The Story of the Human Body

Evolution, Health, and Disease

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Much Depends on Dinner

How the Australopiths Partly Weaned Us Off Fruit

Since Eve ate apples, much depends on dinner.

—BYRON, *Don Juan*

Like me, you probably eat mostly soft and highly processed food, little of it fruit. If you added up the amount of time you actually spent chewing, it would total less than half an hour per day. This is odd for an ape. Every day, from dawn to dusk, a chimpanzee spends nearly half its wakeful hours chewing like a raw foodist.[1] Chimps typically eat forest fruits like wild figs, wild grapes, and palm fruits, none of which are as sweet and easy to chew as the domesticated bananas, apples, and oranges that you and I enjoy. Instead they are slightly bitter, less sweet than a carrot, extremely fibrous, and they have tough outer coverings. In order to get enough calories from eating such fruits all day long, a chimp consumes prodigious quantities, sometimes a kilogram (2.2 pounds) in an hour and then waits about two hours for its stomach to empty before gorging again.[2] Chimps and other apes must also resort sometimes to lower-quality foods such as leaves and gnarly stems when fruit is not abundant. When and why did we stop spending most of the day

eating fruit? How did adaptations for eating different foods affect our bodies' evolution?

Adaptations for eating foods other than mostly fruit are at the heart of the second major transformation in the story of the human body. As we have seen, the first hominins probably needed to eat leaves and stems on occasion, but the trend toward increased dietary diversity accelerated dramatically about 4 million years ago in their descendants, a confusing group of species informally called the australopiths (so named because many of them belong to the genus *Australopithecus*). These diverse and fascinating ancestors occupy a special place in human evolution because their efforts to feed themselves changed what we are adapted for in ways still evident every time we look in the mirror. The most obvious of these shifts are adaptations in our teeth and face for chewing hard and tough foods. Even more important, the benefits of foraging far and wide favored further adaptations for more habitual and efficient long-distance walking than we see in Ardi and other earlier hominins. The combination of these adaptations, which were largely driven by the exigencies of climate change, had momentous implications, setting the stage for the evolution of the genus *Homo* a few million years later and for many important features of the human body. Were it not for the australopiths, your body would be very different, and you would probably be spending much more time in trees, mostly gorging on fruit.

Lucy's Gang: The Australopiths

The australopiths lived in Africa between about 4 and 1 million years ago, and we know much about them thanks to a rich fossil record of their remains. The most famous fossil of all is, of course, the glam girl herself, Lucy, a diminutive female who lived in Ethiopia 3.2 million years ago. Unfortunately for her (but luckily for us), Lucy died in a marsh, which quickly covered her up, preserving slightly more than a third of her skeleton. Lucy is just one among many hundreds of fossils belonging to a species known as *Australopithecus afarensis,* which lived in eastern Africa between 4 and 3 million years ago. *Au. afarensis,* in turn, is just one of more than half a dozen different species of australopiths. Unlike today, when there is only one living species of hominin, *Homo sapiens,* there used to be several species living at any one time, and the australopiths were an especially diverse bunch. In order to give you a quick who's who of these relatives, I've summarized their basic details in table 1. Keep in mind that some of these species are known from just a few fossil specimens, so paleontologists do not entirely agree on how to define them. Because of uncertainties and the differences among the species, a good way to make sense of the various australopiths is to divide them into two general groups: the smaller-toothed graciles and the bigger-toothed robusts. The best-known species of gracile australopiths are *Au. afarensis* (of Lucy fame), which comes from eastern Africa, and *Au. africanus* and *Au. sediba,* which come from southern Africa. The best-known robust australopiths are *Au. boisei* and *Au. robustus,* from eastern and southern Africa respectively. Figure 5 illustrates what a few of these species might have looked like.

Instead of focusing on the names and dates of these species, let's consider what they were generally like as well as some of the varia-

