# 3

# African Roots

## CHAPTER OVERVIEW

Though human beings are distinguished by large brains, great intelligence, and a reliance on culture, fossil evidence shows that large brains were not characteristic of our earliest ancestors. The first steps of the hominid family were literal first steps; walking on two, rather than four feet, was what differentiated them from the apes.

The oldest members of the human family date to more than 6 million years ago, about the time our ancestors diverged from those of the modern apes. The different names we have assigned to these specimens—*Sahelanthropus*, *Ardipithecus*, *Orrorin* and, after 4 million years ago, several varieties of *Australopithcus*—reflect actual physical differences as well as modern arguments about what those differences mean. These creatures share in common the fact that their brains were no larger than those of modern chimpanzees. What they all also seem to share is a skeletal anatomy suited to walking on two feet.

A fork in the hominid road appears about 2.5 million years ago, when a new hominid form is seen in the fossil record. Along with an anatomy suited to upright walking, *Homo habilis* had a brain size beyond the range of the apes and exhibited a greater reliance on culture as seen in the production of stone tools. *Homo habilis* and some of the Australopithecines were contemporaries. While the latter were highly specialized and became extinct, the former are directly ancestral to modern humanity.

## Prelude

### Chapter Sites



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Between running shoes, flip-flops, Uggs, hiking boots, cowboy boots, tennis sneakers, Crocs, Clogs, and a host of other kinds of popular footwear, not many of us walk around in our bare feet all that much, at least not outside. We usually enclose our feet in footwear with hard soles, and we walk on even harder pavement. Walking barefoot on the soft sand of a beach, however, reminds us of the natural process of two-legged walking initiated by our ancestors beginning more than 6 million years ago.

Barefoot, walking is no longer a matter of two flat slabs of leather or rubber or some synthetic material, alternately clomping down on the pavement. Instead, we can sense our feet actually interacting with the earth, gripping into the soil beneath them, pushing us forward in our desire to get from here to there.

In the instant of each step, our heel strikes first, leaving deep impressions as the sand compresses beneath our weight, all of it focused on that small point at the heel. Then the foot rolls forward, the arch lightly curving over the sand, leaving a thin, sharp indentation with the side of the sole. Next, all in a fraction of a second, we rock up onto the balls of our feet, thrusting our center of gravity forward, as we push our alternate leg in front of us. Finally, our toes push down, gripping into the earth, with sand squishing up between and around them, as we propel our bodies forward, ready to catch ourselves in the next step with the other foot.

I remember in particular one time when I walked on a beach with my then 6-year-old son, Josh, and glanced back at our two sets of footprints, one big, one small, as the waves began the inevitable process of erasing them from the sand. Our disappearing trail of footprints reminded me of another such trail, made in a far distant time by two people who passed together across a landscape far different from the Cape Cod beach where my son and I walked. Those footprints, however, were not erased by the tide or blown away by the wind. Those prints, left in a fine volcanic ash on an East African plain in a place called Laetoli, in the modern nation of Tanzania, were preserved, allowing us in the present to examine the way our most ancient ancestors walked (Hay and M. Leakey 1982; M. Leakey and Hay 1979; T. D. White and Suwa 1987).

That these footprints have been preserved is remarkable in itself. The conditions and sequence of events had to be perfect. First, a thin ash layer was deposited about 20 km (a little more than 12 mi) away from an erupting volcano. Soon after, a mild rain fell, turning the ash into the consistency of wet cement. Immediately following this, and before the ash had hardened, two people , and then a third, walked across its surface, leaving their footprints in the still-damp ash. Then the sun came out just in time to dry the ash bed to the hardness of rock before another rainfall might wash it all away. Finally, another ash layer fell, covering the footprint trail and protecting it from the natural erosion that might otherwise have destroyed it. Without any of these steps, the Laetoli footprints would have been as temporary at the footprints little Josh and I left on the beach at Cape Cod. Even ordinarily impassive scientists have characterized the preservation of the 23-meter (about 75-ft) Laetoli trails as "miraculous" (Johanson and Edey 1981).

Those footprints were found more than 3.5 million years after the people, possibly a child and an adult, or perhaps it was a large adult male and a smaller adult female, strode across the surface (R. Leakey and Lewin 1992; Figure 3.1).

We will never know their names or why they were walking, apparently in cadence and, perhaps, giving our imagination free rein, arm in arm across the ash bed (Figure 3.2). Yet, in taking those steps, they achieved a kind of immortality. Perhaps most remarkably, their footprints show that those anonymous folk, whose life journey occurred so many years ago, walked in a fashion that is nearly indistinguishable from the way modern humans walk (Charteris, Wall, and Nottrodt 1981; Day and Wickens 1980; White 1980; White and Suwa 1987). There are no impressions of the knuckles of a quadrupedal ape, no thumb-like big toes. Their footprints are our footprints. Those people were among the earliest **hominins,** with whom all living people share a temporally distant but

▲ **Figure 3.1**

On the left, the Laetoli trackway; the fossilized footprints of at least two human ancestors who walked in a remarkably modern fashion. On the right is the recent trackway of an anthropologist and his 6-year-old son. Though separated in time by more than 3.5 million years, the two sets of footprints clearly show the remarkable continuity of bipedal locomotion in the hominid family. (John Readers/SPL/Photo Researchers, Inc.; K. L. Feder)

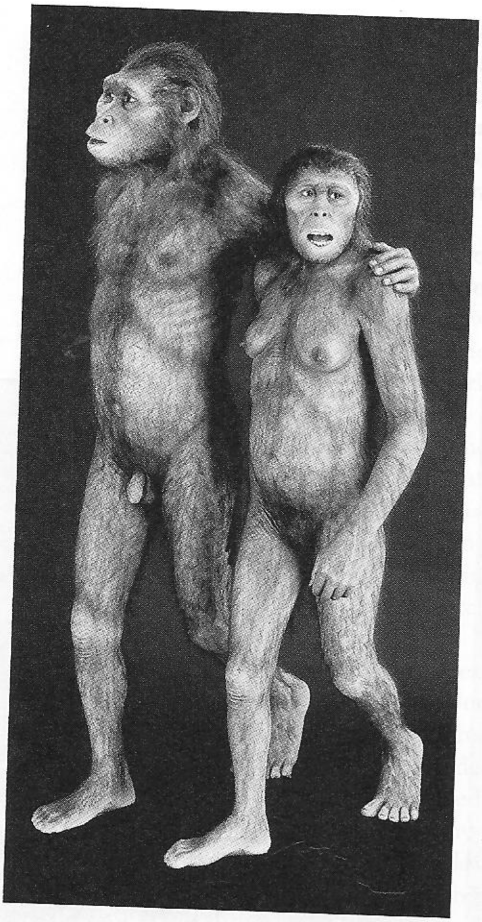


**Figure 3.2**
Based on a careful analysis of their preserved footprints as well as skeletal remains of hominids that lived at the same time, artists have produced models of the human ancestors who left their trail at Laetoli, Tanzania. (Neg. #4744[5]. Photo by D. Finnin/C. Chesek. Courtesy Department of Library Services, American Museum of Natural History)

biologically intimate connection. This chapter is about the first people and the world in which they lived.

## Chronicle

You are sitting down in a darkened movie theater. You've got your popcorn and soda, the ads and previews have just finished, and the main feature begins, a 2-hour movie representing the history of the universe. The very first moment of the film represents the first instant of the beginning of everything, the event cosmologists call "the Big Bang."

Here's the key to understanding the point of this exercise; in our imaginary movie, everything happens proportionally to when it actually happened in the history of the universe. Get it? In such a movie, the earth does not even form until more than 80 minutes after the first flash on the screen and the first living things—just single-celled organisms—don't make their appearance until about 90 minutes into the film. Dinosaurs briefly flash across the screen, and not until the 118-minute mark. The first of the apes do not appear until 119 minutes 50 seconds after the 120-minute-long movie began, and, finally, the earliest members of the human family do not appear until 1 hour 59 minutes 57 seconds into our metaphorical 2-hour movie. The entire human story, from our first upright walking ancestor to this moment, right now, is contained in just the final

*3 seconds* of the film! Though this period may not seem very important from a universal perspective, in human terms we are talking about more than 6 million years, or 300,000 generations of human ancestors (at 20 years per generation). These metaphorical final 3 seconds of the film are the focus of paleoanthropologists and archaeologists.

## Miocene Preface

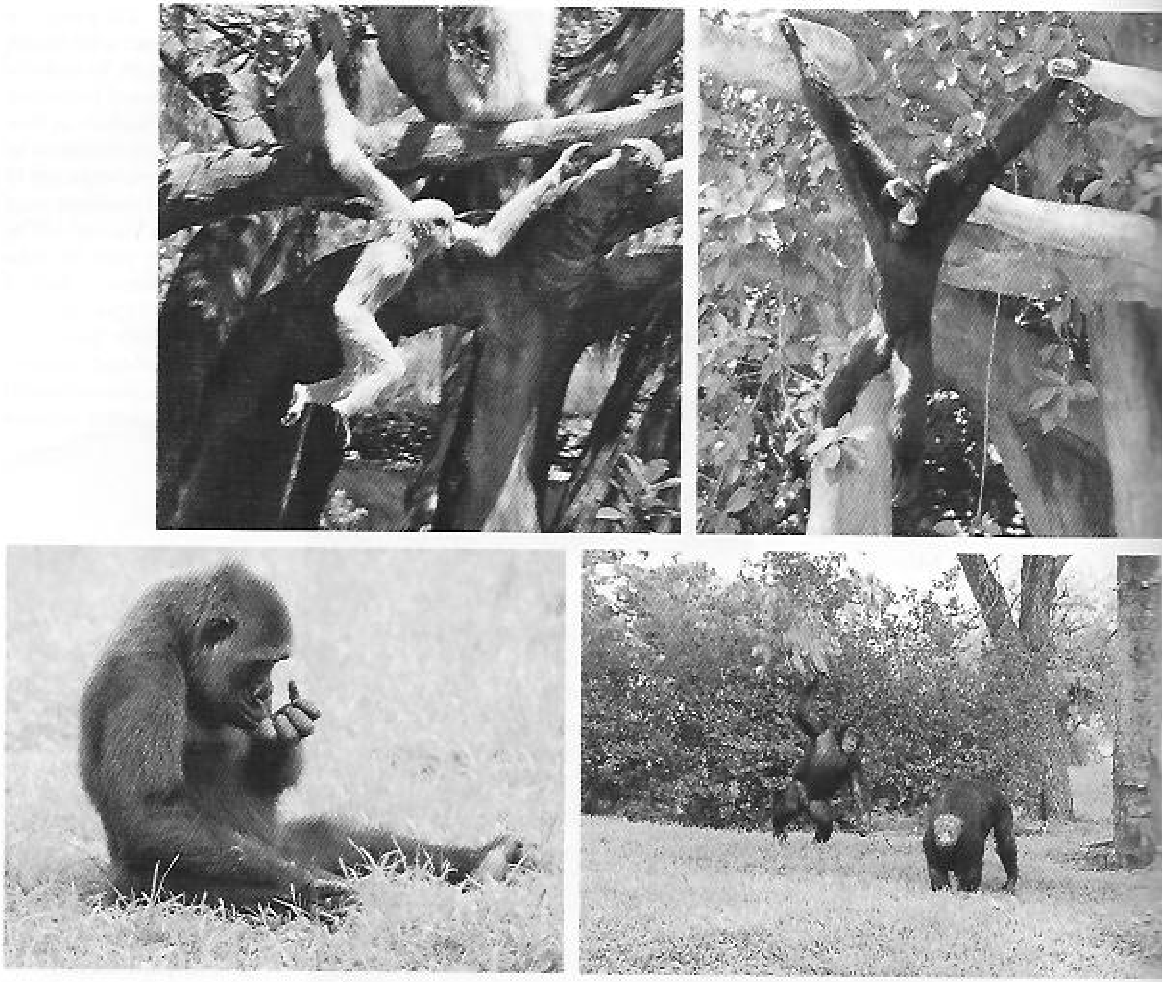
Let's go back to look at the world at the 119-minute 50-second mark in the movie, when our nearest living nonhuman relatives first make their appearance. The world of this period, called the **Miocene** (from about 23 million to 5 million years ago; Figure 3.3), is one we can scarcely imagine. During this epoch, our planet was a matchless place for forest-dwelling creatures, and many ape species evolved to fill the varied **niches** offered by this rich world. Places that today are covered with grassland, prairie, and agricultural crops were then fertile forests, populated by an astounding bestiary of tree-loving species.

