td>
<td>not extreme</td>
<td>not extreme</td>
<td>indeterminate</td>
<td>midfacial breadth greater</td>
</tr>
<tr>
<td>Incisor/lower canine step</td>
<td>present</td>
<td>present</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
</tbody>
</table>

#### Dental Characters

<table>
<thead>
<tr>
<th>Chimp/human LCA (INFERRED)</th>
<th><em>At. kadabba/Sa. tchadensis/ O. tugenensis</em></th>
<th><em>Ar. ramidus</em></th>
<th><em>Au. anamensis</em></th>
<th><em>Au. afarensis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sectorial C/P3 shearing</td>
<td>present, strong in males</td>
<td>sometimes present?</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td></td>
<td>in reduced expression?</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canine size dimorphism</td>
<td>dimorphic</td>
<td>reduced C size dimorphism</td>
<td>further reduction?</td>
<td>further reduction</td>
</tr>
<tr>
<td>Female relative canine size</td>
<td>moderate</td>
<td>moderate</td>
<td>slightly smaller</td>
<td>slightly smaller</td>
</tr>
<tr>
<td>Upper canine shape feminization</td>
<td>males ungendered, higher crowned, medially lower shoulder</td>
<td>male C feminized in shape</td>
<td>male C feminized in shape</td>
<td>male C feminized in shape</td>
</tr>
<tr>
<td>Shoulder height</td>
<td>females mostly mid to low</td>
<td>mostly mid to low?</td>
<td>mid to high</td>
<td>mid to high</td>
</tr>
<tr>
<td>Shoulder flare</td>
<td>weak</td>
<td>weak</td>
<td>distinct flare</td>
<td>distinct flare</td>
</tr>
<tr>
<td>Lingual marginal ridge</td>
<td>weak</td>
<td>intermediate?</td>
<td>fold-like</td>
<td>fold-like</td>
</tr>
<tr>
<td>Main mesial lingual ridge</td>
<td>strong (Secondarily weak in Pan)</td>
<td>strong</td>
<td>basally broad</td>
<td>less prominent</td>
</tr>
<tr>
<td>Crown height</td>
<td>males tall, females moderate</td>
<td>indeterminate</td>
<td>UC height differentially reduced</td>
<td>reduced</td>
</tr>
<tr>
<td>Lower canine shape feminization</td>
<td>males higher crowned, medially low mesial shoulder, weak/ no distal tubercle</td>
<td>feminized</td>
<td>feminized</td>
<td>feminized</td>
</tr>
<tr>
<td>Mesial shoulder height</td>
<td>females vary from low to high</td>
<td>varies from low to high</td>
<td>intermediate?</td>
<td>intermediate?</td>
</tr>
<tr>
<td>Lingual marginal ridge</td>
<td>weak or none</td>
<td>intermediate?</td>
<td>fold-like</td>
<td>fold-like</td>
</tr>
<tr>
<td>Distal crest</td>
<td>weak or none</td>
<td>weak</td>
<td>intermediate</td>
<td>distinct</td>
</tr>
<tr>
<td>Distal tubercle</td>
<td>weak</td>
<td>developed</td>
<td>developed</td>
<td>variable</td>
</tr>
<tr>
<td>Canine enamel thickness</td>
<td>thin</td>
<td>thin</td>
<td>intermediate</td>
<td>thicker</td>
</tr>
<tr>
<td>Lower third premolar</td>
<td>wear</td>
<td>homes UC</td>
<td>rarely homes, distal UC wear steep</td>
<td>No home, distal UC wear steep</td>
</tr>
<tr>
<td>Basal crown size/shape</td>
<td>obliquely elongate</td>
<td>intermediate?</td>
<td>elongation weaker, relatively smaller</td>
<td>basally expanded and large</td>
</tr>
<tr>
<td>Height</td>
<td>tall, with MB cervical extension</td>
<td>intermediate?</td>
<td>MB cervical extension weaker</td>
<td>low, squat, weak extension</td>
</tr>
<tr>
<td>Metacoonid</td>
<td>absent or rudimentary</td>
<td>rudimentary</td>
<td>rudimentary</td>
<td>rudimentary</td>
</tr>
<tr>
<td>Transverse crest</td>
<td>tall, near-transverse to posteriorly directed</td>
<td>near-transverse</td>
<td>near-transverse</td>
<td>near-transverse</td>
</tr>
<tr>
<td>Mesial marginal ridge</td>
<td>weak or none</td>
<td>intermediate?</td>
<td>distinct</td>
<td>distinct</td>
</tr>
<tr>
<td>Upper third premolar</td>
<td>anterior fovea</td>
<td>weak definition</td>
<td>better defined</td>
<td>better defined</td>
</tr>
<tr>
<td>Asymmetry</td>
<td>weak to moderate</td>
<td>weak to moderate</td>
<td>weak to moderate</td>
<td>weak to moderate</td>
</tr>
</tbody>
</table>

Key: **Primitive condition** | **Intermediate derived condition** | **Derived condition**

---

LCA: Last Common Ancestor
Hominid clade: Evolutionary lineage of hominins

*This table continues on the next page.*
Table 1. The assembly of shared derived characters among early hominid taxa—continued.

<table>
<thead>
<tr>
<th>Dental characters (continued)</th>
<th>Chimp/human LCA (INFERRED)</th>
<th>Ar. kadabba/Sa. tchadensis/ O. tugenensis</th>
<th>Ar. ramidus</th>
<th>Au. anamensis</th>
<th>Au. afarensis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lower deciduous molar</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>crown shape</td>
<td>buccolingually narrow</td>
<td>indeterminate</td>
<td>buccolingually narrow</td>
<td>intermediate</td>
<td>broad, with developed anterior fovea</td>
</tr>
<tr>
<td>protoclidial dominance</td>
<td>strong</td>
<td>indeterminate</td>
<td>strong</td>
<td>intermediate</td>
<td>large metacnoid</td>
</tr>
<tr>
<td>talonid</td>
<td>little developed</td>
<td>indeterminate</td>
<td>little developed</td>
<td>intermediate</td>
<td>posterior cusps well defined</td>
</tr>
<tr>
<td>Molars</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>lower molar shape</td>
<td>indeterminate</td>
<td>relatively broader</td>
<td>relatively broader</td>
<td>relatively broader</td>
<td>tends to be very broad</td>
</tr>
<tr>
<td>molar row length</td>
<td>moderate</td>
<td>moderate</td>
<td>moderate</td>
<td>size increase</td>
<td>further increase</td>
</tr>
<tr>
<td>lower M3 development</td>
<td>variable, usually weak</td>
<td>moderately broad</td>
<td>variable, usually weak</td>
<td>moderately broad</td>
<td>large M3 with better developed distal crown</td>
</tr>
<tr>
<td>occlusal foveae</td>
<td>moderately broad</td>
<td>moderately broad</td>
<td>moderately broad</td>
<td>narrower (increased basal flaire)</td>
<td>narrower (increased basal flaire)</td>
</tr>
<tr>
<td>crown height</td>
<td>low</td>
<td>low</td>
<td>low</td>
<td>intermediate?</td>
<td>taller M1 crown height</td>
</tr>
<tr>
<td>Molar enamel thickness</td>
<td>intermediate, variable</td>
<td>intermediate, variable</td>
<td>intermediate, variable</td>
<td>tends to be thicker</td>
<td>thicker</td>
</tr>
<tr>
<td>Canine eruption</td>
<td>males with delayed canine eruption</td>
<td>indeterminate</td>
<td>lacks delayed canine eruption</td>
<td>lacks delayed canine eruption</td>
<td>lacks delayed canine eruption</td>
</tr>
<tr>
<td>Premolar to molar wear gradient</td>
<td>slow P3 wear</td>
<td>slow P3 wear</td>
<td>slow P3 wear</td>
<td>increase of apical P3 wear</td>
<td>increase of apical P3 wear</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Postcranial characters</th>
<th>Chimp/human LCA (INFERRED)</th>
<th>Ar. kadabba/Sa. tchadensis/ O. tugenensis</th>
<th>Ar. ramidus</th>
<th>Au. anamensis</th>
<th>Au. afarensis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Iliac isthmus</td>
<td>superoinferiorly long</td>
<td>indeterminate</td>
<td>short</td>
<td>indeterminate</td>
<td>short</td>
</tr>
<tr>
<td>Pubic symphysis outline</td>
<td>superoinferiorly long</td>
<td>indeterminate</td>
<td>short</td>
<td>indeterminate</td>
<td>short</td>
</tr>
<tr>
<td>Ilium/iliac isthmus orientation</td>
<td>coronal</td>
<td>indeterminate</td>
<td>sagittal</td>
<td>indeterminate</td>
<td>sagittal</td>
</tr>
<tr>
<td>Iliac breadth</td>
<td>moderately broad</td>
<td>indeterminate</td>
<td>slightly broadened</td>
<td>indeterminate</td>
<td>further broadened with expanded sciatic notch</td>
</tr>
<tr>
<td>Anterior inferior iliac spine</td>
<td>not developed</td>
<td>indeterminate</td>
<td>strong, formed by separate ossification center</td>
<td>indeterminate</td>
<td>strong, formed by separate ossification center</td>
</tr>
<tr>
<td>Pubic ramus</td>
<td>mediolaterally short</td>
<td>indeterminate</td>
<td>mediolaterally short</td>
<td>indeterminate</td>
<td>elongated</td>
</tr>
<tr>
<td>Ischiatic tuberosity</td>
<td>not angulated</td>
<td>indeterminate</td>
<td>not angulated (INFERRED)</td>
<td>indeterminate</td>
<td>angulated</td>
</tr>
<tr>
<td>Greater sciatic notch</td>
<td>not developed</td>
<td>indeterminate</td>
<td>weak</td>
<td>indeterminate</td>
<td>well-developed</td>
</tr>
<tr>
<td>Femoral hypotrochanter fossa</td>
<td>lacks true fossa</td>
<td>lacks true fossa</td>
<td>lacks true fossa</td>
<td>intermediate?</td>
<td>true fossa</td>
</tr>
<tr>
<td>Third trochanter and gluteal ridge</td>
<td>strong/rugose 3rd trochanter leading to laterally placed gluteal line</td>
<td>strong/rugose 3rd trochanter leading to laterally placed gluteal line</td>
<td>3rd trochanter weaker but same pattern</td>
<td>3rd trochanter weaker but same pattern</td>
<td>3rd trochanter localized, gluteal line angles medially</td>
</tr>
<tr>
<td>Femoral linea aspera</td>
<td>widely spaced med and lat lips</td>
<td>widely spaced med and lat lips</td>
<td>widely spaced med and lat lips</td>
<td>widely spaced med and lat lips</td>
<td>usually true linea aspera</td>
</tr>
<tr>
<td>Femoral neck cortical distribution</td>
<td>superior cortex relatively thick</td>
<td>superior cortex relatively thick</td>
<td>indeterminate</td>
<td>indeterminate</td>
<td>superior cortex relatively thin</td>
</tr>
<tr>
<td>Hallux</td>
<td>fully adductable, no dorsal doming</td>
<td>indeterminate</td>
<td>fully adductable, no dorsal doming</td>
<td>indeterminate</td>
<td>permanent adduction of hallux, dorsal doming</td>
</tr>
<tr>
<td>Second metatarsal</td>
<td>not robust</td>
<td>indeterminate</td>
<td>shaft and base robust</td>
<td>indeterminate</td>
<td>secondary gracilization</td>
</tr>
<tr>
<td>Metatarsal heads (rays 2–5)</td>
<td>limited dorsal doming</td>
<td>indeterminate</td>
<td>dorsally domed (M3 known)</td>
<td>indeterminate</td>
<td>dorsally domed</td>
</tr>
<tr>
<td>Proximal foot phalangeal cant</td>
<td>proximal orientation</td>
<td>indeterminate</td>
<td>upwardly canted</td>
<td>indeterminate</td>
<td>upwardly canted orientation</td>
</tr>
<tr>
<td>Trapezoid</td>
<td>mediolaterally narrow</td>
<td>indeterminate</td>
<td>mediolaterally narrow</td>
<td>indeterminate</td>
<td>broader</td>
</tr>
<tr>
<td>Capitate</td>
<td>head located palmarly</td>
<td>indeterminate</td>
<td>head located palmarly</td>
<td>head dorsaled and broader</td>
<td>head dorsaled and broader</td>
</tr>
<tr>
<td>Metacarpal heads</td>
<td>moderate dorsal construction</td>
<td>indeterminate</td>
<td>weak, but constriction still seen</td>
<td>indeterminate</td>
<td>constriction lacking</td>
</tr>
<tr>
<td>Metacarpal distal end</td>
<td>moderate/strong proximal collateral ligament facets</td>
<td>indeterminate</td>
<td>intermediate?</td>
<td>indeterminate</td>
<td>weak collateral ligament grooves</td>
</tr>
<tr>
<td>Skeletal size dimorphism</td>
<td>weak</td>
<td>indeterminate</td>
<td>weak</td>
<td>indeterminate</td>
<td>moderate</td>
</tr>
<tr>
<td>Megadontia relative to body size</td>
<td>weak</td>
<td>indeterminate</td>
<td>weak</td>
<td>expressed (INFERRED)</td>
<td>distinct</td>
</tr>
</tbody>
</table>

Key: **Primitive condition** | **Intermediate derived condition** | **Derived condition**
Ardipithecus ramidus

Comparatively few features of *Ar. ramidus* are derived relative to these earlier hominids, although many body parts of the latter are still unrepresented. There are no apparent features sufficiently unique to warrant the exclusion of *Ar. ramidus* as being ancestral to *Australopithecus* (74), and a greatly expanded set of shared derived characters now links *Ar. ramidus* with later members of the hominid clade. Table 1 identifies some of the most important. This pattern robustly falsifies earlier assessments that the Aramis fossils represent an ancestral chimpanzee (13, 75). These results are suggestive of a cohesive hominid evolutionary grade preceding *Australopithecus* (currently >6.0 to 4.2 Ma). By priority, the name *Ardipithecus* may encompass other named genera at this adaptive plateau (12, 15).

The question of whether *Ar. ramidus* is ancestral to later hominids is moot for some cladists because they consider ancestors inherently unrecognizable and therefore recognize only sister taxa (76). The fossils reported here make it even more obvious that *Ar. ramidus* is the clade's sister to *Australopithecines/Homo* because it shares primitive characters with earlier hominids and apes but at the same time exhibits many important derived characters that are shared exclusively only with later hominids (Table 1).