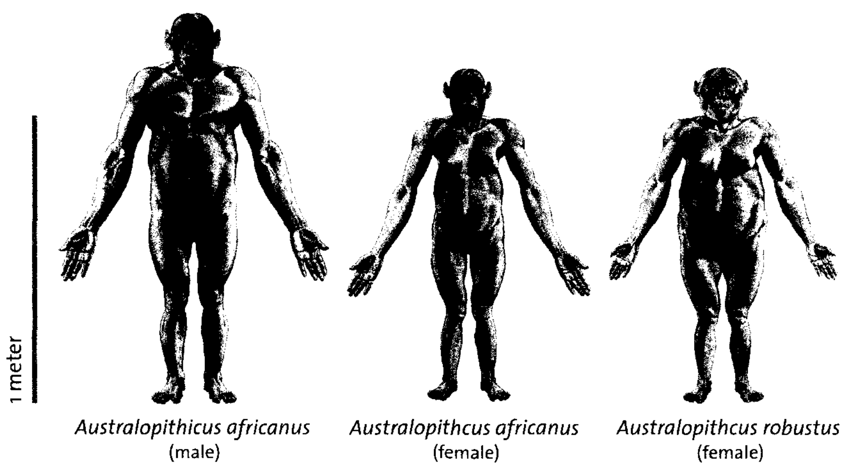


FIGURE 5. Reconstructions of two species of australopiths. On the left, a male and female *Australopithecus africanus;* on the right, a female *Australopithecus robustus.* Note the relatively long arms, short legs, wide waists, and large faces. Reconstructions copyright © 2013 John Gurche.

tions they reveal. If you could observe a group of them, your first impression might be that they were upright apes. In terms of size, they were more like chimpanzees than humans: females averaged 1.1 meters in height (3 feet 7 inches) and weighed between 28 and 35 kilograms (62 to 77 pounds), while males averaged 1.4 meters in height (4 feet 7 inches) and weighed between 40 and 50 kilograms (88 to 100 pounds).[3] Lucy, for example, was just under 65 pounds (29 kilograms), but a partially complete skeleton of a male *from the same species* (nicknamed Kadanuumuu, which means "big man") weighed about 55 kilograms (121 pounds).[4] This means that male australopiths were about 50 percent larger than females, a size difference typical of species such as gorillas or baboons, in which males regularly fight with one another for access to females. Australopith heads were also generally apelike, with small brains only just a little larger than a chimpanzee's, and they retained long snouts and large browridges. Like chimps, their legs were relatively short and their arms were relatively long, but their toes and fingers were neither as long and curved as a chimp's nor as short and straight as a human's. Their arms and shoulders were powerful, well suited to climbing in trees. Finally, if you could be like Jane Goodall and observe them for years, you'd discover that the australopiths had an apelike rate of growth and reproduction: they took about twelve years to grow into adulthood and females probably had offspring every five to six years.[5]

In other respects, however, the australopiths were different not just from apes but also from the first hominins we previously discussed. One very noticeable and important contrast is what they ate. Although there is much variation, the australopiths as a whole probably ate much less fruit and instead relied more heavily on tubers, seeds, plant stems, and other foods that are hard and tough. The key evidence for this inference are their many adaptations for being prodigious chewers. Compared to presumed ancestors such as *Ardipithecus,* they had bigger teeth, more massive jaws, and faces that were wider and taller, with very forwardly placed cheekbones and large chewing muscles. These characteristics, however, vary among species, and are especially extreme in the three species of robust australopiths: *Au. boisei, Au. robustus,* and *Au. aethiopicus.* Put crudely, these robust species are the hominin equivalent of

TABLE 1. Early hominin species

Species	Date (millions of years ago)	Locations found	Brain size (cm³)	Body mass (kg)
Early hominins				
Sahelanthropus tchadensis	7.2–6.0	Chad	360	?
Orrorin tugenensis	6	Kenya	?	?
Ardipithecus kadabba	5.8–4.3	Ethiopia	?	?
Ardipithecus ramidus	4.4	Ethopia	280–350	30–50
Gracile Australopiths				
Australopithecus anamensis	4.2–3.9	Kenya, Ethiopia	?	?
Australopithecus afarensis	3.9–3.0	Tanzania, Kenya, Ethiopia	400–550	25–50
Australopithecus africanus	3.0–2.0	South Africa	400–560	30–40
Australopithecus sediba	2.0–1.8	South Africa	420–450	?
Australopithecus garhi	2.5	Ethiopia	450	?
Kenyanthropus platyops	3.5–3.2	Kenya	400–450	?
Robust Australopiths				
Australopithecus aethiopicus	2.7–2.3	Kenya, Ethiopia	410	?
Australopithecus boisei	2.3–1.3	Tanzania, Kenya, Ethiopia	400–550	34–50
Australopithecus robustus	2.0–1.5	South Africa	450–530	32–40

cows. The most specialized of the robust australopiths, *Au. boisei*, for example, had molars twice the size of yours, and its cheekbones were so wide, tall, and forwardly positioned that its face looks like a soup plate. Its chewing muscles were the size of small steaks. After Mary and Louis Leakey first discovered the species in 1959, people were so impressed with its heavy-duty jaws that it got nicknamed "Nutcracker Man." In terms of the rest of their anatomy, the robust australopith species apparently differed little from their gracile cousins.[6]