### Fossil Apes of the Miocene

Primatologists now estimate that there were more than forty varieties—technically, **genera**—of apes living during the Miocene. Each genus (that's the singular for genera) encompassed multiple species; there are more than 100 ape species recognized and defined for this time (Begun 2003). Compare this situation to the present, with our paltry assemblage of only three genera of large or "great" apes divided into four species (chimp, bonobo, gorilla, and orangutan) and a single genus of the small or "lesser" apes divided into nine species of gibbons and siamangs (Figure 3.4). The Miocene was a time when apes flourished.

| Era | Period | Epoch | Million years ago |
|---|---|---|---|
| Cenozoic | Quaternary | Holocene | 0.01 |
| | | Pleistocene | 2.6 |
| | Tertiary | Pliocene | 5 |
| | | Miocene | 23 |
| | | Oligocene | 38 |
| | | Eocene | 55 |
| | | Paleocene | 65 |
| Mesozoic | Cretaceous | | 135 |
| | Jurassic | | 190 |
| | Triassic | | 225 |
| Paleozoic | Permian | | 270 |
| | Carboniferous | | 345 |
| | Devonian | | 400 |
| | Silurian | | 425 |
| | Ordovician | | 500 |
| | Cambrian | | 600 |
| Precambrian | Proterozoic | | 1,000 |
| | Archeozoic | | 3,000 |
| | Azoic | | 4,600 |

**Figure 3.3** Humans appear extremely late on this standard time scale for earth history. The earliest hominins date to the end of the Miocene.



▲ **Figure 3.4**
A plethora of primates: a gibbon (upper left); a siamang (upper right); a contemplative gorilla (lower left); a branch-wielding chimpanzee (lower right). (K. L. Feder)

## Why the Study of Apes Is Relevant to the Study of Humanity

We are not descended from chimps, bonobos, gorillas, or orangutans. We did not evolve from them. In fact, they have been evolving separately from us for as long as we have been evolving separately from them. But we share with them a common ancestor. Our evolutionary connection is apparent in our appearance, our behavior, as well as in our genes. Human and chimp DNA, in particular, are amazingly similar. In fact, a comparison of modern human, chimp, and gorilla DNA found that human beings and chimps are more similar to each other than either humans or chimps are to gorillas (Wildman, Grossman, and Goodman 2001). Figure 3.5, based in part on DNA evidence, presents a general **phylogeny** for the fossil and modern apes, showing how we currently conceive of their evolutionary relationships. The figure also shows how we view the human position on this phylogeny, and we focus our energies on that branch in the rest of this book.

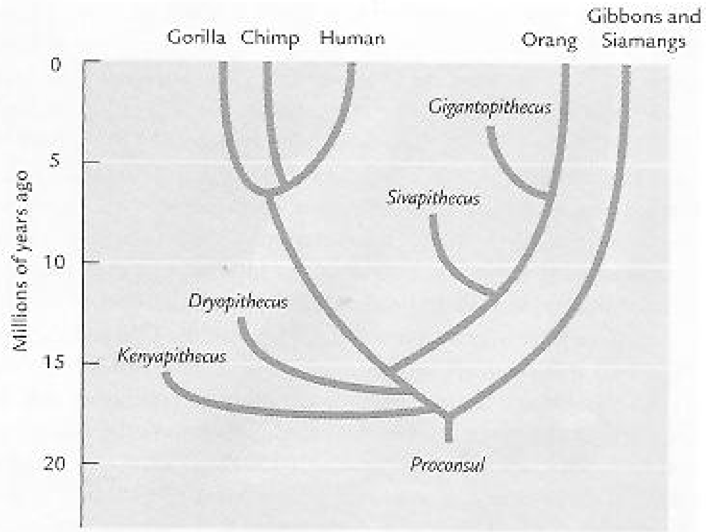



Figure 3.5
A simplified phyolgeny for apes and humans based on the fossil record.

By studying modern apes in a natural setting, primatologists hope to catch glimpses of behaviors the apes share with us: A chimp infant runs to its mother when it is frightened, and two adults embrace and pat each other's backs; chimps live in tightly knit social groups, make and use tools and different geographic groups of chimps make different kinds of tools; and chimps occasionally walk on two feet while carrying objects in their hands. In these shared elements we likely are recognizing behaviors we have inherited from a common ancestor who lived more than 6 million years ago and from whom both chimpanzees and humans descended.

## What Happened to the Apes at the End of the Miocene?

Today, the surviving ape species are threatened with extinction as a result of habitat destruction at the hands of humanity. As the tropical forests of Africa and Asia that are home to the apes are cleared for agriculture to support a burgeoning human population, the apes are pushed into smaller and smaller enclaves. Without a concerted effort by our species—the same species that is responsible for their current precarious position—our nearest living evolutionary relatives may become extinct except in zoos and animal parks.

At the end of the Miocene, the many species of apes that are represented in the fossil record also faced extinction, but not by any human agency; our direct ancestors had not yet evolved. Instead, a natural environmental change began to shrink the rich forest world. Large areas of the extensive forest lands began to contract sometime during the middle or late Miocene, to be replaced largely by grasslands, or **savannas,** by the beginning of the next epoch, the **Pliocene,** about 5 million years ago. And with the contraction of the forests, most of the ape species that had thrived there became extinct.

There is direct evidence to support this scenario. Remember the discussion in Chapter 2 about how most tree species are C3 photosynthesis pathway plants, which tend to select against the $^{13}C$ isoptope of carbon. As a result, when a region, continent, or even the world is dominated by the C3 photosynthesis pathway, $^{13}C$

levels in the soil, in the bones of animals that eat plant by-products, and in the bones of the animals that eat the animals that eat the plants all tend to have lower levels of $^{13}C$ than they do in times when C4 photosynthesis pathway plants—grasses and sedges—dominate (60 percent of C4 species are grasses; Edwards et al. 2010). Thure Cerling, Yang Wang, and Jay Quade (1993) have shown that soils and fossil teeth in south-central Asia (Pakistan) and North America (the western United States) exhibit a simultaneous, dramatic increase between 7 million and 5 million years ago in their concentration of the $^{13}C$ **isotope** (variety) of the element carbon (Figure 3.6). This dramatic increase in $^{13}C$ concentration at the end of the Miocene in soils and animal teeth is an indication of "a rapid expansion of C4 biomass [that is, grasses and sedges] in both the Old and the New World starting 7 to 5 million years ago" (Cerling et al. 1993:334). Recent research has only served to reinforce the apparent magnitude and rapidity of this shift from C3 to C4 plants at this time; it is characterized, for example, by biologist Erika Edwards and her colleagues (Edwards et al. 2010:588) as "explosive and broadly synchronous." In other words, the end of the Miocene is marked by a dramatic, worldwide contraction of forests and their replacement by grasslands. Habitat for forest dwelling species like apes decreased, and many ape species became extinct at this time.

## The Irony of Extinction

Almost certainly, those few ape species that survived the terminal Miocene possessed some characteristics that, by chance, gave them an advantage in the very different world that was establishing itself. Perhaps it was their remarkable ability for **brachiation** that ensured the survival of the ancestors of today's gibbons and siamangs when forests were shrinking and competition for remaining space was fierce. Maybe it was the strength, size, intelligence, and social systems of the

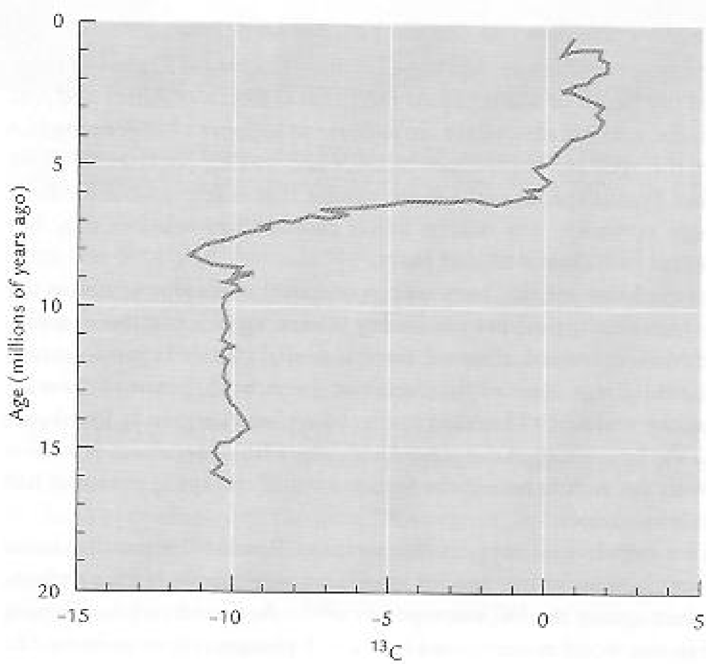



**Figure 3.6** Graph showing the dramatic proportional increase of $^{13}C$ in fossil teeth and soils at the end of the Miocene. Reflecting an expansion of grasslands at the expense of the forests, this probably explains why an arboreal animal family like the apes experienced a wave of extinctions at the end of the Miocene. (From Cerling, Yang, and Quade 1993)

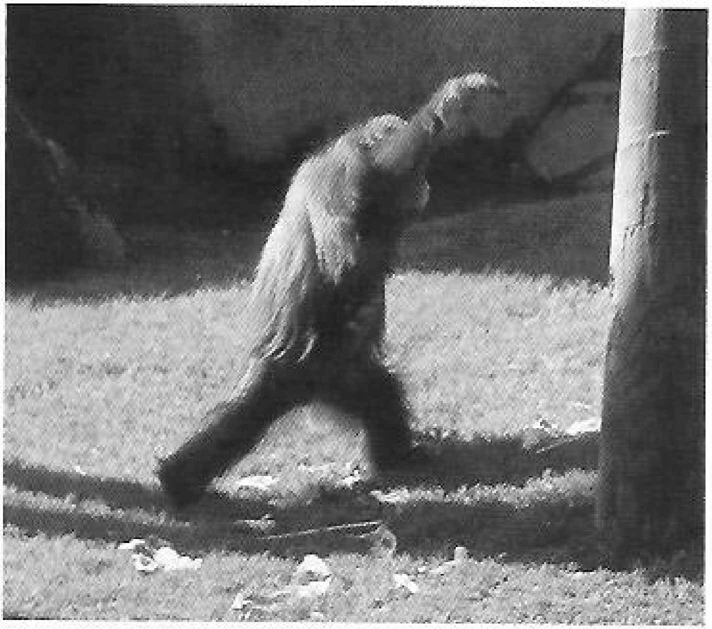


Figure 3.7
This orangutan is seen walking on two feet. Apes possess the capacity for bipedal locomotion, and they will employ that capacity when it suits them, for example, when they need to carry something. But they aren't very efficient at it. It isn't until about 6 million years ago that we see fossil evidence for a skeletal configuration well suited to bipedal locomotion. (K. L. Feder)

ancestors of modern gorillas that allowed for their survival. The intelligence and behavioral flexibility of the ancestors of chimps and bonobos probably provided them with an advantage as the myriad Miocene ape species vied for space in the diminishing forests of 7 million years ago. The modern apes are the descendants of the survivors in this evolutionary struggle. The losers were those who, at the end of the Miocene, found themselves pushed into an alien habitat in which their physical and behavioral characteristics, honed by millions of years of evolution to life in a thick, humid forest, were useless.