Species-level phylogenetics are more difficult to discern given the sparse geographic and temporal distribution of available fossils (Fig. 5). Primitive characters seen in *Ar. ramidus* persist most markedly in its apparent (but still poorly sampled) sister species *Au. anamensis* and, to a lesser degree, in *Au. afarensis*. The known dental and mandibular remains of *Au. anamensis* are temporally and morphologically intermediate between those of *Ar. ramidus* and *Au. afarensis*, with variation that overlaps in both directions. Its constellation of primitive and derived features of the mandible, CP3 complex, lower dm1 (lower first deciduous molar), and postcanine dentition lends support to the hypothesis of an evolutionary sequence of *Ar. ramidus* → *Au. anamensis* → *Au. afarensis* (7, 8, 77). Circumstantial evidence supporting this hypothesis is the temporal and geographic position of *Ar. ramidus* directly below the first known appearance of *Au. anamensis* within the Middle Awash succession. Here, these taxa are stratigraphically superimposed in the same succession, separated by ~80 vertical meters representing ~200,000 to 300,000 years (7). *Au. afarensis* appears later in the same sequence (3.4 Ma, at Maka (53)).

Therefore, at one end of a spectrum of phylogenetic possibilities, *Ar. ramidus* may have been directly ancestral to the more derived chronospecies pair *Au. anamensis* → *Au. afarensis* across the full (still unknown, presumably African) species range (7, 8, 77) (Fig. 5A). Although *Au. afarensis* is well represented in craniodental remains and postcrania, its apparent earlier chronspecies *Au. anamensis* is still woefully underrepresented in both, and because *Ar. ramidus* is so far known only from limited time horizons and locations, its last appearance, date, and potential relationship to these later taxa are still indeterminate. Given the dramatic differences in postcrania anatomies seen in later *Australopithecus* and hinted at in known *Au. anamensis*, it seems likely that a major adaptive shift marked the *Ardipithecus-to-Australopithecus* transition (whenever and wherever the transition might have occurred and whatever its population dynamics). This transition may not have occurred through
pan-specific phyletic evolution (Fig. 5A). Figure 5 presents two other phylogenetic hypotheses that are also, at present, impossible to falsify.

If diagnostic contemporary fossils of *A. anamensis* are found in rocks of >4.4 Ma, the hypothesis that the Afar population of *Ar. ramidus* is the phyletic ancestor of *A. anamensis* (Fig. 5A, B) would be falsified. In such an eventuality, Aramis *Ar. ramidus* would represent a persisting relic population of the mother species (Fig. 5C). Given the lack of relevant fossils, it is currently impossible to determine whether there was a geologically rapid phyletic transition between *Ar. ramidus* and *Australopithecus* in the Middle Awash or elsewhere. Nevertheless, the morphological and ecological transition between these two adaptive plateaus is now discernible.

**Ardipithecus and Australopithecus.** For Darwin and Huxley, the basic order in which human anatomies, physiologies, and behaviors were assembled through time was unknown—indeed unknowable—without an adequate fossil record. They were forced to employ extant ape proxies instead. The latter are now shown to be derived in ways unrelated to the evolution of hominids.

The Aramis fossils help clarify the origin of the hominid clade (27, 31), and reveal some paleobiological dimensions of the first hominid adaptive plateau (*Ardipithecus*). The primitive characters of *Ar. ramidus* simultaneously provide a new perspective on the evolutionary novelties of *Australopithecus*.

Even in the wake of the Aramis and Gona discoveries, the morphological envelopes, phylogenetic relationships, and evolutionary dynamics of early hominid species remain incompletely understood (Fig. 5). However, the paleobiology of *Ar. ramidus*—even when viewed through its geographically and temporally restricted Afar samples—now reveals that the basal hominid adaptive plateau comprised facultatively bipedal primates with small brains, reduced nonhoning canines, unspecialized postcanine dentitions, and arboreally competent limb skeletons. Their ecological niche(s) were probably more restricted—and their geographic distribution(s) possibly smaller and more disjunct—than those of later hominid species and genera.

The derived postcranial elements of *Australopithecus* provide a strong contrast to their more primitive homologs in *Ardipithecus* (78). Relative to the generalized anatomy of the latter, the highly evolved specializations of the foot, ankle, knee, pelvis, wrist, and hand of *Au. afarensis* (79–81) indicate that this species lineage had largely abandoned locomotion in the arboreal canopy (and its resources).

Given the strong selection predicted to have been associated with the emergence of new ranging and feeding patterns in *Australopithecus*, the transition from *Ardipithecus* to *Australopithecus* could have been rapid, and anatomically particularly so in hindlimb structure. The forelimb (especially the hand) was probably under less intensive selection. It is possible that modification of general cis-regulatory pathways may have generated the striking and novel morphology of the hindlimb, especially the foot, because the autopod seems to be the most morphologically compliant to such mechanisms of modification. The dentognathic shifts could have been more gradational, whatever the mode of phylogenesis.

**Homo and Australopithecus** are the only primates with nongrasping feet, and this particular transformation was probably far-reaching, with consequences for key behavioral constancies in higher primates related to arboreal feeding and nesting. Without stabilizing selection for *Ardipithecus*-like arboreal capacities involving slow and careful climbing, the foot, pelvis, and thigh would have experienced directional selection to optimize bipedal locomotion during prolonged walking (also in more limited running bouts). With expanded ranging and social adaptations associated with terrestrial feeding in increasingly open environments, the transition could have been profound, but probably rapid, and therefore difficult to probe paleontologically.

One possible dynamic of an *Ardipithecus*-to-*Australopithecus* transition would have involved microevolution within a dene or regional group of demes. Being more ecologically flexible, the derived, potentially speciated populations would have undergone rapid range expansion, perhaps even encountering relict *Ardipithecus* populations. Unfortunately, the phylogographic details remain obscure given the poor spatial and temporal resolution of the current fossil record (Fig. 5). This provides a strong incentive for pursuing that record by actively increasing sampling of sediments from different African basins with dates between ~5 and~3.5 Ma.

Currently, *Australopithecus* appears relatively abruptly in the fossil record at about 4.2 Ma. Relative to *Ar. ramidus*, available early *Australopithecus* is now revealed to have been highly derived: a committed biped with slightly enlarged brain, a nongrasping arched foot, further derived canines, substantially specialized postcanine teeth with thick molar enamel, and expanded ecological tolerances and geographic ranges. It is widely recognized that this is the adaptive plateau antecedent to *Homo*, which is now definable as the third such major adaptive shift in human evolution. Commitment to the terrestrial ranging behaviors of *Australopithecus* well before the Pleistocene appear to have catalyzed the emergence of what must have been even more highly specialized social and ecological behaviors remarkably elaborated in descendant *Homo*—the ultimate global primate generalist.

**Conclusions.** Besides hominids, the only apes to escape post-Miocene extinction persist today as relic species, their modern distributions centered in forested refugia. The markedly primitive *Ar. ramidus* indicates that no modern ape is a realistic proxy for characterizing early hominid evolution—whether social or locomotor—as appreciated by Huxley. Rather, *Ar. ramidus* reveals that the last common ancestor that we share with chimpanzees (CLCA) was probably a palindrome quadrupedal arboreal climber/clamberer that lacked specializations for suspension, vertical climbing, or knuckle-walking (24–27). It probably retained a generalized incisal/postcanine dentition associated with an omnivorous/frugivorous diet less specialized than that of extant great apes (22, 23). The CLCA probably also combined moderate canine dimorphism with minimal skull and body size dimorphism (22, 23), most likely associated with relatively weak male-male agonism in a male philopatric social system (22, 23, 31).

*Ardipithecus* reveals the first hominid adaptive plateau after the CLCA. It combined facultative terrestrial bipedality (25, 26) in a woodland habitat (28–30) with retained arboreal capabilities inherited from the CLCA (24–27). This knowledge of *Ar. ramidus* provides us, for the first time, with the paleobiological substrate for the emergence of the subsequent *Australopithecus* and *Homo* adaptive phases of human evolution. Perhaps the most critical single implication of *Ar. ramidus* is its reaffirmation of Darwin’s appreciation: Humans did not evolve from chimpanzees but rather through a series of progenitors starting from a distant common ancestor that once occupied the ancient forests of the African Miocene.
Ardipithecus ramidus

56. T. H. Huxley, Westminster Rev. 73, 541 (1860).
69. For example, it has been noted that these methods fail to accurately resolve relationships of modern hominid species without sufficient intermediate forms from a fossil record (72).
70. Enamel thickness of A. ramidus molars ranges largely from what would traditionally be termed “intermediate thin” to “intermediate thick” categories. Lacking the derived thickness pattern of Pan, it forms a suitable ancestral condition for later Australopithecus. The ubiquitous single-rooted lower fourth premolar (P4) in known A. ramidus and Gona A. ramidus is notable, but this is also a known variation of Au. anamensis and A. afarensis. Judging from the clear dominance of double-rooted lower P4s in Au. afarensis (land thereafter an increasing robusticity of the roots themselves in Australopithecus), either there was selection for larger, more complex premolar root systems or such morphologies emerged as pleiotropy of postcanine enhancement.

Without such selection, A. ramidus as a species probably contained regional populations that varied in premolar root number (72).
74. We use generic to express both phyletic proximity and circumscribed adaptive systems, with ecobehavioral and morphological conditions being integral parts of the latter. This use employs the broadly defined genus Australopithecus, without recognizing the now commonly used Paranthropus (22). This is because both “robust” and “nonrobust” Australopithecus species are characterized by a commonly derived heavy masticatory apparatus (albeit to differing degrees), and also because we cannot—even to this day—be certain that the “robust” species are monophyletic.
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SOM Test
Tables S1 and S2

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SOM Test
Tables S1 and S2

References
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Macr...
Ardipithecus ramidus

consistent in their taphonomy and taxonomy across the ~7 km distance from the easternmost (SAG-VP-7) to westernmost (KUS-VP-2) Ar. ramidus localities (3).

Contemporaneous localities between the two tuffs farther south of the modern Sagantole drainage (SAG-VP-1 and -3, at the southeastern paleotransect pole) are relatively impoverished. They lack this diverse and abundant mammal assemblage and contain no tragelaphines, no monkeys, no fossil wood or seeds, no birds, no micromammals, and no Ardipithecus (table S1). Complementary structural, taphonomic, and isotopic data from localities on this pole of the paleotransect suggest a more open landscape that supported more crocodilians, turtles, and hippopotamids, presumably associated with water-marginal settings more axial in the drainage basin (2, 3).

Relative and absolute abundance measures for the large mammals in our collections from the Ardipithecus-bearing Lower Aramis Member localities were assessed by the number of identified specimens (NISP) \((n = 1930)\) and the minimum number of individuals (MNI) based on teeth \((n = 330)\). Proboscideans, giraffids, and hippopotamids are rare (Fig. 1, B and C). The rhinos Ceratotherium efficax and Diceros are represented by few specimens (NISP 6 and 1, MNI 4 and 1, respectively). Unlike most other waterside Plio-Pleistocene assemblages, rhinos are more abundant than hippos at Aramis. The dental mesowear pattern and occlusal morphology of Pliocene Ceratotherium efficax suggest that it was predominantly a grazer but ate less abrasive forage with respect to its highly specialized Pleistocene and extant descendant Ceratotherium simum. The morphological and functional properties of the recovered Diceros sp. molars are similar to those of the extant browsing Diceros bicornis.

Equids are rare. One, Eurygnathohippus sp. nov., is distinguished by its distal limb, which is adapted to open-country running. Its elongate-narrow snout with parabolic symphysis suggests adaptation to selective feeding. The teeth of this equid bear a low-blunt cusp morphology reflecting habitual grazing. Large carnivores and aardvarks are rare, in keeping with their trophic level (as in most other eastern African Plio-Pleistocene assemblages).

Ardipithecus ramidus is represented at Aramis and environs by >110 cataloged specimens representing a minimum number of 36 individuals [14 by upper second molar (M2) count] in the Lower Aramis Member. These numbers are rel-

Fig. 1. Aramis large mammals. (A) Size range illustrated by astragali. The Lower Aramis Member contains a wide range of mammalian taxa, illustrated by this image. Top left, Rhinocerotidae; middle left, Ardipithecus ramidus (ARA-VP-6-500); lower left, small bovid. Included are other artiodactyls, carnivores, and rodents. (B) Relative abundance of larger mammal taxa at Aramis based on dental MNI. (C) Dental NISP based on dental individuals whose tooth crowns are more than half complete. The NISP value reflects all collected specimens identified to the taxon and excludes bulk specimens (tooth crowns less than half complete). Associated dental specimens are counted as one. The MNI values use permanent molars segregated into upper and lower first, second, and third molars, respectively. Numbers for each taxon vary between NISP and MNI, but the relative proportions hold similar. Tragelaphine bovids and cercopithecid monkeys dominate, accounting for more than half of the assemblage, however counted.
atively low compared with many of the other macrovertebrate fossil species we collected. This rarity is consistent with that observed for hominins in other well-known vertebrate assemblages (7). *Kuseracolobus aramisi* and *Pliopapio alemui* are ubiquitous in the assemblage, accounting for 30% of both the larger mammal NISP and MNI. The colobine is numerically dominant within nearly all of the localities, and overall by a ratio of 1.4 to *Pliopapio* (colobinae NISP:cercopithecinae NISP). It is slightly larger (12 kg female, 18 kg male) than this papionin (8.5 kg, 12 kg) based on dental regressions (14). Extant colobines exhibit strong preferences for arboreal habitats; extinct African taxa range from fully arboreal to highly terrestrial (15).

Bovids and primates, particularly tragelaphines and cercopithecids, dominate the larger mammal assemblage based on taxonomically diagnostic craniodental elements (Fig. 1). Together, these taxa account for more than half of the larger mammal specimens, whether counted by NISP or dental MNI. Both cercopithecid and bovid assemblages appear to be attritional and were ravaged heavily by carnivores after death (3).

Bovids help illuminate the local Aramis environment of the *Ardipithecus*-bearing localities. One useful index is the relative abundance of grazing versus browsing taxa, which can indicate the presence of open or closed conditions, respectively (16–19). The most ecologically sensitive of these taxa include grazing, open-habitat tribes such as Alcelaphini and Hippotragini versus the primarily browsing Tragelaphini or the riparian-associated Reduncini. Reduncine bovids commonly dominate in African Plio-Pleistocene faunal assemblages (Fig. 2), in keeping with fluvatile, swampy, or lake marginal depositional conditions.