The other distinctive but also variable characteristic of the australopiths to consider is how they walked. Like Ardi and the other first hominins, they were bipeds, but some species of australopiths walked with a more humanlike striding gait thanks to many features they share with us, such as widely spaced hips, a stiff foot with a partial arch, and a short big toe in line with the other toes. Smoking-gun evidence for australopith bipedalism comes from the Laetoli footprints, a trail made by several individuals—including a male, a female, and a child—who walked across a wet ash plain in northern Tanzania about 3.6 million years ago. These footprints and other clues preserved in their skeletons suggest that australopith species such as *Au. afarensis* walked upright habitually and efficiently. Other australopith species such as *Au. sediba*, however, may have been better suited to climbing trees and walked with shorter strides more along the outside of the foot.[7]

How did the australopiths come to be? Why were there so many species and how did they differ? And, most important, what role did these creatures play in the evolution of the human body? The answers to these questions generally have to do with the continued challenges of finding dinner as Africa's climate kept changing.

The First Junk Food Diet

You and I are unusual in many ways, not the least of which is that when we ask the question "What's for dinner?" we have an unprecedented choice of abundant, nutritious foods available to us. Like other animals, however, our australopith ancestors ate only what they could find, not in fruit-filled forests as their predecessors enjoyed, but in more open habitats with fewer trees. To make matters worse, during the geological epoch in which they lived, the Pliocene (5.3 to 2.6 million years ago), the earth became slightly cooler and Africa continued to become drier. While these changes occurred in fits and starts (as shown by the many zigs and zags of figure 4), the overall trend in Africa during the australopith era was the expansion of open woodland and savanna habitats, widely diminishing and scattering the availability of fruit.[8] This fruit crisis undoubtedly exerted strong selective pressures on the australopiths, favoring individuals better able to gain access to other foods.

So it was that the australopiths (some species more than others) were pushed to forage regularly for lower quality foods—so-called fallback foods that one eats when preferred foods are unavailable. Humans still have to eat fallback foods on rare occasions. Acorns were a common food of last resort throughout Europe during the Middle Ages, and many Dutch people resorted to eating tulip bulbs to avoid starvation during the severe winter famine of 1944. As we have already seen, apes also have fallback foods; they consume leaves, plant stems, herbs, and even bark when ripe fruit is unavailable. An important point about fallback foods is that they can be the difference between life and death, so natural selection tends to act strongly on adaptations that help animals eat them.[9] We often say "you are what you eat," but evolutionary logic dictates that sometimes "you are what you'd rather not eat."

What were the fallback foods of Lucy and other australopiths? And what is the evidence that natural selection for such foods had any appreciable effect on their bodies' evolution? These questions are impossible to answer definitively, but we can make some reasonable inferences. First, there is evidence that the australopiths lived in habitats that had some fruit-bearing trees, so they probably ate fruits when they could get them, just as human foragers still do today in the tropics. It is therefore hardly surprising that their skeletons retain some adaptations for climbing trees like long arms with long, curved fingers, and their teeth have many of the features one typically sees in fruit-eating apes, including wide upper incisors that tilt forward slightly (helpful for peeling), and broad molars with low cusps (helpful for crushing pulp). However, habitats such as woodlands have lower densities of fruiting trees than rain forests, and the fruit tends to be more seasonal. It is almost certain that the australopiths faced shortages of fruit during certain times of year, and these shortages would have been extreme during drought years. Under such conditions, they probably did what the great apes do: fall back on other digestible but less desirable plants. Chimps, for example, will eat leaves (think grape leaves), plant stems (think uncooked asparagus), and herbs (think fresh bay leaves).