All living apes can walk on two feet with varying degrees of success (Figure 3.7). But **bipedal locomotion** is inefficient and tiring for them; the bones and muscles of their hips and legs simply are not compatible with that form of locomotion. The same was probably true for the apes of the Miocene. But at least one and possibly several Miocene ape species could stand up and walk on two legs better than the others. While providing some minor advantages in the forests—and some of their habitats included a **mosaic** of forest and grassland—this ability was particularly valuable as grasslands expanded and replaced the Miocene woodlands. Natural selection, as discussed in Chapter 1, feeds on variability. The nascent ability for upright locomotion within one or more Miocene ape species provided natural selection with the raw material needed to produce a creature fully capable of bipedal locomotion, one that habitually and efficiently walked on two feet. The species that had this ability was the first human ancestor.

## The First Hominins

The first bipeds did not suddenly develop at the end of the Miocene, the product of evolutionary forcing as grasslands replaced forest habitat rendering bipedal locomotion beneficial. They didn't evolve bipedality because they needed to in the grasslands; evolution does not work that way. Novel features are not made to order. Instead, the paleoenvironmental record of carbon isotopes, as well as plant and animal remains dating to the times and places in which our first upright ancestors lived, shows that they were already thriving as bipeds in mosaic environments at the end of the Miocene (Gibbons 2002).

It really was little more than luck that these apes already had the ability to efficiently and, perhaps, habitually walk on two legs. Perhaps because of their ability to walk upright, these apes were able to flourish at the end of the Miocene as the grasslands expanded at the expense of the forests while most other ape species could not. It is the fossil record of this turning point in human evolution that commands our attention here.

### Late Miocene Hominins

In numerous lectures delivered in my classes back in the 1970s and 1980s, I had to tell my students that the fossils simply hadn't been found to allow us to assess the nature of the divergence of our ancestors from those of modern apes. I always held out hope in those lectures, however, that at some point in the future the fossil gap would be filled. Fortunately, that time has come; and while, as yet, the picture is complicated, the fossil gap is beginning to be filled and the story of our earliest ancestors is starting to be resolved (Figure 3.8).

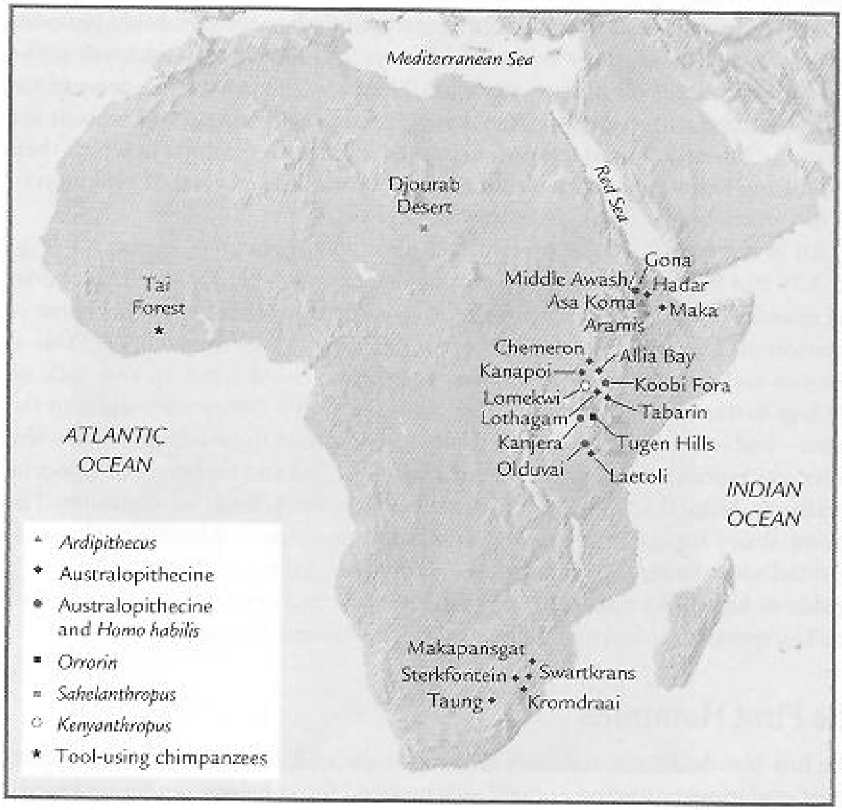



**Figure 3.8** Fossil localities of early hominins.

One of the most important discoveries related to the very early divergence of the hominin from the ape line is the fossil called *Sahelanthropus tchadensis*, found in the African nation of Chad. The original specimen consists of a spectacularly preserved **cranium.** Later, some mandibular and dental fragments from another, very similar individual were found nearby (Brunet et al 2005; Gibbons 2002). This hominin was nicknamed "Toumai" by its discoverers, and the fossil dates to more than 6 million and as much as 7 million years ago about the time, or soon after, when the C3 forests were being replaced by C4 grasslands.

Toumai's nearly complete cranium is about the size of a chimpanzee's, indicating that it possessed a chimp-sized brain (Figure 3.9). However, in the shape of the face, *Sahelanthropus* was decidedly unlike that of a chimp. A bottom of a chimpanzee face, like that of all the great apes, thrusts forward, presenting a profile with, essentially, a snout. *Sahelanthropus* is quite different in this regard, with a very flat face.

A virtual reconstruction of Toumai's skull based on computed tomography (CT) scans, similar to what you might have done at a medical lab or hospital, allowed for the detailed examination of thirty-nine cranial landmarks and then the accurate measurement of their spatial relationships, one to another (Zollikofer et al. 2005). The measurements determined from Toumai's CT scans were then compared to the same measurements performed on modern chimpanzees and gorillas, as well those calculated for a sample of ancient hominin skulls. Toumai's

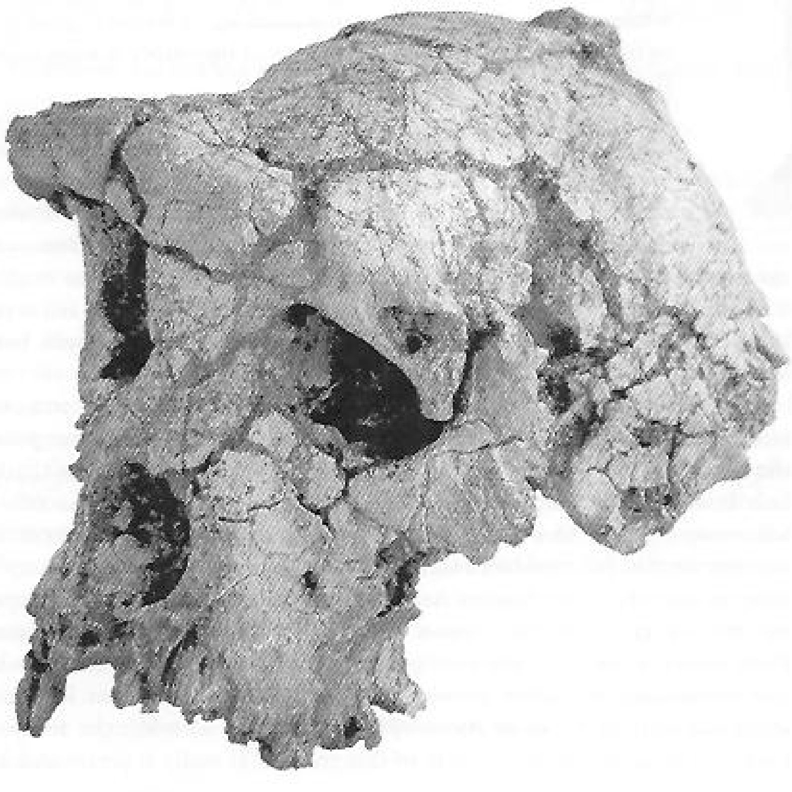
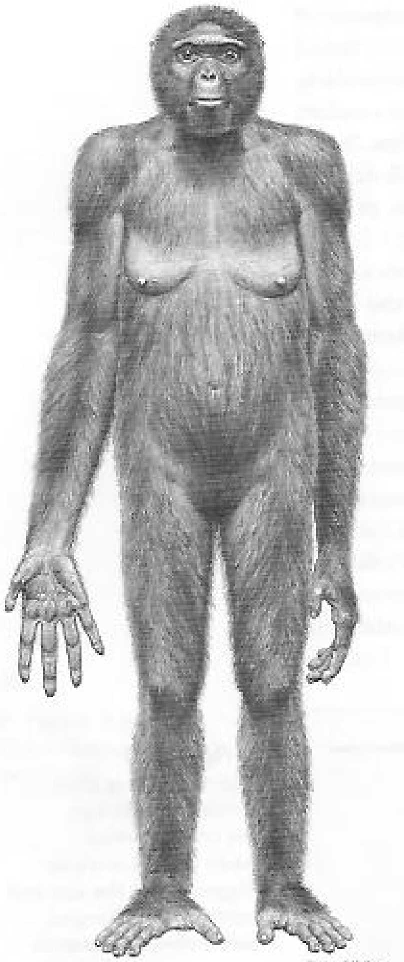


**Figure 3.9**
Dating to more than 6 million years ago, the crucial period when genetic analysis suggests that the ape and human lines diverged, *Sahelanthropus tchadensis* may represent the oldest hominid specimen yet discovered. This cranium was discovered in 2001. (© M.P.F.T)



▲ **Figure 3.10**
Artist's conception of *Ardipithecus*. (© 2008 Jay Matternes)

measurements fell firmly within the range of the hominins and outside of those computed for the apes. Further, at least one of the measurements, the angle between an imaginary line connecting the top and bottom of each of Toumai's eye orbits and another imaginary line drawn at the base of his cranium is perpendicular, just as it is in hominins as a result of their upright orientation. This further implies that Toumai was upright and, therefore, a hominin.

Though bones most directly reflective of locomotor patterns—those of the hips and legs—were not recovered, there is a strong indicator of upright posture in the well-preserved cranium. The position of its **foramen magnum** indicates that *Sahelanthropus* was upright as well. It is positioned not at the back but at the bottom of the cranium. This is another clear indication of upright posture and bipedal locomotion.

So is Toumai our direct ancestor? We can't say because it was not the only hominin living in Africa in the period between 7 and 4 million years ago. Another set of possible hominin bones, these from the Tugen Hills of northwestern Kenya, have been dated to before 5.7 million years ago and may be as much as 6.1 million years old (Aiello and Collard 2001). Called *Orrorin tugenensis* by its discoverers, its status as an early hominin is suggested by its teeth, but the primary evidence used to support this claim is the fragments of three femurs recovered in the excavation. The femurs were quite different from an ape's and, while not exactly like a modern human leg, it was very similar to that of later hominins where the evidence of bipedality is more substantial (Richmond and Jungers 2008).

Paleoanthropologists aren't that good about delayed gratification, so you can imagine how difficult it must have been for them for the last 15 years, waiting for a detailed publication with a series of articles discussing one of the most spectacular—and vexing—discoveries, that of thirty-six members of a 4.4-million-year-old species labeled by its excavators, *Ardipithecus ramidus* (T. D. White et al. 2009). The initial discovery was made in 1992 and now, 17 years later as I write this in early 2010, Ardi, as the most complete specimen is called, stands before us with her unexpected morphology (Figure 3.10).

To begin with, Ardi is literally "standing" before us; the shape and configuration of her pelvis as well as the position of her foramen magnum prove that she was definitely a biped which positions her toward the base of the human line. But Ardi is a complicated specimen, and this can be seen especially in the following features. To begin with, Ardi does not have a human-like hand; her thumbs are not positioned like ours, where we can easily touch the tip of our thumbs to each of our fingers. Ardi couldn't do that; she lacks the "opposability" that characterizes the human capacity for fine and precise manipulation. Even odder, however, is the configuration of Ardi's feet. Even though she was, like us and like our other hominin ancestors, bipedal, her feet look nothing at all like ours or those of *Australopithecus afarensis* who left the footprints at Laetoli mentioned in the prelude of this chapter. It really is pretty shocking to paleoanthropologists; Ardi's feet look like an ape's, with a large and divergent big toe, the characteristic that makes an ape's foot resemble the human hand rather than our foot. But however different Ardi's feet may have been from ours, she walked on two of them like we do, and not on all fours like the living apes.