Whether counted by NISP or dental MNI, *Tragelaphus* (whose modern congeners are associated with wooded habitats) (20) is the numerically dominant Aramis bovid, comprising 85% (NISP) of the bovid assemblage (Fig. 1), followed by *Aepyceros* (whose modern form favors grassy woodland to wooded grassland environments). In contrast, alcelaphine and reduncine bovids that are plentiful at other Plio-Pleistocene sites are rare at Aramis, accounting for a mere 1% (NISP) and 4% (MNI) of all bovids. Aramis is unlike any other known African fossil assemblages in that *Tragelaphus* dominates the ungulates. (20–23) (Fig. 2).

Alcelaphines and reduncines were found at slightly higher frequencies at locality SAG-VP-7 at the eastern end of the *Ardipithecus* distribution (although tragelaphines and aepycerotines still dominate there). This subtle difference between SAG-VP-7 and other more westerly hominid-bearing localities is also indicated by cercopithecid abundance. SAG-VP-7 has relatively fewer cercopithecids and more alcelaphine and reduncine bovids (Fig. 2), potentially signaling that this easternmost *Ardipithecus* locality was a transition zone between two biotopes.

**Functional morphology.** Taxon-based approaches to the inference of paleohabits are usually restricted to using identifiable craniodental remains and assume that habitat preference persists through evolutionary time. Another approach is to evaluate the anatomy of fossils with respect to its implications for functional adaptations. These methods presume that mammals exhibit skeletal and dental adaptations for locomotion and feeding that correlate with their preferred environment (24). Samples of extant taxa are used to quantify the relations between skeletal/dental traits and environmental variables, with the results then applied to fossil forms (25).

Here, we evaluate the “ecomorphology” of the most common large mammals at Aramis, the bovids and cercopithecid monkeys. For the Aramis bovids, we evaluated the astragali and calvaria for evidence of adaptations for locomotion and feeding. Among Lower Aramis Member localities, SAG-VP-7 has relatively lower frequencies of cercopithecids and higher abundances of alcelaphines and reduncines, potentially indicative of ecotonal conditions at this easternmost locality of the *Ardipithecus* distribution.

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**Fig. 2.** Aramis taxonomic abundance. (A) Comparison between the relative abundance (dental) of bovid taxa at Aramis and other Pli-Pleistocene sites (21, 23, 45). The bovid fauna at Aramis is markedly different due to the dominance of tragelaphines. All frequencies are based on NISP, except for Hadar, which is based on MNI. (B) Within-site comparison of the relative abundances of bovids and cercopithecids. Among Lower Aramis Member localities, SAG-VP-7 has relatively lower abundances of cercopithecids and higher abundances of alcelaphines and reduncines, potentially indicative of ecotonal conditions at this easternmost locality of the *Ardipithecus* distribution.
phalanges (25, 26) because other elements that can be revealing (metapodials and femora) were not preserved in sufficient numbers. We used a four-habitat grouping scheme (26) (SOM text S1). Of the 11 available intact bovid astragali with statistically significant habitat predictions (accuracy >95%), 10 are classified as “forest” and one as “heavy cover.” This is a clear signal, since these methods typically produce more varied habitat predictions when applied to fossil samples (27, 28). To lessen possible biases introduced by confining the analysis to specimens sufficiently complete for measurement, we also examined nonmetric traits of the phalanges and classified the entire astragali/phalangeal sample by morphotype (SOM text S1, tables S2 and S3, and fig. S1). These results independently support the conclusion from metric prediction that these animals inhabited a “forest” (in the analytical, not floral, sense). As with bovids, cercopithecoid postcranial features are routinely posited to indicate locomotion (29–31). However, systematic studies of large samples of extant taxa are generally lacking. We therefore consider most proposed correlations between cercopithecoid anatomy and locomotor mode to be of unknown reliability, pending additional study. Even so, the elbow is clearly a key joint for distinguishing between arboreal and terrestrial primate locomotion. Of 10 available cercopithecoid distal humeri, 9 are clearly terrestrial primate locomotion. Of 10 available key joint for distinguishing between arboreal and terrestrial indicators, in the overwhelming majority of the Aramis cercopithecoid postcranial sample (SOM text S2).

**Dental wear.** The morphology, occlusal wear, and stable isotope composition of dental remains also reveal the diet—and, indirectly, habitat preferences—of some Aramis mammals. Differences in mesowear can distinguish among extant browsers, grazers, and mixed feeders (32). The Aramis neotragines, *Giraffa*, and *Tragelaphus* cluster with extant browsers (Fig. 3 and table S3), whereas *Aepyceros* falls between extant mixed feeders and nonextreme grazers. Rare Aramis alcelaphines cluster with nonextreme grazers, whereas the rare bovine and equid fossils are closest to extant coarser grass grazers. The high cusps and colobine-like morphology of *Pliopapio alemu* (all molars with high relief and little basal flare) suggest that the two Aramis monkey taxa had similar diets. We sampled a mixed set of colobine and cercopithecine molars for a blind test of microwear. No significant differences were found between the two taxa. Microwear on the Aramis monkey molars is consistent with both frugivory and folivory but not hard object feeding. A diet of soft (but perhaps tough) foods would be typical of colobines, and the same may have been the case for the papionin (33).

**Enamel isotopes.** The carbon isotopic composition of a mammal’s tooth enamel reflects the relative contributions of grass, trees, and shrubs to its diets. Oxygen isotopes can reveal the degree that a species lives in, or consumes, water from different sources (34). We sampled tooth enamel bioapatite from 177 specimens encompassing a wide range of mammalian taxa within the Ar. ramidus–bearing unit (Fig. 4, SOM text S3, and table S4). These were analyzed blind to taxon. Carbon isotopic ratios for grazers are high, whereas those for mixed feeders, browsers, and forest floor feeders decrease systematically (SOM text S4). Oxygen isotope values are low for water-dependent species such as carnivores and hippos in wet riparian habitats and higher for water-independent browsers and open dry-habitat species.

In the Ardipithecus-bearing Lower Aramis Member assemblage, the aquatic carnivore *Enhydrion* (an otter) has the lowest δ18O of all species. Conversely, the ursid *Agrotherium* (a bear) has the highest carnivore δ18O, consistent with anatomical evidence for an omnivorous diet (35). Among herbivores, giraffids (*Giraffa* and *Sivatherium*) have the highest δ18O and lowest δ13C values, whereas grazing equids (*Eurygnathohippus*), alcelaphines, bovines, hippos, and rhinocerotids show the converse. Among primates, *Kiuscaracolobus* has higher δ18O and lower δ13C than *Pliopapi*, which resembles the difference between modern folivorous Colobini and more omnivorous Papionini (36, 37).

The carbon isotopic composition of four of five *Ardipithecus ramidus* individuals is close to

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**Fig. 3.** Mesowear analysis results for the second molar paracone apex of fossil ungulates. Cusp shape was scored qualitatively as sharp, rounded, or blunt. The relative difference in height between tooth cusp apices and intercusp valleys (occlusal relief) was qualitatively scored as either high or low (large or small distance between cusp apex and intercusp valley, respectively). Histograms show the results on the mesowear variables measured (i.e., the percentages of sharp versus rounded versus blunt cusp shapes and the percentages of high versus low occlusal relief).
that of *Pliopapio*, reflecting diets that included small amounts of $^{13}$C-enriched plants and/or animals that fed on such plants. *Ardipithecus* consumed slightly more of these resources than modern savanna woodland chimpanzees (38) but substantially less than later Plio-Pleistocene hominids (but substantially less than later Plio-Pleistocene). The fifth individual has a $\delta^{13}$C value of $-8.5$ per mil ($\%$), which is closer to, though still lower than, the means for *Australopithecus afarensis*, *Agu: robustus*, and early *Homo* (39, 40). Slightly lower $\delta^{18}$O compared with *Pliopapio* and *Kaseracolobus* suggests that *Ardipithecus* obtained more water from fruits, bulbs, tubers, animals, and/or surface sources.

The isotopic composition of the Aramis mammals between the two tuffs (Fig. 4 and table S4) conforms broadly to patterns expected for their modern congeners across the forest-woodland-savanna spectrum (37, 38) in the East African rift and is consistent with other early Pliocene assemblages (39, 40). Relatively low primate, giraffid, tragelaphine, and Deinotherium $\delta^{13}$C values indicate that small patches of closed canopy forests were present, although woodlands to wooded grasslands probably dominated. Low $\delta^{13}$C values for hyaenids suggest that browsing prey contributed more to their diet compared to their modern congeners in grazer-dominated open savanna environments (37). This is congruent with the numerical dominance of browsing tragelaphines and accords with other evidence for the dominance of woodlands in the 4.4 Ma local environment occupied by *Ardipithecus* (2, 3). A small number of rare grazing species—mainly equids, aelaphines, hippopotagines, and some impala, rhino, and bovines—have high $\delta^{13}$C and $\delta^{18}$O, indicating that they fed on water-stressed C$_4$ plants in drier, open environments (41). These taxa comprise a small portion of the overall assemblage.

The large range of $\delta^{18}$O, particularly the large difference (9.6‰) between water-independent (evaporation-sensitive) Giraffidae (Giraffa and *Sivatherium*) and water-dependent (evaporation-insensitive) Hippopotamidae, suggests a mean annual evaporative water deficit of $\sim$1500 mm (41). Therefore, Aramis was a generally dry woodland setting far from riparian environments. Enamel isotopes of these taxa from nearby pene-contemporary sites at Gona (42) (SOM text S3 and fig. S2) have a $\delta^{18}$O difference of only 4.6‰, reflecting an annual water deficit of $\sim$500 mm (41). Consistently lower oxygen isotope ratios support geological evidence that Gona was close to permanent water (43), but higher carbon isotope ratios for all Gona browsers are inconsistent with greater water availability (SOM text S3).

**Other ecological approaches.** An approach to deducing ancient environment is to first assign each mammal taxon in a fossil assemblage to an ecological category (usually based on diet and locomotion) and then compare the proportions of these categories in the fossil sample to a range of similarly categorized extant communities (44, 45). This approach uses only the presence or absence of taxa, so it is subject to taxonomic and taphonomic biases involving small samples and mixing. Furthermore, the results are often of low resolution because biased local fossil assemblages are compared to variably recorded modern communities that pool multiple habitats (21). *Ardipithecus ramidus* was previously interpreted as inhabiting a woodland or dry forest based on a preliminary Aramis faunal list (about 10% of the sample now available) (46). Although the full faunal list produces results consistent with this finding, these results are not highly robust because the data broadly overlap among distinct environments (e.g., open, riparian, medium-density, and closed woodland) (47).

Other measures of abundance also provide information on the trophic structure of mammalian community represented by the *Ardipithecus*-bearing Lower Aramis Member. Although there are many grazing and carnivorous species (Fig. 5), these taxa are rare (48), so a strict presence/absence evaluation distorts the ecological signal. When measures of relative abundance (NISP and MNI) are included, along with direct information on trophic levels from the stable isotope and mesowear results, a different picture emerges.

These combined data show that the large mammal biomass at Aramis was dominated by browsers and frugivores (including frugivorous animals that consume leaves as a substantial part of their diet). It is unlikely that a plethora of mammals dependent on browse and fruit would have been able to subsist in an environment without abundant trees, the presence of which is witnessed by fossil pollen as well as abundant seeds, wood, phytoliths, and rhizoliths (2).

**Hominid habitat.** Establishing habitat (as opposed to general environment) is crucial for illuminating the paleobiology of any fossil species, including hominids. On the basis of mixed fossil faunas, it has been previously proposed that “early hominids were apparently not restricted to a narrow range of habitats.” (68, p. 571). However, this raises the question of whether the hominids actually occupied a wide range of habitats or whether taphonomic processes and sampling biases have mixed hominid remains with those of species from biotopes that hominids rarely, if ever, frequented. Many fossil assemblages simply do not preserve the necessary temporal and spatial resolution needed to determine whether hominids preferred the riverine forest, lake margin, and...
Ardipithecus ramidus

Fig. 5. Tropic ecovariable distributions by faunal list, dental NISP, and dental MNI. Comparisons of the Aramis trophic structure based on the faunal list versus specimen-level, dental relative abundance data as measured by NISP and MNI. Grazing and carnivorous species are abundant in the faunal list-based trophic structure, whereas browsers and frugivores dominate when NISP and MNI data are incorporated. B, browser; G, grazer; MF, mixed feeder; FG, fresh grass grazer; Fg, Frugivore (includes fruit and leaves); C, carnivorous; I, insectivorous; O, omnivorous; RT, root and tuber.

bushland, savanna, and/or woodland habitats demonstrably available within a few kilometers of most depositional loci within rift valley settings.

For example, Ardipithecus ramidus has also been found at Gona, about 70 km to the north of Aramis, in a valley margin environment where lake deposits interfingered with small fluvial channels or lapped onto basaltic cones and flows (43). At Gona, the dominance of C3 plants indicated by paleosol isotopes contrasts with the C4 plant signal in many associated ungulate grazers (indicated by enamel isotopic data). Levin et al. thus concluded that Ardipithecus was “...may have inhabited a variety of landscapes and was not as ecologically restricted as previous studies suggested” ([42], p. 232). The Gona paleontological and isotopic data show only that a range of habitats was present, and the attribution of Ardipithecus to any particular set of the available biotopes is problematical in this mixed assemblage (49). Fish, birds, browsers, horses, and hominids are all frequently found in a single mixed fossil assemblage in a fluvialite or near-shore deposit. This does not mean that the fish were arboreal or that horses were aquatic. Neither do such data mean that the hominids exploited all potentially available habitats.

The Lower Aramis Member deposits provide fossil samples that evidence a range of environments in the region at 4.4 Ma (2, 3). However, the consistent association of Ar. ramidus with a particular fauna and flora in deposits between SAG-VP-7 and KUS-VP-2 suggests its persistent occupation of a woodland with patches of forest across the paleolandscape (2, 3). Ardipithecus has not been found in the apparently more open settings to the southeast. There is no evidence of any taphonomic bias related to Ardipithecus that might produce this pattern (3) and no evidence of any other spatial or stratigraphic clustering within the 4.4 Ma Lower Aramis Member interval.

Based on a range of independent methods for inferring habitat-based large samples of consilient spatial, geological, and biological evidence generated from diverse sources, we therefore conclude that at Aramis, Ar. ramidus resided and usually died in a wooded biotope that included closed through grassy woodlands and patches of true forest [sensu (6)]. There is no evidence to associate this hominin with more open wooded grasslands or grassland savanna.