Studies of australopith teeth and ecological analyses of their habitats suggest that the australopiths had diverse and complex diets that included not only fruits but also edible leaves, stems, and seeds,[10] but it is highly likely that some of them also started to dig for food, thus adding new, very important, and highly nutritious fallback foods to their diet. Although most plants store carbohydrates aboveground in seeds, fruits, or in the pithy center of stems, some plants like potatoes and ginger store their energy reserves underground as roots, tubers, or bulbs, thus hiding them from herbivores like birds and monkeys and preventing them from being desiccated by the sun. These plant parts are known collectively as underground storage organs, or USOs. USOs are hard to find and they require some effort and skill to extract, but they are rich sources of food and water, and they tend to be available year-round, including dry seasons. In the tropics, one finds USOs in marshes (sedges like papyrus have edible tubers), but also in open habitats such as woodlands and savannas.[11] Many hunter-gatherers rely heavily on USOs, which sometimes make up a third or more of their diet. We now eat domesticated USOs, such as potatoes, cassava, and onions.

No one knows exactly how many USOs were eaten by different species of australopiths, but it is likely that tubers, bulbs, and roots constituted a substantial percentage of their calories and became even more important than fruits for some species. In fact, there is good reason to speculate that a diet rich in USOs—let's call it the Lucy Diet—was so effective that it partly made possible the remarkable radiation of these hominins. In order to appreciate the advantages of the Lucy Diet, it is useful to remember that about 75 percent of the plant foods that chimps eat is fruit, and the rest comes from leaves, piths, seeds, and herbs. If chimp fruits came with nutritional labels, you'd find that they are extremely high in fiber, but they are also moderately rich in starch and protein and low in fat.[12] As you might expect, chimp fallback foods are even higher in fiber and lower in starch, hence calories.[13] USOs, however, are more starchy and energy-rich than many wild fruits, and they have about half the fiber content.[14] Chimpanzees infrequently dig for USOs, which are rare in forests, but when the australopiths started to dig for their dinner they would have been able to substitute USOs for the sorts of fallback foods that chimps eat when they can't get fruits.

To summarize, australopiths as a whole were gatherers who ate a varied diet that included fruit, but some of them also benefited strongly from digging frequently for tubers, bulbs, and roots. They almost certainly foraged for other fallback plant foods too, including leaves, stems, and seeds, and we can guess that, like chimps and baboons, they regularly enjoyed insects such as termites and grubs, and they must have eaten meat whenever it was possible, probably by scavenging, since being slow and unsteady bipeds likely made them ineffective hunters. However, what determined their menu choices? What evidence do we have? And, most important, how did the challenges of getting dinner—a major component of what Darwin termed the "struggle for existence"—influence the evolution of hominin bodies so they could get to these foods and eat them?

What Large Teeth You Have, Grandma!

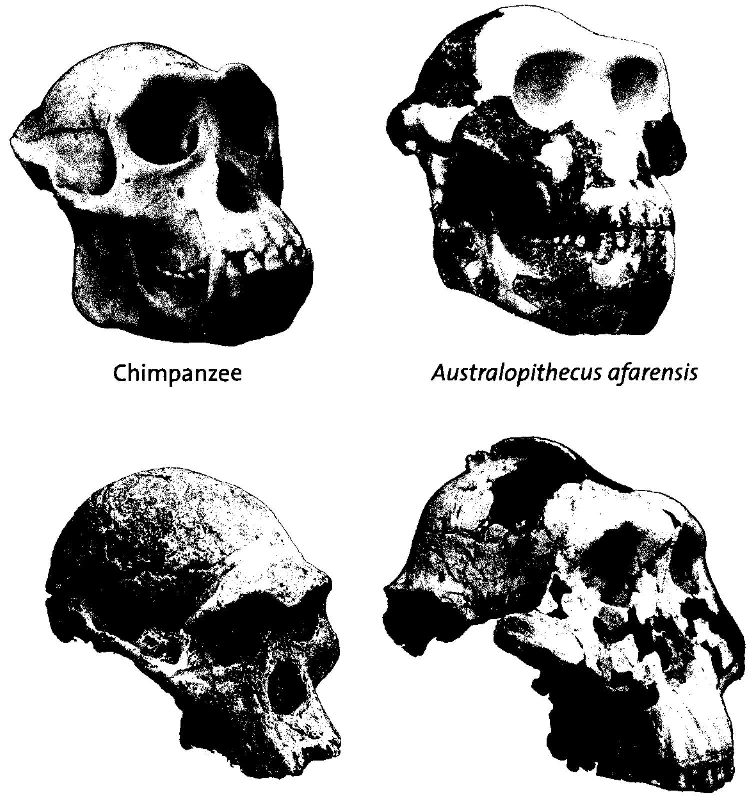
Your body is replete with adaptations to help you acquire, chew, and then digest food. Of all these adaptations, none are as revealing as your teeth. You probably give your teeth little consideration except in terms of how they look or how much pain they cause and cost they incur, but before the era of cooking and food processing, losing your teeth could be a death sentence. Natural selection thus acts strongly on teeth because the shape and structure of each tooth largely determines an animal's ability to break down food into small particles, which are then digested to extract vital energy and nutrients. Since digesting smaller particles yields more energy, you can readily appreciate that the ability to chew as effectively as possible had substantial fitness benefits for animals like the australopiths, who, like apes, probably spent nearly half their day chewing.