In the opinion of geologist Thure Cerling and his colleagues (Cerling et al. 2010), Ardi walked bipedally in an early African savanna habitat. Based on the $^{13}C$ concentration his group calculated from Aramis soils and faunal remains, Cerling suggests that Ardi lived in a place where between 40 and 60 percent of the vegetation consisted of C4 biomass, reflecting what is today called a "tree-bush" or "open savanna" (Cerling et al. 2010:1105d). Ardi's locomotor morphology combined with the $^{13}C$ evidence supports the hypothesis that the replacement of forests by more open habitat after 8 million years ago is inextricably linked to the development of bipedality in our hominin ancestors.

A large team of researchers led by paleoanthropologist Tim White (White et al. 2009—he was also one of the key investigators of the Laetoli footprints)—has published a series of articles about *Ardipithecus* in a special October 2009 issue of *Science*. White and his colleagues believe that *Ardipithecus ramidus* is best explained as:

1. A creature at the base of the hominin line.
2. *Sahelanthropus* and *Orrorin* are probably other species of the same genus, *Ardipithecus*.
3. Ardi and her kind likely spent as much time in the trees as on the ground.
4. *Ardipithecus* did not live in a grassland habitat; its bipedal adaptation developed in an area characterized by woodland habitat.
5. *Ardipithecus* likely evolved into the earliest *Australopithecus* species.

In this scenario, chimps and gorillas diverged from the hominin line before the evolution of *Ardipithecus* and evolved quite separately from the hominins. This would mean that chimps and gorillas are not a very good model for what our human ancestors looked like; their high level of sexual dimorphism with large, aggressive males with substantial canine teeth used in competition with other males and their adaptation for quadrupedal knuckle walking were never a part of our hominin ancestry if *Ardipithecus* is at the base of our evolutionary line. *Ardipithecus* has generated a tremendous amount of interest and controversy. White and his colleagues have provided their colleagues with quite a bit to think about and much to assess. The period between 7 to 5 million years ago is still complicated with a host of hominins, any one of which might be directly ancestral to us. It is too early to determine the precise evolutionary relationships among the 7- to 5-million-year-old probable hominins discussed here. What is clear—and what is most important to understand—is that they all lived at a time soon after the human lineage diverged from that of the apes. Genetic analysis of human beings and chimps shows that we have been evolving separately for no more than about 7 million years. *Sahelanthropus, Orrorin*, and *Ardipithecus*, therefore, appear to be examples of what our ancestors looked like at the genesis of the human family.

## The Genus *Australopithecus*

Dating to sometime between 4.17 and 4.07 million years ago are the exciting discoveries made in Kanapoi and Allia Bay, Kenya, between 1995 and 1997 (M. G. Leakey et al. 1998). The twelve specimens from Allia Bay and the nine from Kanapoi, including teeth, cranial fragments, and some bones below the skull, have been assigned the species name *Australopithecus anamensis*.

The *anamensis* jaw fragments and fossil teeth are apelike, but an upper arm bone exhibits many humanlike features. In addition, and more significant, both ends of a tibia (shin bone) that were recovered are very humanlike; its discoverers identify this bone as clearly indicating bipedal locomotion nearly half a million years before the Laetoli footprints. The environment in which *Australopithecus anamensis* lived was characterized by open woodland or bushland conditions.

### *Australopithecus afarensis*

Far better known and with a far larger sample of remains is a later, somewhat less apelike form of the same genus, *Australopithecus afarensis*—most likely the creature that left the footprint trail described in this chapter's "Prelude." The great majority of these fossils date to the period from 4 million to 3 million years ago. The first *afarensis* fossils were found in the Afar geographical region of Ethiopia, at the site of Hadar (Figure 3.11), highlighted in this chapter's "Case Study Close-up" and the place where the famous *afarensis* fossil, Lucy, was found. Other *afarensis* specimens have been found including a very complete skeleton of a young child found in Dikika, Ethiopia (Alemseged et al. 2006).

Among the key elements of the *afarensis* skeleton that have been found and used to define the species are the pelvis, vertebrae, leg bones, fingers, feet, jaws, skull fragments, a nearly complete cranium, and teeth. Together, these skeletal elements allow us to paint a reliable picture of a creature that, beginning about 4 million years ago, was not becoming bipedal but already was fully upright (see this chapter's "Issues and Debates").

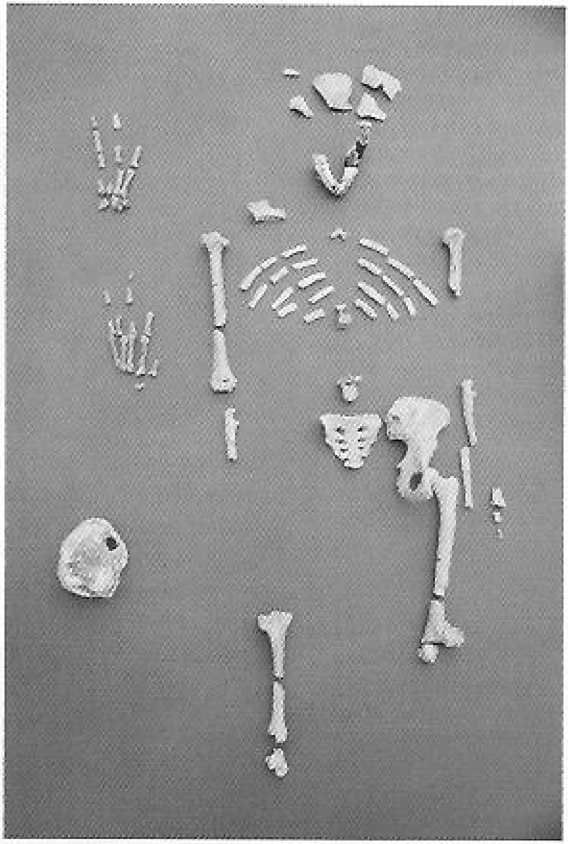
The **postcranial** skeleton (everything below the skull) of *afarensis* is diagnostic of a creature far more like a human than like an ape. The feet of *afarensis* were quite modern, lacking the divergent big toe of the apes and *Ardipithecus*. The ape's big toe is positioned on its foot just as our thumbs are positioned on our hands, allowing the ape to grasp objects with its feet (for example, to grasp tree branches when climbing) far better than we can. *Afarensis* possessed the feet of a walker, not those of a climber. Also, the pelvis was quite similar to ours and is easily distinguished from an ape's (see Figure 3.19); the configuration of the pelvis is an accurate indicator of a creature's mode of locomotion (see this chapter's "Issues and Debates"). Even in the case of the Dikika *afarensis* specimen, which is estimated to have been only 3 years old at the time of death, the bones of the legs and feet are quite human-like and indicate that *afarensis* was bipedal.

A computer simulation of *afarensis* locomotion tested various models, including a chimplike gait and a more fully upright, humanlike mode of walking (Crompton et al. 1998). Using the shapes of the preserved bones of Lucy in the computer simulation of *afarensis* locomotion, these researchers concluded that a humanlike gait was far more likely. Though Lucy certainly possessed some apelike characteristics, she walked on two feet, not clumsily like a chimp but efficiently like a modern human being. (See this chapter's "Case Study Close-up" for more on Lucy.)

Compared to human beings, the apes have proportionally very long arms in relation to their trunk and legs. Long, powerful arms allow the apes to climb or swing through trees as well as to walk quadrupedally on the ground. Human arms are, by comparison, short in relation to human legs; try walking on your hands and feet, and you will soon discover that it's pretty tedious; your legs are far too long and your arms are simply too short. Analysis of the proportions of upper and lower limbs in *afarensis* shows that in this respect as well the species was proportioned far more like modern humans than like apes (Shreeve 1996).

On the other hand, *afarensis* had not left its ape heritage behind entirely. In some specimens the finger bones were long and curved, like an ape's (Susman, Stern, and Jungers 1984). The one preserved finger bone of the Dikika child as well as a well-preserved shoulder blade (scapula) are more ape-like than human; this evidence may indicate that *afarensis* retained some of the **arboreal** ability of its ape ancestors at the same time that it walked bipedally on the ground.

All of the essentially human qualities of the postcranial skeleton of *Australopithecus afarensis* must be contrasted with the almost entirely apelike features of its skull, as exhibited in the nearly complete cranium discovered at Hadar (Kimbel et al. 1994). This cranium, labeled A.L. 444-2 by its excavators, is the most complete *afarensis* skull yet found. It dates to about 3 million years ago, making this specimen one of the youngest yet identified in the *afarensis* fossil species. In its overall form, A.L. 444-2 is certainly more apelike than any subsequent human ancestor, including other, later versions of *Australopithecus* we will discuss. Cranial capacity is apelike, in the range of 400 cc to 500 cc—about the size of a modern chimpanzee and about one-third the human mean for brain size. The upper portion of the face is small when compared to the lower part (as in apes), which is the opposite of the pattern in modern human beings. The jaws jut out and are snoutlike—they are said to be **prognathous**—just like those in an adult ape and again quite different from the relatively flat face of a modern human.



▲ **Figure 3.11**
Photograph of the 45% complete skeleton of the fossil known as Lucy: *Australopithecus afarensis*. Lucy and a series of thirteen other *afarensis* specimens have been dated to 3.18 million years ago. (© Alain Nogues/Sygma/Corbis)

The *afarensis* jaw presents a combination of apelike and humanlike features (Figure 3.12). Humans and apes have the same numbers and kinds of teeth: two incisors, one canine, two premolars, and three molars in each quadrant of the adult mouth. Human teeth, however, in both the upper jaw—the **maxilla**—and the lower jaw—the **mandible**—are positioned in a curving arch that expands to the rear of the mouth; ape teeth present a more boxlike appearance, with the premolars and molars set in nearly parallel rows perpendicular to the incisors. Also, apes have proportionally much larger canine teeth and a gap in the teeth of the opposing jaw to allow room for the large canines when the mouth is closed. This gap, or **diastema,** is not present in the human jaw; our canines are much smaller, and so no gap in the opposing jaw is needed. The *afarensis* jaw is not quite like an

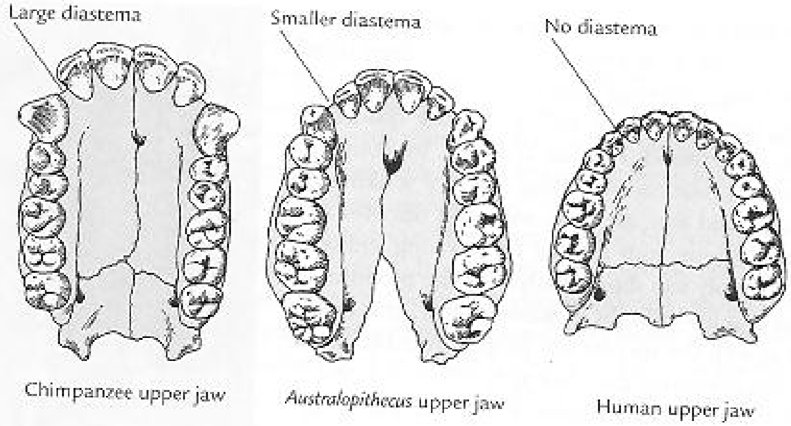



**Figure 3.12** Comparison of the maxillae (upper jaws) of chimps, *Australopithecus*, and modern human beings. The teeth in a chimp's mandible are arranged in a box-like pattern, while those of a modern human being form a curve or arch. (From *Lucy: The Beginnings of Humankind*. © 1981 Donald C. Johanson & Mitland A. Edey. Drawings © Luba Dmytryk Gudz)

ape jaw but not quite like a human jaw either. The configuration of the teeth is more like a box than an arch; there is a small diastema, and tooth size, including that of the canines, that is more apelike than human.