Isotopic data indicate that the Ar. ramidus diet was predominantly forest- to woodland-based. This interpretation is consistent with evidence of the dental and skeletal biology of this primate (1). The ecologic context of 4.4 Ma Aramis hominins, combined with their absence or extreme rarity at Late Miocene and Early Pliocene sites, suggest that the anatomy and behavior of the earliest hominins did not evolve in response to open savanna or mosaic settings. Rather, this clade appears to have originated within more closed habitats favored by these peculiar primates until the origin of Australopithecus, and perhaps even beyond (50).

References and Notes
4. This assemblage is the one co-occurring with Ardipithecus and excludes the small contemporary samples of fossils from the more easterly localities of SAG-VP-1 and -3; see (2, 3) and table S1 for details.
5. Included in the larger mammal subassemblage analyzed here are the following taxa: Artiodactyla, Perissodactyla, Proboscidea, Primates, Carnivora (except Viverridae), and Tubulidentata.
13. Trophic ecovariable distributions by faunal list, dental NISP, and dental MNI. Comparisons of the Aramis trophic structure based on the faunal list versus specimen-level, dental relative abundance data as measured by NISP and MNI. Grazing and carnivorous species are abundant in the faunal list-based trophic structure, whereas browsers and frugivores dominate when NISP and MNI data are incorporated. B, browser; G, grazer; MF, mixed feeder; FG, fresh grass grazer; Fg, Frugivore (includes fruit and leaves); C, carnivorous; I, insectivorous; O, omnivorous; RT, root and tuber.
20. The Aramis tragelaphus cf. moruota has a body size close to that of the living nyala (T. angasi) and is likely a direct descendant of the T. moruota recorded from the Mio-Pliocene of Asa Koma and Kuserale.
27. Y. Haile-Selassie et al., Geobios 37, 536 (2004).
33. Crushing and shearing areas of 10 cercopithecoid molars were all discrete, excepting the one case in which a tooth was laterally damaged after crushing but before shearing (33). Crushing and shearing areas of 10 cercopithecoid molars...software (v. 2.2, 1996). Microwear features included relatively few pits, with narrow pits and scratches. The microwear on the molars of the Aramis
34. Isotopic data indicate that the Ar. ramidus diet was predominantly forest- to woodland-based. This interpretation is consistent with evidence of the dental and skeletal biology of this primate (1). The ecologic context of 4.4 Ma Aramis hominins, combined with their absence or extreme rarity at Late Miocene and Early Pliocene sites, suggest that the anatomy and behavior of the earliest hominins did not evolve in response to open savanna or mosaic settings. Rather, this clade appears to have originated within more closed habitats favored by these peculiar primates until the origin of Australopithecus, and perhaps even beyond (50).
35. References and Notes
relief and has a low level of basal flare in comparison with other papionins.

47. Our analysis also raised numerous questions about the assumptions and procedures underlying such efforts.
48. For example, there are 12 “grazing” taxa compared to only 5 “browsing” taxa, but the former are represented by only 152 specimens, whereas the latter are represented by 758 (NISP).
49. It is evident that in most rift-valley depositional settings, a variety of environments would almost always have been available to hominids. Of primary interest is determining whether any one of these environments was the preferred habitat of these primates. Mixed assemblages cannot usually do this.
51. Supported by NSF (grants SBR-82-10897, 93-18698, 95-12534, 96-32389, 99-10344, and 03-21893 HOMINID-RHOI; and grant SBR 98-71480 for mass spectrometry instrumentation at the Environmental Isotope Paleobiogeochemistry Laboratory and the Japan Society for the Promotion of Science (G.S. and H.S.). We thank L. Bach, H. Gilbert, and K. Brudvik for illustrations; the Ministry of Tourism and Culture, the Authority for Research and Conservation of the Cultural Heritage, and the National Museum of Ethiopia for permissions and facilitation; and the Afar Regional Government, the Afar people of the Middle Awash, and many other field workers for contributing directly to the data.

Supporting Online Material
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SOM Text
Figs. S1 and S2
Tables S1 to S5
References
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Paleobiological Implications of the Ardipthecus ramidus Dentition

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The Middle Awash Ardipthecus ramidus sample comprises over 145 teeth, including associated maxillary and mandibular sets. These help reveal the earliest stages of human evolution. Ar. ramidus lacks the postcanine megadontia of Australopithecus. Its molars have thinner enamel and are functionally less durable than those of Australopithecus but lack the derived Pan pattern of thin occlusal enamel associated with ripe-fruit frugivory. The Ar. ramidus dental morphology and wear pattern are consistent with a partially terrestrial, omnivorous/frugivorous niche. Analyses show that the ARA-VP-6/500 skeleton is female and that Ar. ramidus was nearly monomorphic in canine size and shape. The canine/lower third premolar complex indicates a reduction of canine size and honing capacity early in hominin evolution, possibly driven by selection targeted on the male upper canine.

Fossilized teeth typically represent the most abundant and best preserved remains of hominids and other primates. They provide crucial evidence on variation, phylogenetic relationships, development, and dietary adaptations. Furthermore, because canines function as weapons in interindividual aggression in most anthropoid species, they additionally inform aspects of social structure and behavior.

We have now recovered and analyzed a sample of 145 non-antimeric tooth crowns comprising 62 cataloged dentition-bearing specimens of Ardipthecus ramidus from the Lower Aramis Member of the Sagantole Formation, about five times more than previously reported (1, 2) (Fig. 1 and table S1). All permanent tooth positions are represented, with a minimum of 14 individuals for both the upper canine and upper second molar (M2) positions. Excluding antimeres, 101 teeth have measurable crown diameters. In addition, seven Ar. ramidus specimens with teeth have been described from Gona (3). These are broadly comparable to their Aramis counterparts in size, proportions, and morphology but slightly extend the smaller end of the species range in some mandibular crown diameters.

The major morphological characteristics of the Ar. ramidus dentition have been outlined in previous studies of Aramis and Gona fossils (1, 3, 4). Comparisons of Ar. ramidus with Late Miocene hominids (Ar. kadabba, Orrorin tugenensis, and Sahelanthropus tchadensis) have identified slight but distinct differences, particularly in the canine (4–6). Other subtle features of incisors and postcanine teeth have been noted as phylogenetic or taxonomic distinctions (5–10). However, the most recent and comprehensive evaluation of the available Late Miocene materials concluded that these differences are minor compared with extant ape (and later hominid) genus-level variation and that both Ar. ramidus and Ar. kadabba dentitions exhibit phenetic similarities with early Australopithecus (4).

The expanded Ar. ramidus sample of the present study allows a more definitive phylegetic placement of Ar. ramidus relative to the more primitive Ar. kadabba and the more derived Au. anamensis and Au. afarensis (11). Here, we focus on the paleobiological aspects of the Ar. ramidus dentition, including variation, size, and scaling, probable dietary niche, and canine/lower third premolar (C/P3) complex evolution and its behavioral implications. We also address the alleged phylegetic importance (7) of enamel thickness in Ar. ramidus (1). This is now made possible by the more comprehensive dental collection that includes key associated dental sets.

**Crown size, proportions, and variation.** The Ar. ramidus dentition is approximately chimpanzee-sized (Fig. S1 and tables S2 to S4). Mean canine size is comparable to that of female Pan troglodytes, although the incisors are smaller. Upper and lower first molars (M1s) are P. troglodytes–sized but tend to be buccolingually broader (figs. S1 to S3). The second and third molars (M2s and M3s) are both absolutely and relatively larger (figs. S1 and S4 to S6). Postcanine size and proportions of Ar. ramidus are similar to those of Ar. kadabba and other ~6.0-million-year-old forms (O. tugenensis and S. tchadensis (4–10), as well as to many Miocene hominoids (although Miocene ape lower molars tend to be buccolingually narrower) (fig. S3).

Variation within the Aramis dental sample is low. In modern anthropoids, the coefficient of variation (CV) is lowest in M1 and M2, with single-sex and mixed-sex values usually ranging from about 3.5 to 6.5 (12–14). At Aramis, Ar. ramidus upper and lower M1s and M2s are less variable (CVs ranging from 2.5 to 5.6) than those of Australopithecus afarensis and Au. anamensis (table S2). However, these Australopithecus samples represent multiple sites and span a much greater time than the Aramis fossils (11). The low variation seen in Aramis Ar. ramidus probably reflects spatially and temporally restricted sampling and low postcanine sexual dimorphism as in Pan (15) (table S5).

The Aramis postcanine dentition is also morphologically more homogenous than known Australopithecus species samples. For example, the six relatively well-preserved M1s (Fig. 1) differ little in features otherwise known to vary widely within hominid and modern hominoid species (16, 17), including Carabelli’s expression, occlusal crest development, and hypocone lingual bulge. This suggests that the Aramis Ar. ramidus collection samples regional demes or local populations with persistent idiosyncratic tendencies. The ubiquitous occurrence of single rooted lower fourth premolars (P4) (now seen in eight non-antimeric Ar. P4s) suggests increased frequency of otherwise rare variants from genetic drift, absent substantial selection for larger and/or more complicated root systems (18). Because this anatomy is shared with Gona Ar. ramidus (3), it appears characteristic of this regional population.

**Morphology and evolution of the C/P3 complex.** The C/P3 complex of anthropoids has behavioral and evolutionary importance because canine size and function are directly linked to male reproductive success (19). Therefore, clarifying the tempo and mode of the evolution of the C/P3 complex, from hominid emergence through its early evolution, is important.

Not counting antimeres, 23 upper and lower canines from 21 Ar. ramidus individuals are now known from Aramis. Three more have been described from Gona (3), and seven from the ~6.0-million-year-old Ar. kadabba, O. tugenensis, and S. tchadensis (4–10). There are no examples of a distinctly large male morphotype in any of these collections (Fig. 1 and figs. S7 and S8), suggesting that canine sexual dimorphism was minimal in Mio-Pliocene hominids. In basal crown dimensions, Ar. ramidus canine/postcanine size ratios overlap extensively with those of modern and Miocene female apes (fig. S9). Absolute and relative canine heights are also comparable to those of modern female apes, although canine height appears exaggerated in P. troglodytes [Fig. 1; figs. S8, S10, and S11; and supporting online material (SOM) text S1].

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Canine shape of *Ar. ramidus* is either comparable to female apes or more derived toward *Australopithecus* (11) (Fig. 1 and figs. S12 and S13). The upper canine (UC) is clearly derived in *Ar. ramidus*, because it has a diamond-shaped lateral crown profile with elevated and/or flaring crown shoulders (*n* = 5 from Aramis and *n* = 1 from Gona) [this study and (3, 4, 6)]. However, the lower canine (LC) retained much more of the morphology of the female ape condition (4, 5) (Fig. 1, figs. S11 to S13, and SOM text S1). A hominid-like incisiform LC morphology (high mesial shoulder, developed distal crest terminating at a distinct distal tubercle) is seen in some female apes (e.g., *Ouranopithecus* and *P. paniscus*), whereas the LCs of *Ar. kadabba* and *Ar. ramidus* tend to be conservative, exhibiting a strong distolingual ridge and faint distal crest, typical of the interlocking ape C/P3 complex (4) (Fig. 1 and SOM text S1).

The *Ar. ramidus* P3 is represented by seven observable crowns, ranging from obliquely elongate to transversely broad (1) (fig. S14). The *Ar. ramidus* P3 is relatively smaller than that of *Pan* and typically not as asymmetric or elongate in occlusal view (figs. S15 and S16). In these respects, the *Ar. ramidus* P3 is comparable to those of *Au. anamensis* and *Au. afarensis*. However, *Ar. ramidus* is more primitive than *Australopithecus* in retaining a proportionately higher P3 crown (fig. S16). It appears that there was a decrease of P3 size from the ancestral ape to *Ar. ramidus* conditions, but this reduction was greater in basal crown dimensions than in crown height (SOM text S1).

In *Ar. ramidus*, the combined effect of (i) reduced canine size and projection and (ii) reduced size and mesiobuccal extension of the P3 results in the absence of upper canine honing (defined as distolingual wear of the UC against the mesiobuccal P3 face, cutting into the lingual UC crown face and resulting in a sharpened distolabial enamel edge). Instead, apical wear in *Ar. ramidus* commences early and thereafter expands as wear progresses. None of the known UCs or P3s exhibits evidence of honing (fig. S14). However, both upper and lower canines project beyond the postcanine occlusal plane before heavy wear, resulting in steep and beveled wear slopes, as also seen in examples of *Au. afarensis* and *Au. anamensis* (1, 4, 20).

Two *Ar. ramidus* specimens provide associated maxillary and mandibular dentitions with minimal canine wear. One is almost certainly female (*ARA-VP-6/500*), and the other is a probable male (*ARA-VP-6/300*) (see below). Both individuals possess a UC with a shorter crown height than the associated LC (>10% difference in *ARA-VP-6/500*) (21). In contrast in most anthropoid species, the UC is greater in height than the LC (fig. S17), a condition exaggerated in males of dimorphic species (over 50% in some papionins). Although less extreme in extant great apes (22), the UC still exceeds LC crown height by up to ~20% (fig. S18). In modest samples of modern great ape canines with little to no wear, we found no instances of LC height exceeding that of the UC (30 males and 27 females). This pattern of relative UC and LC height in *Ar. ramidus* appears unique among anthropoids and indicates differential reduction.