Chewing USOs would have been a special challenge. The domesticated roots and bulbs we eat today have been bred to be low in fiber and tender, and cooking makes them even more chewable. In contrast, raw, wild USOs are extremely fibrous and unpleasantly tough to the modern palate. Unprocessed, they require lots of hard chewing—something you can appreciate by trying to munch a raw yam or a rutabaga. You need to chew it over and over, and with lots of force. In fact, some USOs are so fibrous that hunter-gatherers eat them in a special manner known as wadging: chewing them for a long time in order to extract any nutrients and juices and then spitting out the leftover pulp. Imagine wadging your food for hours upon hours because you are hungry and there is little else to eat.

If survival meant the ability to eat tough, hard foods effectively, natural selection would have favored australopiths better able to bite forcefully and to withstand the endless repetitions of powerful chews.

We can therefore infer a great deal about what foods, especially fallback foods, the australopiths and other hominins were selected to eat from the shape and size of their teeth. Most importantly, if there is any one defining characteristic of the australopiths it is big, flat cheek teeth with thick enamel. Gracile australopiths such as *Au. africanus* had molars that were 50 percent bigger than a chimp's, and the rocklike enamel crown of the tooth (the hardest tissue in the body) is twice as thick. Robust australopiths such as *Au. boisei* are even more extreme, with molars that were more than two times the size and up to three times the thickness. To put these differences into perspective, the area of your first molar is roughly the size of a pinky nail, about 120 square millimeters (0.19 square inches), but the same tooth in an *Au. boisei* is the size of a thumbnail, approximately 200 square millimeters (0.31 square inches). In addition to being expansive and thick, australopith teeth were very flat, much less cuspy than chimpanzee teeth, and they had long and wide roots, which helped anchor them in the jaws.[15]

Researchers have devoted much time to studying how and why the australopiths grew such big, thick, and flat cheek teeth, and the unsurprising answer is that these characteristics were adaptations to chew food that was tough and sometimes also hard.[16] Just as thicker, bigger soles make hiking boots more resilient on trails than thin-soled sneakers, thicker and larger teeth are better suited to breaking down harder, tougher foods. Having thick enamel helps teeth resist wear from high pressures and from grit that inevitably clings to foods. In addition, big, flat tooth surfaces are useful because they spread bite forces over a large area and allow you to grind foods with a partly sideways movement, ripping tough fibers apart. Basically, the australopiths, especially the robust species, had giant teeth shaped like millstones, well adapted for endlessly grinding and pulverizing tough food under high pressure. If you had to chew uncooked, unprocessed tubers for half of each day for your entire life, you'd appreciate having these humongous teeth, too. And to some extent, you still do, thanks to your australopith



Chimpanzee | *Australopithecus afarensis*

Australopithecus africanus | *Australopithecus boisei*

FIGURE 6. Comparison of a chimpanzee skull with three species of australopiths. *Australopithecus afarensis* and *Australopithecus africanus* are both considered more gracile, while *Australopithecus boisei* is more robust, with bigger teeth, larger chewing muscles, and a larger face.

legacy. Although human cheek teeth are not as big and thick as those of australopiths, they are actually bigger and thicker than those of chimps.

Most things in life involve trade-offs, including tooth size. There is only so much room in the jaw for teeth, even if you have a long snout like an australopith. In terms of the front teeth, the earliest australopiths, such as *Au. afarensis,* have very apelike incisors that are broad and projecting, well adapted for sinking your teeth into fruits. But as australopith cheek teeth evolved to become bigger and

thicker, their incisors became smaller and more vertical, and their canines also shrank to about the same size as their incisors. To some extent, smaller front teeth reflect the declining importance of fruit in these hominins' diet, but they also reflect the need to make room for bigger cheek teeth. Today, we still have small front teeth with incisor-like canines.