The evidence, then, is quite clear: *Australopithecus afarensis* seems to have been a bipedal ape living between 4 million and 3 million years ago. It looked like a chimpanzee standing on two short but otherwise humanlike legs, with no diverging big toe. What we share with *afarensis* is a mode of locomotion, but not a level of intelligence or a reliance on culture.

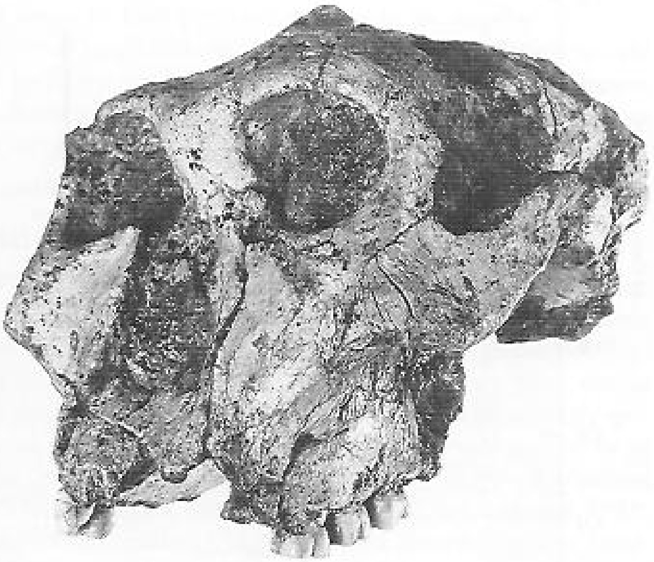
## A Fork in the Hominin Road

At about 3 million years ago, there is evidence of the evolution of a somewhat different form of hominin. We call these new fossils by the name *Australopithecus africanus*. Like its evolutionary progenitors, *africanus* was bipedal and still walked in an essentially modern human fashion. It also retained a basically apelike skull and brain. There are a number of fairly well preserved *africanus* crania, all apelike, with a sloping forehead and large ridges of bone above the eyes (Figure 3.13). On the other hand, the jaw and its teeth are a bit more humanlike and the face not so prognathous as that of *afarensis*, so in some ways it seems more human in appearance. Nevertheless, its brain size still falls into the range of that of the great apes.

*Australopithecus africanus* dates to no more than 3 million years ago and seems to fade out of the picture by about 2.2 million years ago. At that point, a larger bipedal form seems to have taken its place (Figure 3.14). Called *Paranthropus robustus*, it was a biped, and its brain size was a bit greater than in *africanus*. More significant is the difference in the cranial architecture of *robustus*: Where the top of the *africanus* skull is round and smooth, the top of the *robustus* skull sports a thin ridge of bone called a **sagittal crest**. Such a crest allows for a much larger, stronger temporalis muscle, which powers the movement of the mandible while chewing.

Interestingly, though the morphology of the *robustus* chewing apparatus appears to be specialized, analysis of the carbon isotopes in its teeth show a varied diet of both C3 and C4 foods (Sponheimer et al. 2006). In other words, though the teeth and jaws appear to be suited to chewing the tough seeds produced by tropical grasses (C4 plants), direct evidence of the carbon isotopes in the teeth indicate that soft leaves and fruits produced by trees and other C3 plants were an equally important part of the diet. The robust architecture of the chewing appa-

◄ **Figure 3.13**
Cranium of *Australopithecus africanus*, a lightly built or "gracile" *australopthecine* form that followed *afarensis* in southern Africa. *Africanus* flourished after 3 million years ago and appears to have become extinct by 2.2 million years ago. (Transvaal Museum, D. C. Panagos)



◄ **Figure 3.14**
Cranium and mandible of *Paranthropus robustus*. *Robustus* appears to have been a highly specialized hominid, with extremely powerful jaws adapted to processing a diet of hard, gritty foods. *Robustus* may have replaced *africanus*. It became extinct around 1 million years ago. (Transvaal Museum, D. C. Panagos)

ratus might have been an adaptation that allowed robustus to survive on only the tougher C4 plants when C3 foods were not available.

The *robustus* pattern of powerful cranial architecture is even more pronounced in another fossil hominin, *Paranthropus boisei*, whose specimens date from 2.2 million years ago to 1.4 million years ago, making it partially contemporaneous with *robustus* (Suwa et al. 1997). *Boisei* is different enough from *robustus* to warrant separate species status. In other words, there was more than one distinct hominin species living in Africa during the same period, a situation similar to the modern situation for **pongids**, in which there are two extant species of chimp (the common chimp and the bonobo).

## A Forest of Hominins

I am sorry that this all seems so complicated, with so many named species and so little to allow us to draw precise connections among them: which were directly ancestral to us, which were evolutionary dead ends, which were competing contemporaries, and which were members of the same evolutionary lines. I realize it can all seem quite daunting and, unfortunately, it is impossible to come to a definitive determination of how all the various fossil species discussed in this chapter—and others left undiscussed—were related to the lineage of modern human beings. Though a chronological chart can help you sort out when the various species lived (Figure 3.15), there is no nice, neat sequence we can come up

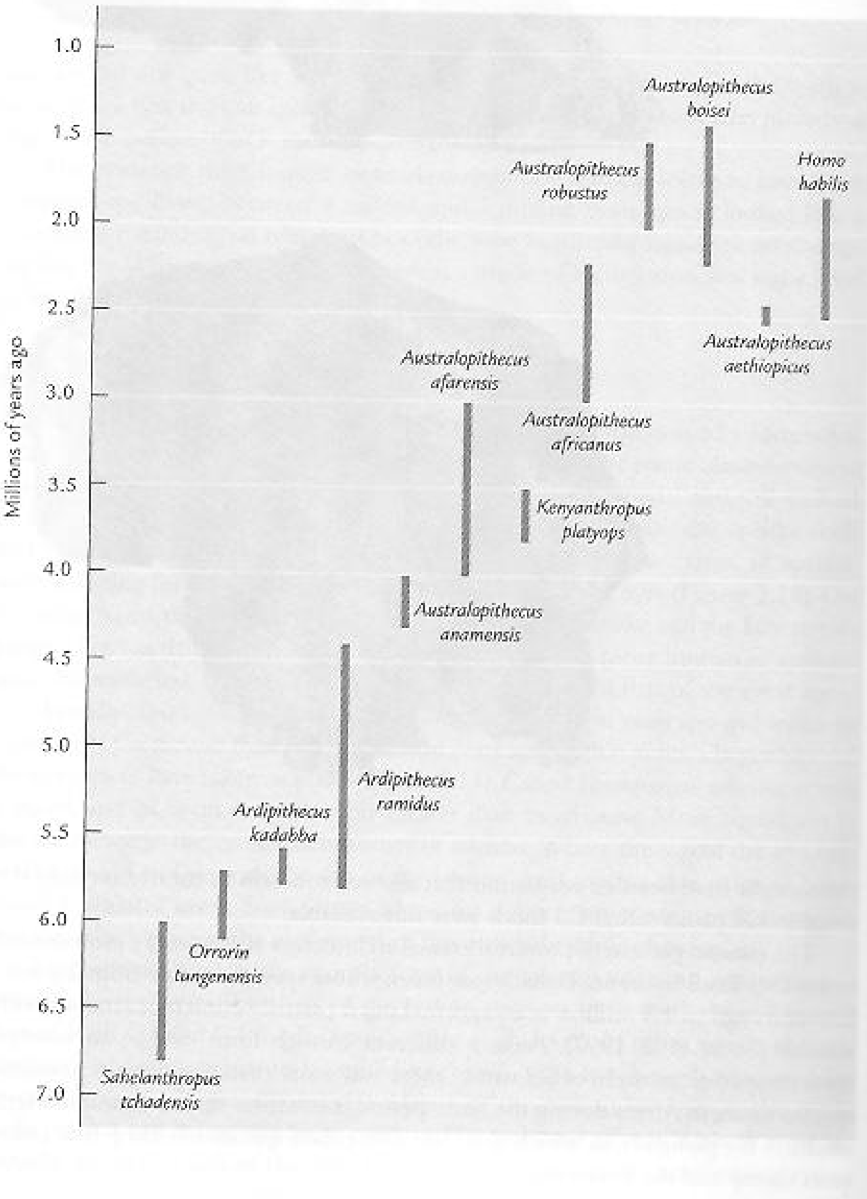



**Figure 3.15** This phylogeny shows the chronological relationships among the fossil hominins discussed in this chapter.

with that shows ancient hominins becoming continuously more modern looking in each of their characteristics through time, leading to individuals that look like modern people. In fact, it appears that there were a number of false starts and dead ends, creatures that were hominins but that became extinct, representing side branches on a densely thick evolutionary bush with modern human beings representing the only surviving branch. We simply don't have large enough samples of the different kinds of hominins that were alive in the period between 6 million and 2.5 million years ago to accurately determine which species faded into extinction and which species are directly ancestral to modern human beings. In all likelihood, there are additional extinct hominin species whose bones have not yet been found or recognized, and one or more of them might be more directly ancestral to us than most or even any of the species so far defined.

With all that is uncertain, a number of elements of the early story of the human family do seem clear. It appears that a number of somewhat different forms of upright-walking creatures with chimp-sized heads, a mix of humanlike and apelike teeth but with tantalizing evidence of a humanlike way of walking on two feet, existed beginning about 6 million years ago. They lived in a variety of environments and seem to have flourished where there was a mosaic of different habitats including forest and grassland. Their ability to walk on two feet and, perhaps, climb trees seems to have provided them with an adaptive advantage over many of the Miocene apes whose forests they shared. Some of these upright walkers that we call hominins also shared the fate of many of the Miocene apes and became extinct. But one of these hominins was a survivor in the evolutionary saga. Its progeny are the focus of the rest of this chapter.

## A Different Path—*Homo habilis*

Soon after 2.5 million years ago, and just as the **australopithecines** were experiencing great changes in their evolutionary pathway, another hominin seems to have branched off from the main line of the *Australopithecus* genus (see Figure 3.15). This breakaway group followed a different evolutionary route, one in which its survival on the African savanna was not the result of an increasingly specialized diet but, instead, was due to an increase in intelligence made possible by an expanding brain. This creature first appears in the fossil record about 2.4 million years ago (Bower 1993b, 1993c; Hill, Ward, and Brown 1992; Schrenk et al. 1993), a little before *africanus* became extinct, which makes it a contemporary of *Paranthropus robustus*. But this new form cannot be mistaken for any variety or form of *Australopithecus or Paranthropus*. With a much flatter face, a steeper forehead, and a larger brain—a mean size close to 700 cc, larger than any ape brain and just about one-half the modern human mean—this clearly is a new and different hominin. It is called *Homo habilis* (Figure 3.16).

Assigning them to the same genus as modern humans means that *Homo habilis* was much more like us than were any of the australopithecines or paranthropines. Whereas taxonomically *Homo sapiens* might live in the same general neighborhood as *Australopithecus* and *Paranthropus*, we live on the same street as *Homo habilis*. The skull of *Homo habilis* was not just larger than that of the australopithecines but was shaped differently as well, with significantly less prognathism, a taller,

▲ **Figure 3.16**
The cranial capacity of this fragmentary cranium shows that *Homo habilis* possessed a brain larger than any ape's. Dated at 2.4 million years ago, *habilis* represents the first hominid with an expanded brain.
(© National Museums of Kenya)

steeper forehead, and a more rounded profile. All of these features seem to presage modern human beings.