![Fig. 1. Representative examples of the Aramis *Ardipithecus ramidus* dentition. (A) Occlusal view micro-CT-based alignment of *ARA-VP-1/300*: top, maxillary dentition; bottom, mandibular dentition. The better-preserved side was scanned and mirror-imaged to form these composites. (B) *ARA-VP-1/300* in buccal view: top, right maxillary dentition (mirrored); bottom, left mandibular dentition. (C) Comparison of canine morphology (micro-CT-based renderings). Top row, lingual view of upper canines, from left to right: male *P. troglodytes* (cast), female *P. troglodytes* (cast), *Ar. kadabba* *ASK-VP-3/400*, *Ar. ramidus* *ARA-VP-6/5*1, *Au. afarensis* L.H. 6 (cast), *Au. afarensis* A.L. 333x-3 (cast, mirrored). Lower rows, distolingual view of lower canines, main row from left to right: male *P. troglodytes* (cast), female *P. troglodytes* (cast), *Ar. kadabba* (*STD-VP-2/61*), *Ar. ramidus* *ARA-VP-1/300*, *Au. afarensis* Sts 50 (mirrored), *Au. afarensis* Sts 51. Lowest two specimens are ape lower canines with hominid-like features: left, *P. paniscus* (cast); right, *Ouranopithecus macedoniensis* RLP-55 (cast). The *Ar. ramidus* upper canine is highly derived, with a diamond-shaped crown with elevated crown shoulders. The lower canine tends to retain aspects of primitive ape features. Further details are given in the SOM figures and SOM text S1. (D) M2 morphology (micro-CT-based renderings) showing relatively little morphological variation among the Aramis individuals. Top row left, *ARA-VP-1/300* (mirrored); right, *ARA-VP-1/18118*. Middle row left, *ARA-VP-1/3288*; right, *ARA-VP-6/500*. Bottom row left, *ARA-VP-6/502* (mirrored); right, *KUS-VP-2/154*. (E and F) Box plot of upper canine maximum diameter and labial height in (mm). *Ar. ramidus* includes Aramis and published Gona materials (2). The ~6-million-year-old hominids are represented by *Ar. kadabba* (*ASK-VP-3/400*) and *O. tugenensis* (BAR 1425'00) (7). Symbols give central 50% range (box), range (vertical line) and outliers. See SOM figures and text S1 for additional plots and details.](www.sciencemag.org)
Ardipithecus ramidus

of the UC in hominids. The UC < LC height relation is retained in modern humans.

Morphological changes in the series *A. kadabba–Ar. ramidus*—early Australopithecus support the hypothesis of selection-induced UC reduction. As detailed above, the UC is clearly derived in *Ar. ramidus*, whereas the LC tends to retain the primitive female apelike condition. *As. anamensis*, geologically younger than *Ar. ramidus* but older than *Au. afarensis*, exhibits a polymorphic condition represented by both primitive and advanced LC morphologies (4, 20) (SOM text S1). The more incisiform morphology becomes universal in *Au. afarensis* and later hominids. Furthermore, compared with both male and female apes, *Ar. ramidus* exhibits a small UC crown (both basal diameter and height) relative to apico-cervical root length, more so than the LC (figs. S19 and S20). This observation provides further support to the interpretation that the UC crown was differentially reduced (SOM text S1).

A broader comparison of *Ar. ramidus* with extant and Miocene apes illuminates aspects of C/P3 complex evolution. Compared with cercopithecoids, hominoids tend to have smaller P3s with less extensive honing (fig. S15). Compared with other modern and Miocene apes, both species of *Pan* appear to show P3 reduction. The P3 of *Ar. ramidus* is even smaller, suggesting further reduction of the C/P3 complex from an ancestral ape condition. At first sight, the comparatively small P3 size in *Pan* appears paradoxical, because amongst the modern great apes both male and female *P. troglodytes* have relatively large and tall canines (figs. S9 and S10 and SOM text S1). However, this apparent paradox is removed by a broader perspective on tooth and body size proportions. Both *Pan* species share with atelines and *Presbytis* (sensu stricto) small postcanine size relative to body size (Fig. 2, figs. S21 and S22, and SOM text S2), low postcanine dimorphism, and low to moderate canine size dimorphism (figs. S23 to S25). Conversely, papionins exhibit the opposite condition: large postcanines, large canines, and extreme dimorphism. We therefore hypothesize that the basal *Pan* condition was characterized by a somewhat reduced C/P3 complex as part of a generally small dentition relative to body size and that the canines were secondarily enhanced leading to modern *P. troglodytes*.

**The ARA-VP-6/500 skeleton and sexual dimorphism.** Of the 21 individuals with canines, *ARA-VP-6/500* has UC and LC that are strikingly small; its UC ranks either 12th or 13th (of 13), and its LC ranks seventh (of eight) in size (table S6). However, postcranially, *ARA-VP-6/500* is a large individual with an estimated body weight of ~50 kg (23). Was *ARA-VP-6/500* a small-canined male or a large-bodied female?

We began our evaluation of *ARA-VP-6/500* (24) by estimating the degree of dimorphism in the *Ar. ramidus* canine (SOM text S3). Even in modern humans, the canine is metrically the most dimorphic tooth. Mean basal crown diameter of human male canines is about 4 to 9% larger than that in females (table S5). Our analysis indicates that *Ar. ramidus* was probably only marginally more dimorphic than modern humans (tables S6 to S9 and SOM text S3), with a probable range of 10 to 15% dimorphism (in canine mean crown diameter). This is substantially less dimorphic than modern great apes, whose male canines (mean crown diameter) are larger than those of females by 19 to 47%.

On the basis of the above dimorphism estimate, the probability of a male having canines as small as those of *ARA-VP-6/500* can be evaluated by bootstrapping (2). Assuming 12% dimorphism in mean canine size (table S8), the probability that *ARA-VP-6/500* is a male is <0.03 (if the UC is ranked 12th of 13) or <0.005 (if ranked 13th) (table S9 and SOM text S4). We conclude that *ARA-VP-6/500* is a large-bodied male, a conclusion also corroborated by cranial anatomy (25). This shows that skeletal size dimorphism in *Ar. ramidus* must have been slight (11), as is the case in both species of *Pan* (26, 27).

The *ARA-VP-6/500* skeleton and dimorphism estimates allow us to place the *Ar. ramidus* dentition within a broader comparative framework. Scaling analyses (2) show that the UC of *Ar. ramidus* was relatively small in both sexes (fig. S22 and SOM text S2). In particular, male UC height of *Ar. ramidus* is estimated to be close to that of female *P. paniscus* and *Brachyteles* and to be much lower than that of male *P. paniscus* (which has the least projecting male canine among extant catarrhines) (Fig. 2).

**Canine development and function.** In cercopithecoids with highly dimorphic canines, canine eruption is typically delayed in males, beginning after the age of eruption in females (28) and apparently corresponding with species-specific patterns of body size growth spurts (29–31). Once male canine eruption is initiated, it then proceeds at a higher rate than in females, but it can still last for several years depending on species (31). As a consequence, males attain full canine eruption as they approach or achieve adult body size, both of which are necessary for reproductive success (19).

Sexually distinct patterns of canine eruption in relation to body size growth have yet to be well documented in modern great apes but appear to broadly share the cercopithecoid pattern described above (28, 32–34). Initiation of canine eruption in *P. troglodytes* differs by about 1.5 to 2 years between the sexes (35). In males of both *P. troglodytes* and *P. paniscus*, full canine eruption appears to coincide broadly with M3 eruption (observations of skeletal materials), with polymorphism in the eruption sequence of the two teeth. By contrast in females of both species, full canine eruption is attained before M3 eruption.

**Fig. 2.** Size and scaling of the *Ardipithecus ramidus* dentition. Natural log-log scatter diagram of relative upper canine height (y axis) against relative postcanine length (x axis): left, females; right, males. Both axes represent size free variables (residuals) derived from scaling tooth size against body size across a wide range of anthropoids (2). A value of zero represents the average female catarrhine condition. Positive and negative residuals represent relatively large and small tooth sizes, respectively. The diagonal line indicates the direction of equivalent canine and postcanine proportions independent of size. The five great ape taxa plotted are from left to right: *P. paniscus*, *P. t. troglodytes*, *P. t. schweinfurthii*, Gorilla gorilla, and *Pongo pygmaeus*. *Ar. ramidus* is plotted by using mean postcanine size and canine crown heights of probable female *(ARA-VP-6/500)* and male *(ARA-VP-1/300)* individuals. A hypothetical female body weight of 45 kg or 50 kg was used (right and left stars, respectively). *Ar. ramidus* is shown to have small postcanine tooth sizes, similar to those of Atelis, *Presbytis* sensu stricto, and *Pan*. Relative canine height of *Ar. ramidus* is lower than that of the smallest-canined nonhuman anthropoids, *P. paniscus* and *Brachyteles arachnoides*. See SOM text S2 for further details.
The relative timing of canine eruption in *Ar. ramidus* is revealed by two juveniles. The *ARA-VP-6/1* holotype, a probable male (table S6), includes an unworn UC whose perikymata count is 193, higher than that in *Au. africanaus/aferensis* (maximum 134, n = 4) (36) and lower than those in small samples of female *P. troglodytes* and *Gorilla* (minimum 204, n = 10) (37). The *ARA-VP-6/1* UC crown formation time was 4.29 or 4.82 years, depending on estimates of enamel formation periodicity (fig. S26). This is a comparatively short formation time, around the minimum reported for modern female apes (38).

The eruption pattern of a second individual, *ARA-VP-1/300*, can be assessed from the presence or absence of wear facets and/or polish. The *ARA-VP-1/300* canines were just completing eruption, its M2s were worn occlusally, and its unerupted M3 crowns were barely complete (Fig. 1 and fig. S27). Compared with extant apes, both its UC and LC development are advanced relative to both M2 and M3 (fig. S28) (39).

The combined morphological and developmental evidence suggests that selection for delayed canine eruption had been relaxed in *Ar. ramidus*. We hypothesize that canine prominence had ceased to function as an important visual signal in male competitive contexts.

**Tooth size and diet.** We consider relative incisor and postcanine sizes to be potentially useful in inferring dietary adaptations, although consistent patterns across primates have not been obtained (40). In particular, postcanine megadontia has been considered a defining feature of *P. troglodytes* (41). We evaluated incisor and molar sizes of *Ar. ramidus* in comparison to those of *Pan* and *Australopithecus*. Among anthropoids, *Pan* and *Pongo* are unique in having large incisors relative to both postcanine and body size, a condition not shared by *Ar. ramidus* (fig. S29).

This suggests that *Ar. ramidus* was not as intensive a frugivore as are *Pan* and *Pongo*, incisor length probably being functionally related to removal of fruit exocarp (42) and/or feeding behavior such as wading.

Although the M1 area, normalized by individual postcanial metrics, lies well within the range of extant chimpanzees, the total postcanine area of *ARA-VP-6/500* falls between *Pongo* and *P. troglodytes* (Fig. 3). *Ar. ramidus* is not only less megadont than *Pongo* and *Au. aferensis* but, together with *Pan*, *Ateles*, and some *Pithecia* species, lies at the small end of the range of variation of large-bodied anthropoids (fig. S30). The most megadont anthropoids include robust *Australopithecus*, such as *Au. boisei*, as well as *P. paniscus* and *Alouatta*. *Ouranopithecus* was probably as megadont as *Australopithecus* species, whereas *Dryopithecus* and *Pierolapithecus* probably had relative postcanine sizes closer to *Ar. ramidus* and thus better approximate the dentition–body size relationship of the last common ancestor of humans and chimpanzees. We conclude that *Ar. ramidus* was substantially less megadont than *Australopithecus*.

**Molar structure and enamel thickness.** Molar structure, enamel thickness, and tooth wear further illuminate dietary adaptation in *Ar. ramidus*. Compared with the distinct occlusal structure of the molars of each of the modern ape species (see below), *Australopithecus* occlusal morphology is more generalized, with low, bunodont cusps and moderate to strong basal crown flare. Such morphology also characterizes *Australopithecus* as well as a diversity of Miocene apes (43). *Gorilla* molars have much more salient occlusal topography and enhanced shearing crests. *Pan* molars are characterized by broad, capacious occlusal basins flanked by moderately tall cusps, effective in crushing relatively soft, fluidic mesocarp while retaining the ability to process more fibrous herbaceous materials (Fig. 4) (44, 45). These features are accentuated in *Pan* by the characteristically thin enamel of its occlusal basin (45, 46).

To further elucidate molar structure and dietary adaptations of *Ar. ramidus*, particularly in comparison with *Pan* and *Australopithecus*, we used micro–computed tomography (micro-CT) to study molar enamel thickness and underlying crown structures (2). Although the weak contrast of fossil enamel and dentin makes micro-CT– based evaluations difficult, we were able to assess several *Ar. ramidus* molars with this method. These and analyses of CT sections and natural fracture data (2) indicate that *Ar. ramidus* enamel is considerably thinner than that of *Australopithecus* but not as thin as in *Pan* (as originally reported in (1)) (Fig. 4 and figs. S31 and S32).

Of particular importance is that *Ar. ramidus* molars do not exhibit enamel distribution patterns characteristic of *P. troglodytes* and *P. paniscus*. Both *Pan* species have similar crown structure and enamel distribution patterns (Fig. 4), although *P. paniscus* molars exhibit a higher cuspal topography, perhaps related to greater reliance on fibrous food (46, 47). *Ar. ramidus* lacks the thin occlusal fovea enamel of *Pan* and in this regard is similar to both *Australopithecus* and Miocene forms such as *Dryopithecus* (Fig. 4). The *Pan* condition is most likely derived, probably associated with an increased reliance on higher-canopy ripe fruit feeding.

Despite the generalized molar structure common to both *Ar. ramidus* and *Australopithecus*, the adaptive difference between the two is expressed by enamel tissue volume, which we consider to broadly track net resistance to abrasion. Modern ape species exhibit a near-isometric relation between molar durability (measured as volume of enamel tissue available for wear per unit occlusal area) and tooth size, despite diverse dietary preferences and crown anatomy (Fig. 4). *Ar. ramidus* falls near this isometric continuum, but *Australopithecus* does not. *Australopithecus* molars achieve greater functional durability from increased enamel volume. *Au. boisei* occupies an extreme position distant from the modern ape baseline. Thus, both tooth size and enamel thickness and volume suggest a substantial adaptive shift from *Ardipithecus* to *Australopithecus*.

This is further expressed in molar macro- and microscopic wear patterns. In contrast to *Australopithecus*, *Ar. ramidus* molars did not wear flat but instead retained stronger buccolingual wear slopes. The Aramis *Ar. ramidus* dentition also exhibits consistently weak M1 to M3 wear gradients (48). Microwear of the *Ar. ramidus* molars tends to differ from that of *Au. aferensis*, the latter characterized by a dominance of buccolingually oriented scratches (49). In contrast, the *Ar. ramidus* molars tend to exhibit finer and more randomly oriented striae (fig. S33). Collectively, the wear evidence suggests that *Ar. ramidus* consumed a less abrasive diet and engaged in less masticatory grading than *Australopithecus*. 