If your molars are big and thick in order to chomp for many hours a day on tough, hard, fibrous food, you also need big, strong chewing muscles. Not surprisingly, the australopith skulls such as those in figure 6 bear many traces of having had massive chewing muscles that could generate lots of bite force. The temporalis, the fan-shaped muscle along the side of the head, was so large in many australopiths that bony crests grew off the top and back of the skull to give the muscle more room to insert. In addition, this muscle's belly, which runs between the temples and the cheekbone to insert on the jaw, was so thick that the cheekbones (the zygomatic arches) of the australopiths were displaced far to the side, making their faces as wide as they were tall. The large cheekbones of the australopiths also provided plenty of room to vastly expand another major chewing muscle, the masseter, which runs from the cheekbone to the base of the jaw. In addition to being large, australopith chewing muscles were also configured to generate forces efficiently.[17]

Have you ever chewed something so hard and for so long that your jaw muscles ached? It turns out that when animals, including humans, generate such high bite forces they cause bones in the jaw and face to deform slightly, causing microscopic damage. Minor levels of deformation and damage are normal and cause bones to repair themselves and grow thicker.[18] Repetitive high deformations, however, can damage the bone seriously, potentially causing a fracture. Therefore, species that generate high chewing forces tend to have upper and lower jaws that are thicker, taller, and wider, thereby lowering the stresses caused by every bite, and the australopiths are no exception. As you can see in figure 6, the australopiths had massive jaws, and their large faces were heavily reinforced with thick pillars and sheets of bone that allowed them to chew tough, hard foods all day long without breaking their faces.[19] This facial buttressing is impressive in the gracile australopiths, but the robust australopiths have faces and jaws so heavily built they resemble armored tanks.

In short, australopiths, like chimps and gorillas, probably loved fruit, but they must have eaten whatever foods they could get their hands on. There was no single australopith diet, and the half dozen or so species that we know about undoubtedly ate varied diets that reflected the diverse ecological conditions in which they lived. But as climate change caused fruits to become rarer, tough fallback foods, especially USOs, must have become increasingly important resources for these ancient relatives—a heritage we still retain to some extent.[20] But how did they get these foods in the first place?

Tottering for Tubers

As you forage in a market, changing your diet mostly involves reaching for a different box of this or that, perhaps even venturing down an unfamiliar aisle. Hunter-gatherers, in contrast, spend hours every day traveling long distances in search of food. In this respect, chimpanzees and other forest-dwelling apes are more like modern shoppers than hunter-gathers because they rarely travel far to fill their bellies, regardless of whether they eat their preferred diet of fruit or "fall back" on less desirable leaves, stems, and herbs. A typical female chimpanzee walks about 2 kilometers (1.2 miles) a day, mostly going from one fruiting tree to another; male chimps walk an additional kilometer or so (closer to 2 miles) each day.[21] Otherwise, both sexes spend most of the day feeding, digesting, grooming, and otherwise interacting. When fruit is scarce, chimps and other apes resort to fallback foods that are ubiquitous, but doing so requires little change in how far they travel. In essence, apes are surrounded by foods they mostly choose to ignore.

Switching from a diet primarily of fruit to one chiefly of tubers and other fallback foods must have had an enormous impact on australopith travel needs. There were many species of australopiths, but all of them lived in partly open environments that ranged from woodlands adjoining rivers or lakes to grasslands. In addition to being less filled with fruit-bearing trees, these habitats were also more seasonal than the rain forests in which apes usually live. As a result, the australopiths must have foraged for foods that were more dispersed, and they almost certainly had to walk longer distances every day to find enough to eat, sometimes in open landscapes that would have exposed them to dangerous predators and withering heat. But at the same time, australopiths probably still had to climb trees, not just for food, but also to find safe places to sleep.

The demands of traveling far to get enough food and water are evident in many important adaptations for walking that evolved in several species of australopiths and which are still evident in humans today. As we saw before, early hominins like Ardi and Toumaï were bipeds of some sort, but Ardi (and thus perhaps Toumaï) did not walk entirely like us but probably took shorter strides using mostly the side of her foot to bear her weight. Ardi also retained lots of features for tree climbing, such as grasping feet with divergent big toes that likely compromised her ability to walk as efficiently as we do. However, a number of adaptations for more habitual and efficient bipedalism first appear starting about 4 million years ago in some australopiths, indicating that there was strong selection to make at least some of these species better long-distance walkers. These adaptations are such important features of the human body today that they are worth considering to help make sense of how and why we walk as we do.