### The Ability to Make Tools

You might think that one of the key behavioral features that distinguishes people from other animals rests in our ability—and need—to use tools. In actuality, however, a number of animal species have been observed using tools in the wild. Sea otters will often grab a flat, smooth stone, rest it on their stomachs while they float on their backs in the water and use the stone as a sort of anvil on which they smash open shells for the seafood within. Woodpecker finches have been seen using cactus spines held in their beaks to probe for insects in tree bark. Some chimps use stones to hammer open nutshells to get at the nutmeat within, even placing the nuts on stone anvils to magnify the effect.

Some chimpanzees go beyond this, not only using tools but actually making them by physically modifying a raw material to a desired shape or form. For example, chimps will strip the bark off of twigs, which they then poke into termite mounds like fishing rods. The stripped twigs are wet and sticky, and termites will adhere to them. After pulling the twigs out of the mound, chimps eat the termites which they apparently think are a delicious treat (Goodall 1986). Central African chimps have been seen crafting wooden clubs to crack open beehives from which they then collect honey using twigs, sometimes using a complex array of as many as five separate tools—pounder, perforator, enlarger, collector, and swab—in a precise sequence in order to extract the honey (Bower 2009; McGrew 2010).

Though there is no direct evidence of such tool use among the Australopithecines, there is no reason to believe that they were not capable of similar work. It isn't until about 2.5 million years ago, however, that the first stone tools have been found in the archaeological record. The first appearance of these formally produced, consistently patterned stone tools closely coincides with the earliest appearance of *Homo habilis*, a species that possessed both the hand anatomy and the increased intelligence needed to carry out the sophisticated process of forethought and action in the production of permanent tools. In all likelihood, they were the makers of these first stone tools.

## Oldowan Technology

These oldest stone tools date back to about 2.6 million years ago at Gona, Ethiopia (Quade et al. 2004; Semaw et al. 1997). Tools like these were first recognized, defined, and described by the famous paleoanthropologist team of Louis and Mary Leakey (M. Leakey 1971). They called the tools **Oldowan,** after the place where they were first found and where the Leakeys had devoted so much of their research energy, Olduvai Gorge in Tanzania (Figure 3.17). The Leakeys originally defined Oldowan tools as a series of specifically shaped, sharpened rocks that served as chopping tools. Mary Leakey (1971) classified Oldowan choppers into a number of types based on shape and inferred function—cutting, chopping, scraping, and so forth. More recent work, however, by Nicholas Toth (1985) and Kathy Schick (Schick and Toth 1993) shows clearly that, though some of the "Oldowan choppers" may have been used as tools, the vast majority functioned as **cores** from which **flake** tools were produced.

**Figure 3.17** *Homo habilis* is also known to have been a tool producer. Here is a chopper from the Oldowan tradition of *Homo habilis*. (© Institute of Human Origins)

The maker of the tool, or the **knapper,** begins with a more or less spherical nodule of stone. Holding this **object piece** in one hand, the knapper strikes it with a **hammerstone,** usually a fortuitously shaped harder rock (or just one less likely to break as a result of its shape). Without much trouble, the knapper can knock a flake off the stone (Figure 3.18). Then the knapper turns the object piece around in his or her hand so the interior surface of the rock that was just exposed with the first hammerstone blow is facing up. Next, using that surface as a **striking platform,** the knapper strikes down on it with the hammerstone, thereby removing a stone flake from the opposite side of the object piece. Repeating this several times can produce a number of sharp, relatively straight-edged flakes useful for cutting, scraping, sawing, chopping, and the like. Microscopic analysis of a large collection of Oldowan flakes shows that many were used for these purposes (Keeley and Toth 1981; Toth 1985). The flakes exhibit a polish on their edges that is typically caused by cutting plant material, butchering animals, and woodworking. Stone flakes are sharper, stronger, and more durable than the teeth or nails nature provided our ancestors. Although one doesn't need to be a genius to figure out how to make stone tools, it does take what researcher John Gowlett calls an "appreciation of the properties of stone" (1986:251). Try it yourself (be careful and always wear eye protection) and you'll see how challenging it can be. It takes a while even for modern people with our much larger brains to get a feel for how how to break stone in a way that consistently results in the desired endproduct: sizeable, sharp-edged tool blanks. The production of Oldowan tools took some knowledge of the characteristics of different rocks, an understanding of their breakage patterns,

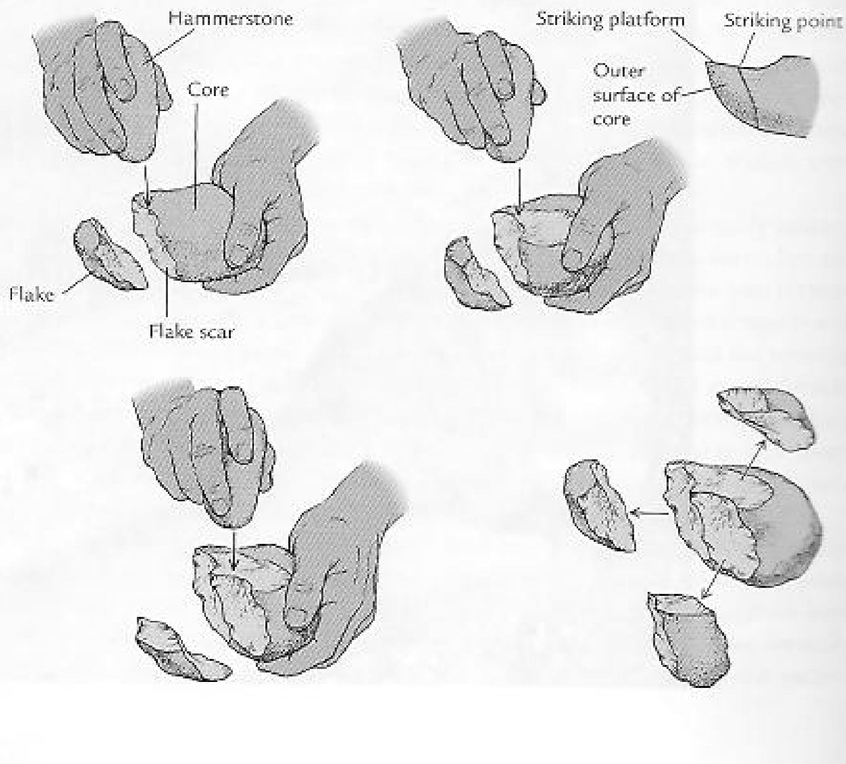



**Figure 3.18**
The process by which flakes were removed from a stone core in the Oldowan tradition. A nucleus of a hard stone was struck with another stone in just the right locations to allow for the removal of sharp, thin flakes. (From "The First Technology" by Nicholas Toth. Copyright 1987 by Scientific American, Inc. All rights reserved; drawing by Edward L. Hanson)

forethought in planning the sequence of blows, a bit of hand–eye coordination, and flexibility to change the planned sequence when problems cropped up. More fundamentally, this process takes enough intelligence to recognize that a round, dull rock can be transformed into a large number of straight, thin, sharp pieces of rock suitable for many different uses. Clearly, this is the thought process of an intelligent being.

I am certain that most of us would not know what kinds of rock would be useful in toolmaking, and we wouldn't know where to find any of it even if we did know the kinds that work best. In the experimental archaeology course I teach in which students learn about stone-tool technology by attempting to actually replicate stone tools, I instruct them to go off into the wilds of Connecticut and collect stones from which they think they might be able to produce sharp-edged stone blades. We won't talk about the one student who actually bought rocks at a local rock shop (the price tag was still on one of them). Most students return to the class with sandstone and schist and other rock types common in our region but that shatter or crumble when struck, producing no usable tools. The point is, it takes knowledge and experience to recognize rocks with the best qualities for making tools. There is a lithic learning curve, and *Homo habilis* was pretty far along on that curve.

The hominins at Gona selected the best stone in their territory, rock that fractures readily, regularly, and predictably to produce sharp, thin flakes. Flaking was not random but was done according to a sensible pattern of removal from a core. In fact, the Gona researchers propose that the 2.6-million-year-old tools found there almost certainly do not represent the first or even a very early attempt by these hominins to make stone tools. These researchers suggest that further study may likely reveal evidence of even older toolmaking, more representative of the initial experimentation performed by our ancestors as they literally invented stone toolmaking (Semaw et al. 1997).

To Schick and Toth (1993), the archaeological record at *Homo habilis* sites suggests quite a bit of forethought and planning in the manufacture of stone tools. In their view, Oldowan was not a simple or "expedient" technology in which tools were made haphazardly and only to fill an immediate need from whatever happened to be available. If this had been the case, then flakes and the cores from which they originated would all be found together where they were made and used, and they would have been produced from raw materials found nearby. But this is not the case. For example, stone tools found at the Kanjera South site in Kenya weren't made from the local limestone, from which sharp, durable tools cannot be made. Instead, the tools found at the site were made from far more durable raw materials from which sharp edges can be produced: quartzite and rhyolite. Those rock types were available no less than 13 kilometers distant from the site, implying quite a bit of planning and forethought by the tool makers, and not just a little bit of applied geological knowledge (Gibbons 2009c). The analysis of the wear patterns on stone tools to determine their uses was discussed in Chapter 2. The wear patterns present on the Kanjera South tools suggest their use in the processing of plant materials, perhaps in the cutting of fibrous tubers.

The cores found at *Homo habilis* sites appear to have been moved around to wherever flakes were needed; it is common to find flakes but not their source cores at a site. The cores, apparently, were carried to the next place tools might be needed. This process shows a high level of planning and intelligence. As Schick and Toth maintain, "This is a much more complicated pattern than many would have suspected from this remote period of time. It bespeaks to us an elevated degree of planning among these early hominins than is presently seen among modern nonhuman primates" (1993:128).

### The Fate of *Homo habilis*

The existence of *Homo habilis* was rather short in evolutionary terms: Occurring first in deposits that are about 2.4 million years old, their remains disappear entirely sometime after about 1.8 million years ago. But the evidence does not imply that *Homo habilis* simply became extinct, leaving no evolutionary descendants. In fact, *habilis* appears to have evolved into another hominin species. This evolutionary jump and the new species that resulted are the focus of the next chapter.

**Issues and Debates**

## What Were the First Steps in Hominin Evolution?

The evidence regarding how the hominin family began is unequivocal. The first hominins were, fundamentally, bipedal apes; the first steps of our evolution were literally "first steps." The physical evidence shows that creatures dating to at least 6 million years ago had a skeletal anatomy, reflected in the morphology of their femurs as well as the positioning of their skulls on their vertebral columns, suitable for walking on two feet, in a manner similar to the way modern human beings walk. At the same time, these creatures possessed brains of a size and configuration virtually indistinguishable from those of some species of fossil and modern apes. The consensus on this is clear.

## How Do We Know the Hominins Were Upright?

The configuration of the skeleton is quite different for creatures who walk quadrupedally and for those who are habitual bipeds. The most important part of the skeleton in this regard is the pelvis, made up of a left and a right **innominate bone** (Figure 3.19). The innominate bones of a primate quadruped—for example, a chimpanzee—have a long and narrow top blade (the **ilium**) that connects to the base of the pelvic bone (the **ischium**), creating a flat plane. A human innominate, on the other hand, has an ilium that is short and broad and, when compared to a chimp's, flares out at the top and seems twisted to the side, producing a complex curve away from the plane of its ischium (Lovejoy 1988).

The configuration of the innominate bone in an animal determines the position of the large gluteal muscles, which in turn determines how the creature could most easily get around. Thus, the position of the ilium on the innominate bone of an extinct animal allows us, with some accuracy, to deduce how that creature walked—in other words, whether it got around on four legs or two.

There really is very little argument about the pelvis of *Australopithecus afarensis* as well as that of the other australopithecines with preserved pelvises; they have an innominate bone very similar to that of a modern human being (Lovejoy 1988; Lovejoy, Heiple, and Burnstein 1973; see Figure 3.19).