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**Fig. 3.** Relative postcanine dental size in *Ar. ramidus*. Postcanine size is compared directly in reference to associated postcanine elements; x axis is natural log of the size variable (body size proxy) of Lovejoy et al. (23), derived from four metrics of the talus and five metrics of the capitular; y axis is natural log of the square root of the sum of calculated areas (mesiodistal length multiplied by buccolingual breadth) of lower M1 (left) and lower P4 to M3 (right). A, *Ar. ramidus* ARA-VP-6/500; L, *Au. aferensis* A.L. 288-1; c, *Pan troglodytes* troglodytes; g, *Gorilla gorilla* gorilla; o, *Pongo pygmaeus* (males blue, females red).
Ardipithecus ramidus

Enamel thickness and phylogenetic implications. Since the initial description of Ar. ramidus as a new species of Hominidae (1), its relatively thin molar enamel has been a focus of attention. Some authors have suggested that its thin enamel might be a shared derived feature with Pan (7). The fuller study of molar enamel thickness and patterns outlined above establishes the following: (i) Although Ar. ramidus enamel is thinner than that of Australopithecus, it is not as thin as Pan’s; (ii) the thin enamel of Pan molars can be considered a part of a structural adaptation to ripe fruit frugivory (46) and therefore differs from the Ar. ramidus condition. Furthermore, the distinct internal structure of Pan molars seems lacking in Ar. kadabba, O. tugenensis, and S. tchadensis (4, 8, 10). Hence, the Pan condition is best considered derived relative to the ancestral and early hominid conditions.

Conclusions. Multiple lines of morphological evidence suggest that Ar. ramidus was a generalized omnivore and frugivore that did not rely heavily on either ripe fruits (as in Pan or Pongo), fibrous plant foods (as in Gorilla), or hard and

Fig. 4. Enamel thickness and distribution patterns in Ar. ramidus. Left panels: micro-CT–based visualizations of maxillary first molars in arbitrary size. (A) Outer enamel surface; (B) enamel thickness in absolute thickness scale superimposed on topographic contours; (C) enamel thickness in relative scale to facilitate comparison of pattern. The molars labeled in (A) are as follows: 1 and 5, Au. africanus Sts 24 (mirrored) and Sts 57; 2, Dryopithecus brancoi; 6, Ar. ramidus ARA-VP-1/528; 3, Pan troglodytes; 4, Pan paniscus; 7, Gorilla gorilla; 8, Pongo pygmaeus. The Pan species share a broad occlusal basin and thin occlusal enamel. Both Ar. ramidus and D. brancoi are thinner-enameled than Australopithecus but share with Australopithecus a generalized distribution pattern. (D) Maximum lateral enamel thickness, showing that Ar. ramidus enamel is thicker than those of Pan and D. brancoi and thinner than that of Australopithecus species. Horizontal line is median; box margins are central 50% range. (E) Ratio of occlusal (volume/surface area) to lateral (average linear) enamel thicknesses, showing that Pan is unique in its distinctly thin occlusal enamel. (F) Molar durability (enamel volume per unit occlusal view crown area) plotted against projected occlusal view crown area. An isometric line (slope of 0.5) is fitted through the centroid of the three measured Ar. ramidus molars. The least squares regression (y = 0.418x- 1.806) of the combined modern ape sample is also shown. This slope does not differ significantly from isometry. Ar. ramidus and D. brancoi are close to, and Australopithecus species considerably above, the regression line, indicating greater enamel volume available for wear in Australopithecus molars. See (2) for further details.
These inferences are corroborated by the isotopic Ar. ramidus sources in woodland habitats and small patches of forest, thus differing from both savanna woodland-dwelling chimpanzees (>90% C3) and Australopithecus spp. (>30% C4) (51).

Conversely, extant Pan and Gorilla, each with its distinctive dental morphology, are best considered derived in their dietary and dental adaptations. This is consistent with the Ar. ramidus postcranial evidence and its interpretations (11, 23) and strengthens the hypothesis that dental and locomotor specializations evolved independently in each extant great ape genus. This implies that considerable adaptive novelty was necessary to escape extinction in the Late Miocene forest and woodland environments. These analyses also inform the social behavior of Ar. ramidus and its ancestors. The dental evidence leads to the hypothesis that the last common ancestors of African apes and hominids were characterized by relatively low levels of canine, postcanine, and body size dimorphism. These were probably the anatomical correlates of comparatively weak amounts of male–male competition, perhaps associated with male philopatry and a tendency for male-female codominance as seen in P. paniscus and ateline species (52, 53).

From this ancestral condition, we hypothesize that the P. troglodytes lineage secondarily enhanced its canine weaponry in both sexes, whereas a general size reduction of the dentition and cranium (25) occurred in the P. paniscus lineage. This suggests that the excessively aggressive inter- and intragroup behavior seen in modern P. troglodytes is unique to that lineage and that this derived condition compromises the living chimpanzee as a behavioral model for the ancestral hominid condition. The same may be the case for Gorilla, whose social system may be a part of an adaptation involving large body size, a specialized diet, and marked sexual dimorphism.

In the hominid precursors of Ar. ramidus, the predominant and cardinal evolutionary innovations of the dentition were reduction of male canine size and minimization of its visual prominence. The Ar. ramidus dental evidence suggests that this occurred as a consequence of selection for a less projecting and threatening male upper canine. The fossils now available suggest that male canine reduction was well underway by 6 million years ago and continued into the Pliocene. Further fossils will illuminate the tempo and mode of evolution before 6 million years ago.

References and Notes
2. Materials and methods are available as supporting material on Science Online.
4. Y. Haille-Selassie, G. Suwa, T. D. White, in Ardipithecus kadabba: Late Miocene Evidence from the Middle Awash.
Ardipithecus ramidus

The Great Divides: Ardipithecus ramidus Reveals the Postcrania of Our Last Common Ancestors with African Apes

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Genomic comparisons have established the chimpanzee and bonobo as our closest living relatives. However, the intricacies of gene regulation and expression caution against the use of these extant apes in deducing the anatomical structure of the last common ancestor that we shared with them. Evidence for this structure must therefore be sought from the fossil record. Until now, that record has provided few relevant data because available fossils were too recent or too incomplete. Evidence from Ardipithecus ramidus now suggests that the last common ancestor lacked the hand, foot, pelvic, vertebral, and limb structures and proportions specialized for suspension, vertical climbing, and knuckle-walking among extant African apes. If this hypothesis is correct, each extant African ape genus must have independently acquired these specializations from more generalized ancestors who still practiced careful arboreal climbing and bridging. African apes and hominids acquired advanced orthoarogy in parallel. Hominoid spinal invagination is an embryogenetic mechanism that reoriented the shoulder girdle more laterally. It was unaccompanied by substantial lumbar spine abbreviation, an adaptation restricted to vertical climbing and/or suspension. The specialized locomotor anatomies and behaviors of chimpanzees and gorillas therefore constitute poor models for the origin and evolution of human bipedality.

Thomas Huxley published Evidence as to Man’s Place in Nature (1) only 4 years after Darwin’s On the Origin of Species. Its frontispiece featured a human skeleton and four suspensory adapted apes, each posed upright and each obviously more human-like than any primate (today further confirmed by comparative genetic analysis). Until now, the few available fossils of apes in deducing the anatomical structure of the last common ancestor that we shared with them.

Evidence for this structure must therefore be sought from the fossil record. Until now, that record has provided few relevant data because available fossils were too recent or too incomplete. Evidence from Ardipithecus ramidus now suggests that the last common ancestor lacked the hand, foot, pelvic, vertebral, and limb structures and proportions specialized for suspension, vertical climbing, and knuckle-walking among extant African apes. If this hypothesis is correct, each extant African ape genus must have independently acquired these specializations from more generalized ancestors who still practiced careful arboreal climbing and bridging. African apes and hominids acquired advanced orthoarogy in parallel. Hominoid spinal invagination is an embryogenetic mechanism that reoriented the shoulder girdle more laterally. It was unaccompanied by substantial lumbar spine abbreviation, an adaptation restricted to vertical climbing and/or suspension. The specialized locomotor anatomies and behaviors of chimpanzees and gorillas therefore constitute poor models for the origin and evolution of human bipedality.

Challenges, however, were mounted.Straus enumerated disconcertingly primitive human features in “The Riddle of Man’s Ancestry” (4), and Schultz doubted that brachiation “…opened the way automatically for the erect posture of modern man” (5), pp. 356–357). Although withdrawal of the ulna from its primitive pisotriqetral recess was thought to be the sine qua non of suspension (6), a functional equivalent was discovered to have evolved in parallel in the wrists of never-suspensory lorises (7). African ape knuckle-walking (8), considered by many too bizarre to have evolved independently in Gorilla and Pan, came to be viewed in light of emergent molecular phylogenetics (9) as a natural successor of suspensory locomotion—and by some as the almost-certain default engine of bipedality (10).

A flood of morphometric analyses appeared to confirm arguments for knuckle-walking hominid ancestors [reviewed in (11)], even though hints of the behavior were also seen in captive orangutans (12). Knuckle-walking was surmised to be a natural consequence of irreversible modifications of the forelimb skeleton to facilitate advanced suspension and vertical climbing (11). It was thereby hypothesized to be an adaptive signal of the first two phases of a deterministic succession leading to bipedality: advanced suspension/vertical climbing → terrestriality/ knuckle-walking → bipedality.

A compendium of observations of chimpanzees and bonobos performing upright stance and locomotion followed. Accumulating molecular biology propelled this troglodytian paradigm (conceived as a natural succession to its older, suspensory counterpart) to near-consensus. Chimpanzee-human protein homologies and DNA base sequence comparisons (9, 13–16) established Homo and Pan as likely sister clades (today further confirmed by comparative genomics (17, 18)). The only question remaining seemed to be whether the bonobo or chimpanzee represented the best living proxy for the last common ancestor (19–22).

The Chimpanzee model and Australopithecus. The discovery and recognition of the then-primitive Australopithecus afarensis during the 1970s (23) pushed the hominid record back to 3.7 million years ago (Ma). Although its postcranium was recognized to harbor unusually sophisticated adaptations to bipedality [reviewed in (24)], a feature confirmed by human-like footprints at Laetoli (25, 26), many interpreted these fossils to represent the closing argument for the troglodytian paradigm [see, e.g., (27)]. Only the recovery of earlier, chimpanzee-like fossils from the Late Miocene seemed necessary to complete this scenario [even though newer Australopithecus fossils have led at least one discoverer to doubt a chimpanzee-like ancestry (28)]. Until now, the few available fossils of appropriate antiquity have remained largely uninformative (29-31).

The Ardipithecus ramidus fossils from 4.4 Ma Ethiopia are obviously not old enough to represent the chimpanzee/human last common ancestor (CLCA); the older common ancestor of hominids and both Gorilla and Pan is hereafter the GLCA). However, their morphology differs substantially from that of Australopithecus. The Ar. ramidus fossils therefore provide novel insights into the anatomical structure of our elusive common ancestors with the African apes. For that reason, and because of its phylogenetic position as the sister taxon of later hominids (32), this species now provides opportunities to examine both the suspensory and troglodytian paradigms with greater clarity than has previously been possible. Here we first provide evidence of limb proportions, long considered to bear directly on such issues, and then review key aspects of the entire Ar. ramidus postcranium. Comparing the basic proportions and postcranial anatomy of Ar. ramidus (Fig. 1) with those of apes enables us to propose the most probable anatomy of the last common ancestors of Gorilla, Pan, and the earliest hominids. Much of the relevant information on Ar. ramidus is based on the partial skeleton from Aramis (32).

Body mass. The geometric means of several metrics of the capitale and talus are strongly related to body mass in extant primates (correlation coefficient r = 0.97; fig. S1), and can be used to estimate body mass in ARA-VP-6/500, as well as in A.L. 288-1. Restricting the sample to large-bodied female hominoids predicts that ARA-VP-6/500 had a mass of about 51 kg. The metrics for A.L. 288-1 fall below those of all extant hominoids. We therefore used the female anthropoid regression to estimate the body mass of A.L. 288-1 (26 kg), which is consistent with previous estimates (33) (table S1). Based on several shared metrics, ARA-VP-7/2, a partial forelimb skeleton (32), was slightly smaller than ARA-VP-6/500 [supporting online material (SOM) Text S1].

Given the apparent minimum body size dimensions of Ar. ramidus (32, 34), the predicted...
body mass of ARA-VP-6/500 serves as a reasonable estimate for the general body mass of *A. ramidus*. Although *ARA-VP-6/500* was one of the larger individuals of the Aramis sample (32), it was probably more representative of its species than was *A.L. 288-1* [the latter clearly lies at the lower end of the *Au. afarensis* species range based on larger samples (35)]. Unfortunately, *ARA-VP-6/500* tells us little about the body mass of the CLCA and GLCA because these predate *A. ramidus* by wide margins and may have still been primarily arboreal. The limited available (mostly dental and cranio-mandibular) samples indicate that the size of Late Miocene hominids (29–31) was similar to that of *A. ramidus* (34), and estimated body weight for the 6 Ma Orrorin femoral remains is 30 to 50 kg (36). Although body mass in early Miocene forms appears to have varied greatly (37, 38), it is likely that the CLCA and GLCA were either equal to or smaller than *A. ramidus*, and possibly even substantially so. Only additional fossils can resolve this issue.

**Limb segment proportions.** Radial, ulnar, and tibial lengths can be accurately determined for *ARA-VP-6/500* (SOM Text S1). The specimen’s radius/tibia ratio (0.95; fig. S2) is similar to those of generalized above-branch quadrupeds such as the Old World monkey *Macaca* (0.90 to 0.94; table S2) and the Miocene ape *Proconsul heseloni* (0.88 in *KNM-RU 2036*) (38). The ratio is unlike that of African apes (*P. troglodytes*, 1.11 ± 0.04; *Gorilla*, 1.13 ± 0.02) (39) and is, remarkably, 17 standard deviations below that of *Pongo* (1.47 ± 0.03).

The *Arbipithecus* skeleton’s nearly intact tibia allows estimation of femoral length because the crural index (CI: tibia length/femur length × 100) is highly conserved in African apes and humans (5, 40) (81 to 84; SOM Text S1). Tibial length in *A.L. 288-1* can likewise be estimated from its effectively complete femur. Although no humerus was recovered for *ARA-VP-6/500*, one belonging to *ARA-VP-7/2* is almost complete and can be used to estimate humerus length in *ARA-VP-6/500* by simple proportion of shared elements (SOM Text S1). The *A.L. 288-1* humerus is intact, and its radius length was previously estimated by regression (41). These data allow calculation of the more familiar intermembral index (IMI; forelimb length/hindlimb length × 100). The IMIs of both specimens resemble those of *Proconsul* and Old World monkeys (table S3).