Let's begin with efficiency. When apes walk, they are unable to stride like humans with relatively straight hips, knees, and ankles; instead they shuffle forward with these joints bent at an extreme angle. A gait that resembles the way Groucho Marx walked is amusing to watch, but it is also tiring and costly for reasons that help illuminate the fundamental mechanics of walking. Figure 7 illustrates how during walking, legs function like pendulums that alternate their center of rotation. When the leg is swinging forward, the center of rotation is the hip. But when the leg is on the ground and supporting the body above, it becomes an upside-down pendulum whose center of rotation is the ankle. This reversal allows us and other mammals to save energy with a clever trick. During the first half of every step, the leg's muscles contract to push the leg down, vaulting the body over the foot and ankle. This vaulting action raises the body's center of mass, storing up potential energy in the same way you build up potential energy in a weight by lifting it off the ground. Then, during the second half of each step, this stored energy is mostly returned in the form of kinetic energy as the body's center of mass falls (as if you were to drop the weight). Pendular walking is thus very efficient. However, walking becomes much more costly when you shuffle like a chimp with extremely bent hips, knees, and ankles because gravity is always pulling your body down, trying to flex those joints even more. Groucho gaits require you to contract your butt, thigh, and calf muscles constantly and forcefully to maintain your leg as a stiff, upside-down pendulum. In addition, flexing the leg's joints shortens your stride, so you travel less far per step. Experiments that measure the energy cost of walking show that a bent-hip and bent-knee gait is considerably less efficient than walking normally: a male chimp that weighs 45 kilograms (100 pounds) spends about 140 calories to walk 3 kilometers (nearly 2 miles), around three times as much as a 65 kilogram (145 pound) human requires to walk the same distance.[22]

Unfortunately, we'll never be able to watch australopiths walk or entice one to wear an oxygen mask to measure its cost of locomotion. Some researchers think these ancestors walked like upright chimps, with flexed hips, knees, and ankles.[23] Several lines of evidence, however, suggest that some species of australopiths strode efficiently, like you and I, with relatively straight (extended) joints. A number of these clues come from the foot, which has many features we retain today. Unlike apes and Ardi, whose big toes are long and diverge outward to help them grasp on to things and climb trees, species like *Au. afarensis* and *Au. africanus* had human-shaped big toes that were short, hefty, and in line with the other toes.[24] Like us, they also had a partial longitudinal arch in the foot, capable of stiffening the middle of the foot while they walked.[25] A stiffened arch and upwardly oriented joints at the base of the toes indicate that australopiths, like humans, were able to use their toes effectively to push the body forward and upward at the end of each step. And, crucially, some australopith species, such as *Au. afarensis,* had a big, flat heel bone, adapted for coping with high-impact forces caused by heel striking.[26] This kind of heel, characteristic of humans as well, tells us that when Lucy walked, she must have swung her leg forward in an extended, humanlike manner with a lengthy stride. However, at least one other australopith species,

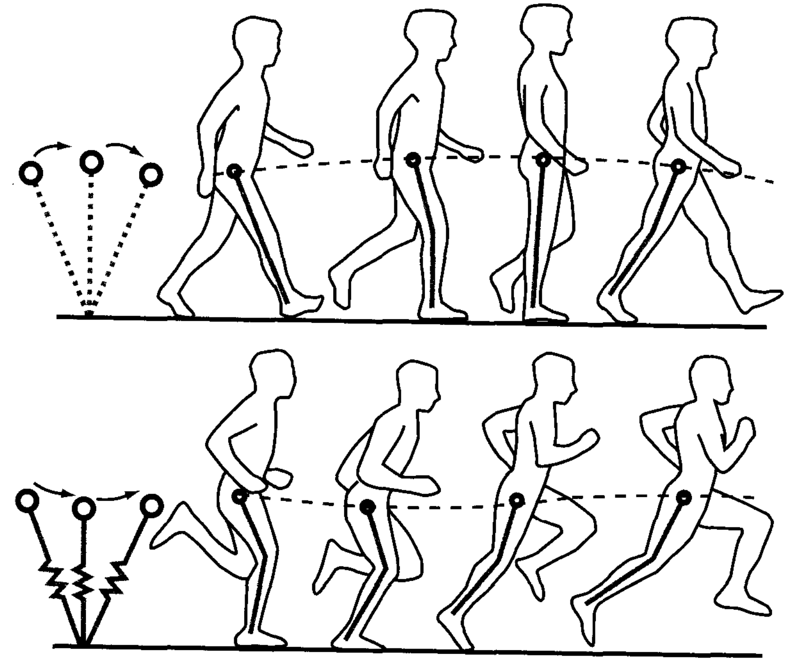


FIGURE 7. Walking and running. In walking, the leg functions during the stance like an upside-down pendulum, elevating the center of mass (circle) in the first half of the stance before it falls in the second half. In running, the leg acts more like a spring, stretching as the center of mass falls in the first half of the stance and then recoiling to help push the body up in the second half of the stance and then into a jump.