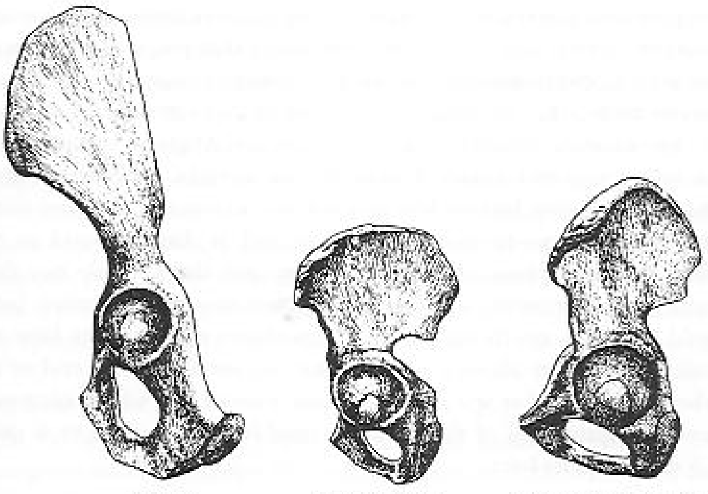



**Figure 3.19** Comparison of the pelvis of a gorilla, *Australopithecus*, and a modern human. Though there certainly are some differences, the pelves of the extinct and the modern hominid are far more similar than either is to that of the gorilla. This is true for the simple reason that pelvis determines the configuration of the muscles that attach to the upper leg, which, in turn, determines how an animal locomotes. Gorillas are quadrupeds. *Australopithecus* and modern human beings are bipeds. (From *The Antiquity of Human Walking* by John Napier. Copyright © April 1967 by Scientific American, Inc. All rights reserved; drawing copyright Enid Kotsching)

## Is There Other Evidence for Bipedality?

Though the pelvis is the best place to look for evidence of locomotion, fossil discoveries are not made to order, and we don't always find this skeletal element. Other parts of early hominin anatomy, however, are also useful to assess a creature's locomotor pattern. For example, the femur of *Orrorin* has characteristics that indicate bipedality 6 million years ago. The Laetoli footprints (see Figure 3.1) are virtually indistinguishable from footprints of a modern human; individually they exhibit the typical pattern of a human foot, and together they match the human stride (Charteris, Wall, and Nottrodt 1981; Day and Wickens 1980; T. White 1980; T. D. White and Suwa 1987). The prints display a humanlike arch and lack any hint of the divergent big toe that characterizes the apes.

As we saw earlier, the location of the foramen magnum determines the position of the vertebral column, which in turn indicates whether a species is quadrupedal or bipedal. Fossil hominin crania as far back as *Sahelanthropus* possess a foramen magnum located at the base of the cranium, in nearly the same position as in modern human beings, who, of course, are bipedal.

Fragments of the **femur** (upper leg) and **tibia** (lower leg) of *afarensis* show clearly that its upper and lower leg joined at an angle more like that in modern human beings than that in apes (Johanson and Shreeve 1989). The preserved foot bones of *afarensis* are longer and more curved than the modern human form, but, like the footprints, they exhibit a modern arrangement of the big toe. In fact, when the large, well-preserved foot from the site of Hadar (see the "Case Study Close-up" in this chapter) is scaled down to the size of the Laetoli prints, it is a perfect match (Johanson and Shreeve 1989:197).

## Why Bipedalism?

It's one thing to cite physical evidence to show that the earliest hominins walked on two feet. It's another thing to explain why bipedality evolved in the first place. If you are an ape, what is it about walking on two feet in the savanna or an environment marked by a mosaic of grassland and forest that increases your likelihood of survival and, in turn, the probability that you will reproduce and pass on the genetic disposition for bipedal locomotion to another generation, for whom greater proficiency for that mode can be further acted on by natural selection?

Seventeenth-century natural historian and Anglican minister John Ray, who we mentioned in Chapter 1, believed that upright walking was an endowment from God, giving human beings a unique advantage, enabling them to see for greater distances—to spot resources as well as dangers—and to carry objects. Modern explanations of why this ability was the key selective factor in early hominin evolution are a bit more complex, though they often (coincidentally) build on Ray's assertions. Modern hypotheses elaborate on how the ability to walk on two feet allowed our ancestors to survive at the end of the Miocene when so many other ape species became extinct and why it continued to be the central adaptive trait of the hominins until brain expansion took over more than 3.5 million years later.

### The Upright Provider

Consider the hypothesis proposed by Owen Lovejoy (1981, 1984, 2009), who suggests that the key advantage to bipedal locomotion, including that seen in *Ardipithecus*, was that it freed the hands to carry things, allowing males to carry food back to a camp or village where females and their offspring could be provisioned.

Among modern primates, chimp females raise their children alone. They are often good mothers, devoting much time and energy to the health and well-being of their offspring. Male chimps, on the other hand, generally have little to do with infants. Because chimp society is sexually promiscuous, the males don't know which, if any, infants they have sired. So, from an evolutionary perspective, why should they waste time providing for offspring that probably do not carry their genes?

Any help a chimp mother can get in providing for her offspring will improve the likelihood of survival of all of her children. It makes sense for her to solicit assistance from other chimps in her group, including adult males.

But how can a female chimp convince a male to do this? In Lovejoy's view, she must assure him that the offspring are his and that, by helping them, he ensures that half his genes get passed along as well. Only a pattern of sexual fidelity—in other words, monogamy—can do this. Basically, it's a trade: Females increase the likelihood their children will survive by remaining sexually faithful to one male. The male receives exclusive sexual access to a female and an increased probability that he will father offspring. All he has to do is faithfully provision the female and the children he has sired with her. This ability to bring food and other resources back to the female and the young is made feasible, in Lovejoy's view, by the freeing of the hands—which, in turn, is made possible by walking on two feet.

Remember, individual animals are not making a conscious choice to enhance their contribution to the evolutionary gene pool by the practice of monogamy. Females merely are choosing to associate with males who help them care for their children, and males help females who provide them with sex. These behaviors increase the probability that offspring survive to adulthood. In terms of natural selection, it should be apparent that those late Miocene apes who acted in a way that increased the likelihood of their offspring's survival were more successful than those who did not: Their population increased while other groups became extinct. Because the provisioning behavior was made possible by upright walking, that ability would be strongly selected for.

There is at least one glaring defect in Lovejoy's hypothesis (Tanner 1981; Zihlman and Tanner 1978): When a male is away gathering food, what is to prevent a female from having sex with other males? In fact, such behavior may be to her advantage because it would increase the number of males willing to provision her and her offspring. Sex is used in many of the social primates to make alliances and maintain friendships. In such a scenario, sexual fidelity might even be disadvantageous, particularly if the male doesn't do a good job of provisioning. Ultimately, it is difficult to understand how a more rigid pattern demanding sexual fidelity actually could have been maintained in ancient hominin societies.

### The Upright Scavenger

Anthropologist Pat Shipman (1984, 1986) has proposed another hypothesis. Using the scanning electron microscope, Shipman has examined the remains of animal bones recovered at early hominin sites. She found microscopic evidence of tooth marks from predators and scavengers, as well as cut marks from stone tools, made when hominins removed the meat. In some instances she found carnivore and stone-tool marks on the same bones, either with the tool marks superimposed on the carnivore tooth marks or with the tool marks made first. In other words, sometimes carnivores had access to the bones only after the hominins had processed them (indicating hominin hunting behavior), and sometimes the hominins got at the bones after carnivores had already chewed on them, evidence that the hominins were scavenging the carcasses of animals killed by other carnivores.

Walking on two feet was likely advantageous to hominins who were opportunistic scavengers. Scavengers need to find their quarry, and that means walking great distances and scanning a broad territory for evidence of a predator kill. Bipedalism is highly energy-efficient, in part because it involves only two limbs and yields greater endurance for walking long distances. In addition, because scavengers always need to be wary of the return of the predator who did the killing in the first place, as well as of other large, aggressive scavengers—like hyenas or jackals, who might compete for the same kill—it is wise to get in and out quickly: Cut the meat off the bone as fast as possible and carry it back to a safe place to eat. The free hands of a bipedal hominin can carry both the tools for extracting the meat from the carcass and the meat.

### The Efficient Walker

Primatologist Peter Rodman and anthropologist Henry McHenry (Johanson, Johanson, and Edgar 1994) have proposed what may be the simplest and most elegant hypothesis of all. After analyzing the energy expended by chimps when they walk quadrupedally and by humans with their upright gait, Rodman and McHenry determined that human locomotion was simply more efficient than chimp locomotion, meaning we expend less energy to accomplish the same task. Following on this hypothesis, researchers have recently calculated the actual difference in energy expenditure between quadrupeds and bipeds. It turns out that, while using half as many limbs, a human being walking on two legs expends only one-quarter the energy of a chimp walking on all fours (Sockol, Raichlen, and Pontzer 2007).

As the Miocene forest shrunk, some ape species may have thrived by exploiting the resources of the growing savanna, where food resources were more dispersed. An energetically efficient way of moving across increasing distances in the search for food became adaptively advantageous. The ability to walk efficiently on two feet may have provided that advantage.

## The Endurance Runner

The Olympic marathon race (26 mi, 285 yd; 42.195 km) is run to commemorate a legendary marathon run by a Greek herald 2,500 years ago. A Greek herald named Phidippides ran the approximately 26-mile route from Marathon to Athens to announce the stunning victory of the Greeks over Persian invaders, and then promptly dropped dead.

More recently, marathon running has become extremely popular (mostly without the dying part); for example, there were more than 25,000 competitors in the Boston Marathon in 2008. Thousands more compete in marathons all over the world, and many more than that train for long-distance running, though they will never actually compete. Not being a runner, I can scarcely comprehend the attraction of what, to me, seems like a particularly agonizing way to spend your time. Nevertheless, I do understand that in the human ability to run for great distances—not necessarily quickly when compared to the sprinting abilities of, for example, a horse or a cheetah, but consistently, over the course of many hours—we are unique among the primates. No monkey or ape species can run, bipedally or quadrupedally, for great distances.

In fact, human physiology seems supremely well adapted to running (Bramble and Lieberman 2004). Running is not just ramped-up walking; it is a very different manner of locomotion made possible by a unique combination of skeletal morphology, muscle configuration, and tendon placement (Zimmer 2004). For example, our tendons are arranged in a manner very different from those of chimps; they act like springs, allowing our legs to store energy with each stride. Our legs are proportionally much longer than those of the apes, allowing for longer strides and a faster pace, without expending the additional energy required to run faster by moving shorter legs more quickly. Running produces a pounding on our joints with each stride, but our skeletons are adapted to this as well. The surfaces where our leg bones meet—their **articular surfaces**—are proportionally broader in humans than in apes, allowing the great impacts of running to be dampened by spreading them out over a larger area. Bipedal running can be an unsteady way of moving about, and here too humans seem uniquely well-adapted to maintain stability, especially with a pelvic configuration that allows for large and powerful gluteal muscles that work to keep us upright.

Bramble and Lieberman point out that the skeletal features that adapt us so well for running are absent even in the demonstrably bipedal australopithecines, appearing first in *Homo habilis*. They suggest that the ability to run would have been highly advantageous both in hunting and in scavenging. Particularly before the development of long-distance weaponry—things like bows and arrows, developed much later—the need to catch up to prey, to get close enough to hurl rocks or other projectiles, provided good long-distance runners with a decided advantage (Carrier 1984). Scavengers, too, benefit from endurance running; based on clues provided by smell and the presence of circling vultures, wild dogs and hyenas regularly run great distances to exploit carcasses (Bramble and Lieberman

2004:351). Hominins who could run great distances would be able to better compete with these other scavengers for access to those carcasses.

So, the next time you compete in a marathon, or just watch one on TV, consider the possibility that the pounding, the agony, and the relentless pushing it takes to accomplish the run may be made possible because of evolutionary forces that enabled our ancestors on the plains of Africa more than 2 million years ago to successfully compete with animals larger, stronger, and faster than us.