*ARA-VP-6/500* also allows interpolation of other key limb proportions. The brachial indices (BI: radius length/humerus length × 100) of *Proconsul*, *Equatorius*, *A.L. 288-1*, and *ARA-VP-6/500* are each within the observed range of *Pan* (fig. S3). It is therefore likely that the BI has remained largely unmodified since the GLCA, especially in light of the relationship of radius length to estimated body mass (fig. S4). In contrast, the BIs of *Homo* and *Gorilla* are both derived, albeit by obviously different routes (fig. S3). Humans have greatly shortened radii in conjunction with their novel antebrachial/manual proportions for grasping and manipulation ([41], 42 and see below). *Gorilla* appears to have experienced both humeral elongation and possibly slight radial shortening (figs. S4 and S5), most likely to reduce joint stresses at the elbow imposed by the immense mass of adult males. The BIs of *Pan* and *Ar. ramidus* are similar (fig. S3), but *Pan* exhibits a much higher IMI (table S3). Therefore, both *Pan* and *Gorilla* have undergone forelimb elongation and hindlimb reduction since the GLCA (table S2 and figs. S4 to S6). The IMIs of hominids appear to have remained primitive until 2.5 Ma (41, 43). The relatively high BI of *Pongo* reflects its entirely different evolutionary history.

**Manual anatomy and proportions.** Compared to estimated body size, the manual phalanges of *Ar. ramidus* and *Gorilla* are long relative to those of the Miocene ape *Proconsul* (fig. S7). They are relatively even more elongate in *Pan*, but dramatically abbreviated in *Homo*. These conclusions are supported by similar calculations using the means of observed body mass (table S3). There is no evidence that the manual phalanges of *Au. afarensis* were elongated relative to those of *Ar. ramidus*.

In contrast to their manual phalanges, the posterior (medial) metacarpals 2 to 5 (MC2-5) of *Proconsul* and *ARA-VP-6/500* are substantially...
shorter than those of any extant ape (figs. S8 and S9). Viewed in the context of relative limb length patterns (see above), as well as the anatomical details of the hand (44), the short M5s of *Ar. ramidus* strongly suggest that *Pan* and *Gorilla* independently acquired elongate M5s as a part of an adaptation to vertical climbing and suspensory locomotion. Elongation of M2-5 in African apes demanded heightened resistance to torsion and consequent fixation of the carpo-metacarpal joints within the central joint complex (CJC) (44).

The retention of the primitively short M5s in *Ar. ramidus* suggests that the GLCA/CLCA also did not have elongate M5s, and engaged in a form of above-branch quadrupedal locomotion involving deliberate bridging and careful climbing. We hypothesize that this was retained from Middle Miocene precursors of the GLCA. A retained short metacarpus would optimize palmar conformity to substrates, an adaptation later abandoned by extant African apes.

The thumb metacarpal of *ARA-VP-6/500* was more aptly proportioned for manual grasping than are those of extant apes (figs. S10 and S11) (44). In extant apes, elongation of the posterior (medial) metacarpus may have been achieved by increased expression of *Hoxd11* or one of its targets, which do not affect the first ray (SOM Text S2) (42, 45). However, the M1 of apes does seem moderately less robust than that of *Ar. ramidus*, and its soft tissues have undergone substantial involution (4, 42). This suggests that some degree of down-regulation of *Hoxd13* may have been responsible for elongation of the posterior (medial) metacarpus.

*Ar. ramidus* greatly illuminates the natural history of the thumb in higher primates. Its robusticity in hominids, while certainly enhanced during the past 3 million years, is nevertheless at least partially primitive. In contrast, in taxa adapted to vertical climbing and suspension, lengthening of the palm has become so dominant as to eclipse some of the thumb’s function, a condition that has reached its apogee in *Ateles* and, to a lesser extent, large-bodied extant apes. These findings strongly suggest that the target of recently discovered major cis-regulatory modification of gene expression in the first ray (46) was not manual but pedal—it is the human hallux, not our largely primitive pollex, that is highly derived (47).

Additional relevant hand anatomy leads to the same conclusions. *Ar. ramidus* is the only hominid fossil thus far recovered with a metacarpal head reminiscent of the metacarpophalangeal (MP) joint structure seen in many Miocene hominoids [such as *Equatorius*, *Proconsul*, *Dryopithecus*, and *Pierolapithecus* (48)]. The collateral ligament facets in these taxa collocate with deep symmetric invaginations of the metacarpal head’s dorsum. This morphology is typical of Old World monkeys and is thereby associated with substantial dorsiflexion of the MP joint, an obvious manifestation of their palmigrady. The trait is only moderately expressed in *Orudipithecus*. Modern human and orangutan MP joints are substantially less constricted, and neither taxon exhibits appreciable locomotor-related MP dorsiflexion.

Constricted metacarpal head morphology appears to be primitive because it is still partially present in *Ar. ramidus*, albeit substantially reduced compared to early Miocene hominoids and Old World monkeys. Its retention suggests moderately frequent MP dorsiflexion, a finding consistent with the remarkable adaptations to palmigrady seen in the *Ar. ramidus* wrist (see below and (44)).

The metacarpal heads of knuckle-walking apes are also somewhat constricted by their collateral facets, but are heavily flattened and broadened to withstand excessive compression during dorsiflexion. Constriction by their collateral ligament facets is therefore only minimal. Moreover, the origins of their collateral ligaments have been substantially expanded volarily, presumably because such positioning improves their capacity to restrict abduction or adduction during MP dorsiflexion imposed by knuckle-walking. Joint flattening enhances cartilage contact and is likely at least partially a cartilage-modeling trait [cartilage modeling; Type 4 (49)].

Loss of MP dorsiflexion in *Pongo* is readily explicable by its extreme metacarpal and phalangeal elongation and curvature. These can safely be presumed to have eliminated any appreciable functional MP dorsiflexion. Modern humans lack any dorsiflexion because our hands play no important role in locomotion. The trait is also absent in *Au. afarensis*, suggesting that either its hand no longer played any role in locomotion, or that such use no longer included an MP dorsiflexive component of palmigrady. The former seems far more likely, given the paramount adaptations to bipedality in the species’ lower limb (24, 50, 51).

The primitive metacarpal head morphology within the overall primitive hand anatomy (44) of *Ar. ramidus* carries obvious implications for reconstruction of GLCA/CLCA locomotion. The unique combination of marked midcarpal mobility, ulnar withdrawal, and moderate MP dorsiflexion in *Ar. ramidus*, probably mostly primitive retentions, implies that the GLCA/CLCA locomotor pattern was also characterized by some form of arboreal palmigrade quadrupedality, unlike that in any extant descendant great ape.

Finally, it is clear now that phalangeal length of *Ar. ramidus* is not related to suspensory locomotion, but instead reflects a more general grasping adaptation. This renders phalangeal length most regarding the hypothesis that manual (or even pedal) phalangeal lengths are an active signal of suspensory locomotion in *Au. afarensis* [contra (52, 53)]. It is more probable that selection had not reduced their length in the younger species, and that such reduction did not occur until selection for tool-making became more intense later in the Pliocene (43, 54).

**Pedal proportions.** Pedal phalangeal evolution appears to have closely paralleled its manual counterpart in each clade (compare figs. S7 and S12). However, pedal phalanges of African apes and hominids appear to have been substantially abbreviated, rather than elongated. Functional demands of terrestrial locomotion, perhaps similar to those acting on papiolions (which also exhibit pedal phalangeal shortening), are a probable explanation. *Pongo* represents a marked contrast, with substantial pedal phalangeal elongation. It is thus reasonable to infer that the GLCA/CLCA’s pedal phalanges were longer than those of the partially terrestrial extant African apes and *Ar. ramidus*.

The metatarsals of *Ar. ramidus*, chimpanzees, and gorillas presents a striking contrast to their metacarpus. Like the foot phalanges, the metatarsals also appear to have been universally shortened in all hominoids subsequent to *Proconsul* (figs. S13 and S14) (47). The basis of this universal shortening, however, is somewhat unclear, because tarsal evolution contrasts dramatically in hominids and African apes. The modern ape foot has obviously experienced functional reorganization into a more hand-like grasping organ. The *Ar. ramidus* foot did not. This suggests that substantial elements of a more lever-based, propulsive structure seen in taxa such as *Proconsul* and Old World Monkeys [robust plantar aponeurosis; retained quadratus plantae; robust peroneal complex (47)] were preserved in the GLCA/CLCA. These structures were sacrificed in both African ape clades to enhance pedal grasping for vertical climbing (55, 56). The moderate shortening of the metatarsus in *Ar. ramidus* and both African apes may therefore simply reflect negative allometry of metatarsal (M1) lengths with an increase in body size. The human foot has been lengthened primarily by tarsal elongation (5, 47), presumably because of the likely high failure rate of metatarsal shafts during forceful fulcrumation.

In summary, a comparison of the pedal proportions of *Ar. ramidus* and the extant African apes suggests that the GLCA/CLCA hindlimb remained dominant for body mass support during bridging and arboreal clambering, to the extent that it later proved permissive to bipedality in transitionally terrestrial hominids.

**Trunk structure.** Knowledge of the role of selector genes in early vertebral column formation [especially the role of the *Hox* code on column differentiation (57, 58)] has advanced our ability to interpret the vertebral formulae of extant hominoids. It now appears that the modal number of lumbar vertebrae in *Australopithecus* was six, and that a four-segment sacrum was also probably common (57, 58). This axial formula is unlike that of any extant ape. Comparison of the axial columns of extant species further indicates that postoccipital somite number in the GLCA/CLCA was probably either 33 or 34, and that lumbar column reduction occurred independently in chimpanzees, bonobos, gorillas, and hominids. This probably resulted from either transformation of vertebral identities,
or a combination of such transformation and reduction in the number of somites contributing to the lumbosacral region (fig. S15). The most likely vertebral patterns for Ar. ramidus are therefore those also inferred for the GLCA/CLCA and Australopithecus.

Pelvic structure indicates that Ar. ramidus retained a primitive spine. Its iliac and acetabular regions establish not only that it was habitually bipedal when terrestrial, but also that this was achieved by combining situational anterior pelvic tilt to accentuate substantial lordosis during upright walking (59). Such rotation placed the still partially primitive anterior gluteal musculature into a position of functional abduction for single support stabilization. In contrast to Ar. ramidus, Au. afarensis is known to have exhibited highly evolved mechanisms of hip abduction, confirmed by the distinctly stereotypic trabecular profile of its femoral neck (24).

The Ar. ramidus pelvis retained other elements in common with extant African apes (and presumably the GLCA/CLCA). These include a long, expansive and rugose ischial region and shorter pubic rami (but not a long pubic corpus) (59). The species’ highly flexible lower lumbar column, coupled with its narrower interacetabular distance, still must have provided a moderately reflexive hindlimb for arboreal climbing. Not until hominids became habitually terrestrial bipeds with broad interacetabular distances, reduced and angulated ischial tuberosities (possibly indicating hamstring deceleration of the hindlimb at heel strike), and extremely shortened, flared, and broadened ilia did they then exchange such flexibility for the much more rigid constraints of lower-limb stabilization that characterize Australopithecus (50, 51).

The combined pelvic and vertebral data imply that the morphological elements of extant great apes emerged separately rather than in concert. Vertebral column invagination and its associated gracilization of the retroauricular pelvic space preceded specialized iliac modification and the radical lumbar column shortening seen in the African apes (58). The ARA-VP-6/500 pelvis shows that hominid ilia shortened and broadened to establish permanent lumbar lordosis. African ape ilia were instead modified to increase abdominal stiffness. The posterior pelvic changes and pronounced lordosis in hominids subsequently promoted even more dramatic vertebral column invagination (60). This trend is eventually reflected in more dorsally oriented transverse processes of hominid thoracic vertebral compared to those of apes (60). In extant apes, vertebral column invagination and shortening were acquired both independently and non-contemporaneously, the first being a deeply rooted embryogenetic mechanism that postero-lateralized the pectoral girdle for a more lateral-facing glenoid; the second, an independent means of increasing abdominal rigidity. We hypothesize that hominids never participated in the second (SOM Text S3), having rather evolved from a careful climber in which deliberate bridging placed no undue stress on the lower spine. Not until the ancestors of African apes embarked (separately) on their adaptations to vertical climbing and suspension did the lumbar spine undergo its dramatic reduction in length.

The last common ancestors. Integration of the data and observations reviewed above allows us to hypothesize about the postcranial adaptations and locomotion of the GLCA and CLCA. The extensive array of highly distinctive specialization seen in modern Gorilla and Pan (in part shared with Pongo) indicates that these are derived features most likely related to vertical climbing and suspension.

Not only does Ar. ramidus fail to exhibit these specialized modifications, it exhibits others (e.g., a palmar position of the capitae head that facilitates extreme dorsiflexion of the mid-carpal joint rather than its limitation; a robust os peroneum complex limiting plantar conformity to substrates rather than its facilitation) that are effectively their functional opposites. The expression of some of these characters (e.g., capitae head position) is even more extreme than it is in either the Miocene apes preceding Ardipithecus or in Australopithecus that follows. It is therefore highly unlikely that Ar. ramidus descended from a Pan/Gorilla-like ancestor and then (re)evolved such extreme characters. Conversely, some other detailed differences in Pan and Gorilla structure [e.g., scapular form (61), iliac immobilization of lumbar vertebrae (58), appearance of a prepollex (62)] suggest that each of these ape clades independently acquired their anatomical adaptations to vertical climbing and/or suspension.

Therefore, we hypothesize that Ar. ramidus retains much of the ancestral GLCA and CLCA character states, i.e., those that relate to above-branch quadrupedality. In particular, contra Gorilla and Pan, the GLCA carpometacarpal, mid-carpal, radiocarpal, and ulnotrochlear joints must have lacked notable adaptations to suspension and/or vertical climbing (44). The GLCA foot seems to have been only partially modified for manual-like grasping. Its hindlimb remained fully propulsive at its midtarsal and tarsometatarsal joints (47). Although its shoulder joint must have been fully lateralized, its lumbar column nevertheless was still long (58) (fig. S15). Its limb proportions were still primitive (see earlier). If body size was as large as in Ar. ramidus, it may have been too large for habitual, unrestricted above-branch quadrupedality, but this remains uncertain. Assuming considerable reliance on arboreal subsistence, it is likely that body mass did not exceed 35 to 60 kg [i.e., combined probable range of Ar. ramidus and 6 Ma Orrin (36)].

The GLCA picture that emerges, therefore, is one of generalized, deliberate bridging with quadrupedal palmigrady and preference for large-diameter substrates. This may have involved either suspension or vertical climbing, but without sufficient frequency to elicit morphological adaptations specific to these behaviors. It is likely that these hominoids ranged mostly in the lower canopy, and perhaps were even partially terrestrial. However, their mode of terrestrial locomotion remains unknown.

The GLCA therefore represents a foundation for two adaptive paths. Gorilla and Pan independently specialized for both suspension and vertical climbing (and eventually knuckle-walking). Gorillas might have acquired larger body size in relation to mixing higher-canopy frugivory with a more terrestrial herbaceous or folivorous dietary component. Lacking definitive fossil evidence, it is currently impossible to determine when the large body mass of Gorilla evolved, but it probably occurred in concert with its more herbaceous diet. The 10 Ma Chororapithecus, which shows incipient signs of Gorilla-like molar morphology (63), may be an early representative of the Gorilla clade. If so, then this clade’s shift toward increased body mass and terrestriality must have occurred early in its phyletic history.

The other adaptive pathway retained palmar flexibility, with a short metacarpus that lacked notable syndesmotic restriction. This was combined with retention of an essentially rigid mid-tarsal joint that was insufficiently flexible to perform vertical climbing (55, 56), but was fully satisfactory for less specialized careful climbing, clambering, and bridging. This is the hypothesized structure of the CLCA, from which Pan would have evolved a greater reliance on vertical climbing and suspension than occurred in the Gorilla clade, never reaching as large a body size.

In contrast to Pan, the forebears of Ar. ramidus early in the hominid clade must have relied increasingly on lower arboreal resources and terrestrial zones, without being dependent on higher-canopy resources (such as ripe fruits). From the comparative evidence now available from Ar. ramidus and Pan dental anatomy and isotopes, we posit that the chimpanzee clade increasingly developed a preference for (or dependency on) ripe fruit frugivory, whereas hominids retained a more primitive dental complex adequate for the range of transitional arboreal/terrestrial resources (34).

The likely K-selected demographic adaptation of all hominoids in a setting of almost certain competition with the surging Old World monkey radiation would have been a major factor (64, 65) driving such very different evolutionary trajectories of early African apes and hominids. The earliest fossil evidence for cercopithecid radiation (an early colobine) is now close to 10 Ma (66). A much better record of both fossil hominoids and cercopithecids from the late Middle to early Late Miocene is needed to clarify these suggested patterns of ape-cercopithecid evolution.

Orthogrady, suspension, knuckle-walking, and bipedality. Ar. ramidus affords new insights into ape and hominid bauplan evolution.
Ardipithecus ramidus

(Fig. 2 and Table 1). The most fundamental is the clear demonstration that the GLCA lacked the suspensory adaptations long recognized to be common to all extant apes.

The chimpanzee and gorilla clades each independently increased their reliance on higher-canopy resources, and modified characters originally associated with advanced bridging to those more useful in vertical climbing and suspension. These include an elongated posterior (medial) metacarpus, broadened radiocarpal joint with reduced midcarpal mobility, syndesmatically and morphologically buttressed carpometacarpal joints, expanded long antebraconal flexor tendons, a redistributed long pollical flexor tendon (to the elongated second ray), a modified enthesis donors, a redistributed long antebrachial flexor ten-

sions, a retroflexed troch-orate mechanisms of negotiating gaps in trees (Fig. 2 and Table 1). The most fundamental is the long-held view that dorsal transposition of the lumbar transverse processes onto their pedi-

cles implies orthograde is now falsified, because Ar. ramidus establishes that such relocation is a direct correlate of ventral invagination of the entire spinal column within a context of above-

branch quadrupedal palmigrady that established increased shoulder mobility for bridging and clambering (SOM Text S3).

In hominids, from an above-branch quadrupedal ancestry, advanced orthograde was the independent consequence of terrestrial bipedality made possible by a mobile lumbar spine and largely primitive limbs. It is sobering to consider one profound implication—if emergent hominids had actually become as adapted to suspension or vertical climbing as are living apes, neither bipedality nor its social correlates would likely have evolved. It is therefore ironic that these locomotor modes have played so promi-

nent a role in explanations of bipedality. In retrospect, it seems clear that they would instead have likely prevented it (SOM Text S3).

Conclusions. Ar. ramidus implies that African apes are adaptive cul-de-sacs rather than stages in human emergence. It also reveals an unanticipated and distinct locomotor bauplan for our last common ancestors with African apes, one based on careful climbing unpreserved in any extant form. Elaborate morphometric statistical procedures were the culmination of a 20th-

century trend toward objectivity, in which metrics came to be regarded as more informative than careful comparative anatomy—a trend accom-

panied by too many presumptions and too few

Fig. 2. Branching diagram to illustrate cladistic relationships of extant hominoids. Branching order among the extant forms shown here is well established by molecular evidence. The two fossil forms are possible phyletic ancestors of the human clade, but are shown here in a sister relationship to the extant forms. Circled numbers indicate evolutionary derivations, itemized in Table 1, hypothesized to have occurred on each lineage. (Illustrations: Copyright 2009, J. H. Mattenmes)
1. **Basal node.** An inferred generalized ancestor of the great ape clade, which lived probably more than 18 Ma. We infer this primate to have been an above-branch palimpsest, plantigrade quadruped, with generalized limb proportions, an anteriorly oriented pectoral girdle, and long lumbar vertebral column with transverse processes located ventrally on their bodies. It would have also been characterized by an extensive postauricular iliac region for a massive erector spinae, a long olecranon process, an anteriorly oriented trochea, a capitate head located mid-body, and a primitive central joint complex in the wrist. It would have featured a full wrist mortise with pisotriquetral contact and a moderately long midtarsus for fulcrumation on its metatarsal heads. It was presumably tailless (80).


3. **Extant African ape and hominid clade (GLCA).** Minor abbreviation of midtarsal length, elongation of manual phalanges, and shortening of posterior (lateral) metatarsus. Invagination of spine with posteralateralization of pectoral girdle, mediolateral proportionality shift of sacroiliac region, cranio-caudally shortened vertebral centra, and relocation of lumbar transverse processes to corporeal/epacromial junction or onto pedicle. Abbreviation of olecranon and elevation of lateral margin of trochea. Ulnar withdrawal with elimination of wrist mortise (i.e., loss of pisotriquetral contact) and deepening of carpal tunnel. Fusion of os centrale to scaphoid.

4. **Gorilla clade.** Elongation of forelimb (by disproportionate elongation of humerus) and abbreviation of hindlimb (global change in limb proportions), moderate elongation of posterior (medial) metacarpus, moderate shortening of manual phalanges. Abbreviation of lumbar vertebral column (average 3.5 elements) by means of sacralization of lumbar and reduction in axial length by one segment (58). Entrapment of most caudal lumbers by articulation with cranially extended ilia and reduction in breadth of sacral ala. Moderate increase in cranial orientation of scapular spine and glenoid plane, reduction of deltopleural crest. Retroflexion of ulnar trocheal notch with attendant abbreviation of olecranon process, expansion of long digital flexor (emergence of “flexion tubercle” on ulna), subduction or gracilization of long flexor tendon of thumb to expanded long digital flexor, increased osseo-ligamentous resistance to torque in CJC via distal prolongation of the volar portion of the capitae with corresponding evagination of the Mc3 base (creating a mediolateral block-to-joint rotation by novel abutment of Mc2 and Mc3), dorsalization and enlargement of capitae head, frequent formation of prepollex (62) on trapezium, anterior relocation of collateral ligament attachments of metacarpophalangeal joints (with simultaneous expansion of attachment facets on metacarpals), expansion of metacarpal heads, reduced capacity for dorsiflexion in midcarpal joint. Introduction of lateral spiral pilaster with loss of third trochanter, elimination of os pereonale complex and substantial shortening of midtarsus, especially proximomedial abbreviation of navicular and cuboid, and abbreviation of dorso-palmar dimensions of metatarsal bases. Gracilization of plantar aponeurosis with loss of plantaris and reduction/elimination of quadratus plantae.

5. **Basal chimpanzee/bonobo clade.** Abbreviation of forelimb and abbreviation of hindlimb (global change in limb proportions) but less extreme than in 4. Substantial elongation of posterior (medial) metacarpus and further elongation of manual phalanges. Chimpanzees exhibit higher intermembral index than bonobos and are probably derived in this regard. Abbreviation of lumbar vertebral column (three or four elements) by transformation of vertebral type and/or reduction in axial length by one segment [chimpanzees and bonobos differ substantially in number of axial elements, and bonobo is clearly primitive in this regard (58)]. Entrapment of most caudal lumbers by articulation with cranially extended ilia and reduction in breadth of sacral ala. Further immobilization by novel lumbo-inguinal ligaments (61). Elongation of iliac ischium. Dramatic mediolateral narrowing of scapula, marked increase in cranial orientation of scapular spine and glenoid plane, reduction of deltopleural crest (intermuscular fusion). Retroflexion of ulnar trocheal notch with attendant abbreviation of olecranon process, expansion of long digital flexor (emergence of “flexion tubercle” on ulna), subduction or gracilization of long flexor tendon of thumb to expanded long digital flexor, increased osseo-ligamentous resistance to torque in CJC via distal prolongation of the volar portion of the capitae with corresponding evagination of the Mc3 base (creating a mediolateral block to joint rotation by novel abutment of Mc2 and Mc3), dorsalization and enlargement of capitae head, elimination of mobility in hamate/Mc4/Mc5 joint, possible gracilization of Mc1, reduced capacity for dorsiflexion in midcarpal joint, reduction and anterior relocation of collateral ligament “grooves” of metacarpophalangeal joints (but expansion of attachment facets on metacarpals), expansion of metacarpal heads. Introduction of lateral spiral pilaster with loss of third trochanter, elimination of os pereonale complex and substantial shortening of midtarsus, especially proximomedial abbreviation of navicular and cuboid, abbreviation of dorso-palmar dimensions of metatarsal bases. Gracilization of plantar aponeurosis with loss of plantaris and reduction/elimination of quadratus plantae.

6. **Hominid clade, Late Miocene.** Substantial supero-inferior abbreviation of iliac ischium and pubic symphysis. Increased sagittal orientation and mediolateral broadening of ilium with novel growth plate for anterior inferior iliac spine, introduction of slight (obtuse) greater sciatic notch, (infurred) facultative lumbar lordosis, probable broadening of sacral alae to free most caudal lumbar for lordosis. Possible increased size and robusticity of fibularis longus, increased robusticity of second metatarsal base/shaft and doming of dorsal metatarsal heads related to toe-off.

7. **Hominid clade, Mid-Miocene.** Shortening of ischial length and angulation of ischiocentral tuberosity, further mediolateral expansion of iliac fossa with introduction of substantial (acute) greater sciatic notch, further invagination of lumbar vertebral column and fixation of lordosis (no longer facultative). Reduction of thoracic column from 13 to 12 elements associated with reduction in axial length by one segment [or this occurred at 6 (58)]. Elongation of pubic rami and femoral neck. Posterior relocation of third trochanter and emergence of true hypotrochanteric fossa. Elevation of quadriceps attachments to form “true” linea aspera, signaling fundamental shift in knee extensor/hip extensor proportions conducive to primary propulsion by quadriceps. Probable emergence of subischial dominant knee and transverse ischiopubic plate (or these occurred at 6). Expansion of fibularis longus attachment to include markedly remodeled medial cuneiform and permanent addition of great toe, elevation of sustentaculum tali to create mediolateral and longitudinal planter arches, likely development of “spring ligament,” marked inflation of calcaneal tuber (with secondary introduction of distinct lateral plantar process) for energy absorption at heel strike, gracilization of second metatarsal base, relocation of fibularis longus tendon to more proximo-planter location (with inferred attendant change in short and long plantar ligaments [see 47]) to support novel transverse arch during toe-off and foot-flat, introduction of “dual phase” metatarsofalucrumation (addition of transverse axis to oblique axis of fulcrumation). Dorsalization and expansion of capitae head and broadening of trapezoid for greater palmar span, slight dorsalization in reduction mobility of Mc5/hamate joint, anterior relocation and near elimination of collateral ligament “grooves” for metacarpophalangeal joint.

8. **Hominid clade, Plio-Pleistocene.** Elongation of lower limb, global modification of pelvis to expand birth canal (late) including abbreviation of femoral neck and pubic rami. Reduction of modal lumbar column by one (from six to five typically by sacralization of most caudal lumbar). Slight reduction in glenoid angulation of scapula, increased robusticity of thumb, transfer of styloid body from capitae to third metacarpal, palmar rotation of hamulus, loss of growth plate from pisiform, increased robusticity of terminal phalangeal tufts in carpus. Substantial abbreviation of posterior metacarpus, antebrachium, and carpal phalanges. Substantial anteroposterior thickening of navicular and length and eccentricity of calcaneal process of cuboid. Increased robusticity of MTJ. Reduction in frequency of calcification of os peroneum, abbreviation of tarsal phalanges—especially intermediates.
Ardipithecus ramidus fossils. Contemporary morphogenetics now show that organisms as diverse as sticklebacks and fruit flies can display remarkable parallel evolution merely because they share fundamentally similar genomic toolkits (73, 74). Knuckle-walking in chimpanzees and gorillas appears now to be yet one more example of this phenomenon.

In retrospect, it is impressive that the straightforward cogency of Schultz and the detailed dissections of Straus more accurately predicted the early course of human evolution than the more objective quantitative and technologically enhanced approaches heralded in the last quarter of the 20th century. Recent work in genetics and developmental biology has identified fundamental mechanisms by which morphological structures emerge during evolution. In the study of fossils, such insights have had their primary value as heuristic guides with which to construct and test hypotheses. Understanding the morphogenesis underlying profound shifts in the hominoid bauplan evidenced by A. ramidus may take years, perhaps even decades, but is likely to further transform our understanding of human natural history.

Ardipithecus has thus illuminated not only our own ancestry, but also that of our closest living relatives. It therefore serves as further confirmation of Darwin’s prescience: that we are not only one terminal twig in the tree of life, and that our own fossil record will provide revealing and unexpected insights into the evolutionary emergence not only of ourselves, but also of our closest neighbors in its crown.

References and Notes
18. N. Patterson, D. J. Richter, S. Greene, E. S. Lander, D. Reich, Nature 441, 1103 (2006).
39. P. troglodytes and P. paniscus differ in a number of skeletal proportions and characters (75, 76). Our sample of Pan was limited to P. troglodytes, and our use of the genus nomen Pan herein refers only to P. troglodytes, except where otherwise noted.
49. The trait nomenclature system used here is taken from M. A. McCollum, M. Selby, and B. A. Rosenman for aid in data collection and exceptionally helpful discussions.

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