## Were the Early Hominins Hunters?

In all likelihood, hunting was not the dominant mode of subsistence among our most ancient ancestors. Dental morphology shows that *Ardipithecus* and *Orrorin* were browsers who consumed soft fruit and leaves, not carnivores who concentrated on animal flesh (Gibbons 2002). The preserved teeth of *Australopithecus afarensis* imply a diet of mostly fruits, leaves, roots, insects, and small mammals. The habitat in which *Australopithecus anamensis* lived implies a diet of fruit, insects, and small mammals.

Even for the toolmaking *Homo habilis*, there is no evidence that hunting dominated the subsistence quest. Neither the Oldowan choppers nor the used flakes would have been handy as spearpoints. Moreover, a detailed **taphonomic** analysis conducted by archaeologist Lewis Binford (1987) has shown that animal bones found at early hominin sites typically are not those we would expect to find at the hunting camps of proficient hunters. The animal skeletal elements found are not those that would have been associated with the best cuts of meat, such as upper limbs. Binford determined that the excavated animal bones were mostly lower limbs and parts of skulls and mandibles, among the least meaty of animal parts. Moreover, many of the tools found at *Homo habilis* sites would have been more suitable for extracting marrow than for removing meat from bones; marrow inside the shafts of long bones, typically left behind by carnivores, is a staple for many scavengers. Binford concluded from this that early hominins were probably not proficient hunters, but, instead, opportunistic scavengers of the carcasses of animals killed by large carnivores.

This doesn't mean that our early ancestors weren't capable of hunting. Anthropologists Henry Bunn and Ellen Kroll (1986) analyzed stone flakes and bones from the 1.8-million-year-old FLK site in Olduvai Gorge and found substantial evidence for reliance on meat; bones representing the meatiest parts of animals bore ample evidence of stone-tool cut marks. The evidence for hunting seems a bit stronger for small animals, with a pattern of scavenging but also some hunting of larger animals.

We needn't be too concerned about the finer points of early hominin subsistence. All researchers would probably agree that hunting was not predominant in the subsistence base of the australopithecines or in *Homo habilis*. Though we have to be careful when generalizing from nonhuman primates, we do know that chimpanzees in the wild occasionally engage in cooperative hunts (Goodall 1986). As paleoanthropologist Daniel Stiles (1991) has pointed out, there is no reason to believe our hominin ancestors were less capable than chimps in their ability to plan, coordinate, and carry out a hunt. The first hominins were not born killers, but they probably did rely on meat to a certain degree, some of it scavenged, some from hunting. The early hominins probably were opportunistic foragers, taking whatever food they could, whenever the opportunity presented itself.

## Where Did the Idea for Stone Tools Come From?

It is not intuitively obvious that a more or less spherical, relatively small, single nodule of stone can be transformed into a large number of consistently contoured stone flakes that cumulatively provide several feet of sharp tool edge. It takes some amount of reflection, study, and deliberation to figure out that stones with certain properties, when struck in the right way, at the right place, with just the right amount of force, and at the right angle can produce useful tools that can cut, pierce, or scrape far more effectively and efficiently than our teeth and nails. That *Homo habilis* was able to figure this all out is implied by the archaeological record of Oldowan tools. The question remains, then, "What might have inspired our first tool-using ancestors in this intellectual process?"

Though chimps in the wild have never been observed intentionally modifying stone to make tools, as mentioned earlier in this chapter, they do use rocks to crack open hard-shelled nuts. Chimps in the Taï Forest of the African nation of Côte d'Ivoire, for example, use extremely hard igneous rocks that they have to collect from outcrops and then transport to the location of the nut-producing *Panda* trees (Mercader, Panger, and Boesch 2002). The chimps position the nuts on bedrock outcrops or exposed tree roots that serve as anvils and then crack the nuts open by striking them with the igneous hammers (Figure 3.20). Occasionally, slices of these hammers accidentally flake off, unintentionally producing sharp-edged stone flakes.

This got the researcher of the chimp behavior thinking. Nuts are a nutritious and abundant food source. When *Panda* nuts are in season in the Taï Forest, chimps have been calculated to obtain more than 3,000 calories of food per day from this food source (Mercader et al. 2002:1452). The researchers of chimp nut-cracking sensibly suggest the possibility that some Miocene apes and early hominins could have exploited the same or similar nut foods in their subsistence pursuit. The only viable way to access the rich meat of some species of nuts is to strike the nuts with a hard hammer. Certainly, Miocene hominins might have practiced the same nut-cracking behavior as the chimps in the Taï Forest. These same researchers have proposed that nut-cracking hominins might have been inspired by accidentally breaking their stone hammers and unintentionally producing sharp flakes that could be used as tools. Perhaps they recognized the utility of the sharp flakes and then set about the process of trying to figure out how to intentionally and consistently produce sharp stone flakes—for butchering an animal, cutting fiber, and so on. It is interesting to consider the possibility that the invention of stone tools ultimately was the by-product of an accident.

## Case Study Close-up

HADAR, LOCATED IN THE AFAR TRIANGLE of northeastern Ethiopia, is one of the most spectacular fossil hominin sites ever excavated. All by itself, the Hadar site disproves the notion that the pronouncements of paleontologists are based on a tiny handful of unrecognizable bone fragments or indistinguishable teeth. This one site produced 250 hominin fossil bones representing 14 individual members of the species *Australopithecus afarensis* (Johanson and Shreeve 1989:21). Perhaps most significantly, Hadar produced Lucy.

The remains of the fossil that her discoverers named Lucy were found in 1974. Close to one-half of her skeleton was recovered, including parts of the skull, the lower jaw, ribs, vertebrae, arm bones, left innominate, left femur (upper leg),

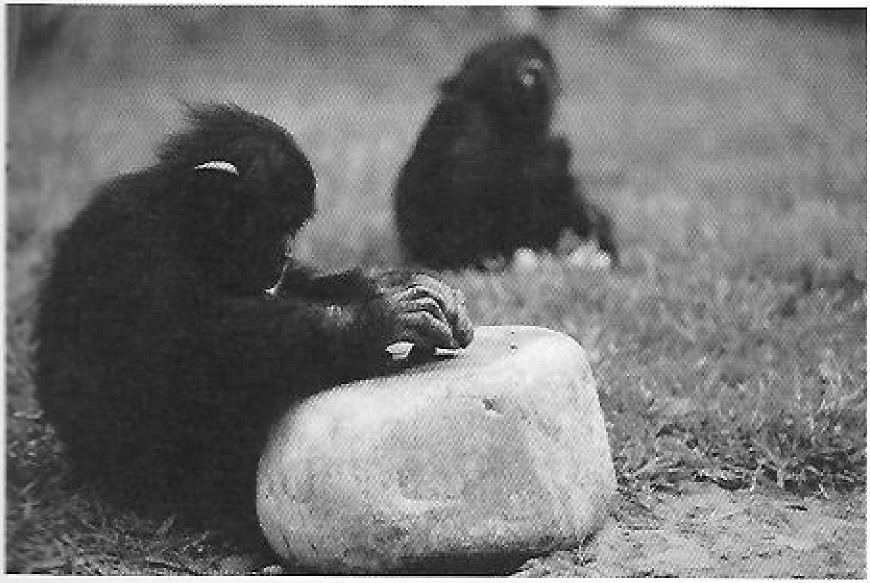


**Figure 3.20**
Chimpanzees living in the Tai forest of the African nation of Côte d'Ivoire use rock hammers and root and stone anvils to pound open nutshells to extract the rich and nutritious nutmeats. In this process, chimps may accidentally break the stones, producing, again accidentally, sharp-edged flakes of stone that litter the surroundings of the nut-processing stations. It is possible that our human ancestors used stones to perform the same task, producing flakes that they realized were, themselves, a valuable byproduct of the activity, useable as tools. It may then have been a short intellectual leap for our ancestors to intentionally and directly produce stone tools.
(Kennan Ward)

and parts of the lower right leg (see Figure 3.11). The following year, fragmentary remains of 13 more individuals were found, including 9 adults and 4 children. Dubbed "the First Family," all these individuals were deposited at the same time and seem to have died together.

The Hadar fossils provided the name for this hominin species, *Australopithecus afarensis*, after the Afar region of Ethiopia, where the site is located. Lucy and the First Family fossils constitute solid support for the interpretation presented in this chapter: Dating to more than 3.18 million years ago, these early hominins were, essentially, bipedal apes.

Lucy has received most of the attention as a result of her remarkable degree of preservation, but her size is not typical of the group found at Hadar. Lucy, an adult, was tiny by modern standards, standing only a little over 110 cm (3½ ft) tall, with an estimated weight of about 30 kg (65 lb), small even by *afarensis* standards. But Lucy is a female in a species that exhibits a large measure of **sexual dimorphism**—that is, a big difference between males and females. For example, among gorillas—a species with strong dimorphism—males are commonly twice the size of females. An analysis by Henry McHenry (1991) shows that sexual dimorphism among the known *afarensis* specimens is less than that exhibited by gorillas and orangutans but more than in chimpanzees and much more than in modern human beings where, on average, males are only about 10% to 15% larger than females. Lucy falls within the broad range of sizes represented in the First Family fossils. Though she is a small female, she is clearly a female.

The Hadar specimens show what these ancient hominins looked like: They were bipedal. Their arms were proportionally longer than those of modern humans, with hands quite modern in appearance except for fingers that curled more like an ape's fingers. Their jaws were an amalgam of ape and human. They had ape-sized brains housed in skulls that exhibited large, apelike bony ridges above the eyes and a highly prognathous profile.

Hadar presents an astonishing picture of more than a dozen individuals who probably knew each other and perished together in the dim mists of our own beginnings. Like the footprints at Laetoli, they have achieved a kind of immortality as a result of the lucky accident of the preservation of their bones. And like the Laetoli prints, that lucky accident affords us, 150,000 generations later, the luxury to contemplate where and how we began.

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## Summary

Humanity began its evolutionary journey in Africa more than 6 million years ago as an "upright ape." Bipedal locomotion—not brain size or intelligence, the things that *most* distinguish us from the other animals—was what *first* differentiated us, the hominins, from the apes. *Sahelanthropus*, *Orrorin*, and *Ardipithecus* are among the candidates for the designation "oldest hominin," all dating to about 6 million years ago. By 4.2 million years ago, *Australopithecus anamensis* certainly was upright and may have been ancestral to all later forms of hominins. The ability to walk on two feet was advantageous in many ways: Hominins could travel with greater energy efficiency, which assisted in scavenging. Hominins seem uniquely adapted for long-distance running, and this ability to cover great distances may have been highly advantageous. With the hands freed, they could carry tools to where they were needed and bring back food to provision the young.

Around 2.5 million years ago, an environmental change in Africa, sparked by worldwide cooling, induced a burst of evolution in the hominin family. A number of varied species branched off from *Australopithecus afarensis* after this time. One branch, *Homo habilis*, had a brain size larger than any ape's. With its larger brain, *Homo habilis* was able to produce the first stone tools—simple but revealing a level of planning and forethought that reflects the great intelligence of this first member of our genus.

## To Learn More

### Technical Summaries

If you are interested in how Ardipithecus is causing paleoanthropologists to rethink the origins of the hominin line, look at the suite of articles available in the special, October 2, 2009 issue of *Science* magazine.

### Popular Summaries

For a terrific summary of current thinking about the evolution of the apes, see David Begun's (2003) "Planet of the Apes" in *Scientific American*. As always, National Geographic presents a superbly illustrated and well-written piece on the exciting, new discoveries in paleoanthropology in an article in its July 2010 issue (Shreeve 2010). The article focuses on *Ardipithecus*. For very well written, broad discussions of the paleoanthropology and archaeology of the first hominids, books written by some of the best-known scientists in the field are good choices: Donald Johanson and Kate Wong's (2009) *Lucy's Legacy* is a terrific, recent summary of the story of Lucy's discovery and her significance in human evolution evolution. Also, see the beautiful coffee-table book written by