Au. sediba, had smaller, less stable heels and probably walked on a turned-in foot with a less marked heel strike and a shorter stride.[27]

Another set of adaptations for efficient walking that we still retain is evident in many of the lower limbs of australopith fossils.[28] Australopiths had femurs that were angled inward, placing their knees near the body's midline, so they didn't have to walk with a wide stance, swaying from side to side like a toddler or a drunk.[29] Their hip and knee joints were large and well buttressed, able to deal with the high forces caused when walking with just one leg on the ground. For the most part, their ankles had a nearly humanlike orientation with more stability but less flexibility than chimp ankles, presumably to help prevent dangerous ankle sprains.

Finally, it is clear that australopiths had several adaptations to stabilize their upper bodies when they were bipedal. We don't yet know whether long, curved lumbar spines, which position the trunk above the hips, evolved in the first hominins, but they were certainly present in australopith species such as *Au. africanus* and *Au. sediba*.[30] In addition, australopiths also had wide, basin-shaped pelves that curved out to the side. As we discussed before, wide hips that face sideways allow the muscles along the side of the hip to stabilize the upper body when only one leg is on the ground. Without this shape, we'd always be in danger of falling sideways, and we'd have to waddle awkwardly like a chimp.

All in all, australopith species such as *Au. afarensis* probably walked rather efficiently using a somewhat humanlike gait, a conclusion evocatively preserved by the famous footprint trails from Laetoli, Tanzania. Whoever made these trails (a good bet is *Au. afarensis*) appears to have been able to stride with extended hips and knees.[31] However, it would be a mistake to conclude that australopith locomotion was exactly the same as ours, and they still must have climbed trees to get fruit, to seek refuge from predators, and maybe to sleep at night. It should not be surprising that their skeletons retain some features inherited from apes that were useful for climbing trees. Like chimps and gorillas, they had relatively short legs and long arms with long, slightly curved toes and fingers. Many australopith species had powerful forearm muscles and upwardly oriented shoulders, well adapted for hanging or pulling themselves up. Adaptations for tree climbing are especially prominent in the upper body of *Au. sediba*.[32]

Selection for striding gaits in the australopiths left several legacies in the human body. Most important, their ability to walk effectively and efficiently played a key role in the arc of human evolution by transforming hominins into endurance walkers, well adapted for long-distance trekking through open habitats. Remember that selection to reduce the cost of walking is evidently of little consequence for chimps, probably because they walk only a mile or two in any given day, and they also need to climb and leap in trees. But if the australopiths had to travel long distances regularly in search of fruit or tubers, increased economy of locomotion would have been very advantageous. Imagine that a typical australopith mother weighed 30 kilograms (66 pounds) and had to travel 6 kilometers

(3.7 miles) a day, twice as far as a chimpanzee mother. If she walked as efficiently as a human female, she would save about 140 calories a day (which adds up to nearly 1,000 calories a week). If she were only 50 percent more economical than a chimp, she would still save 70 calories a day (nearly 500 calories a week). When food was scarce, such differences could have a large selective benefit.

As we have already discussed, being bipedal had other highly consequential costs and benefits for hominin bodies. The biggest disadvantage to being upright is the inability to run fast by galloping. The australopiths must have been slow. Whenever the australopiths ventured down from trees, they were easy pickings for such carnivores as lions, saber-toothed cats, cheetahs, and hyenas that hunt in open habitats. Perhaps they were able to sweat and thus could wait until midday to move about when these predators would have been unable to cool down as effectively. In terms of advantages, tramping around upright makes it easier to carry food, and a vertical posture exposes less surface area to the sun, which means that bipeds heat up less than quadrupeds from solar radiation.[33]

The final major advantage of being a biped, emphasized by Darwin, was that it freed the hands for other tasks, including digging. USOs often lie several feet belowground, and it can take twenty to thirty minutes of hard work to excavate them with a stick. I suspect that digging was not a problem for the australopiths. The shapes of their hands are intermediate between those of apes and humans, with longer thumbs and shorter fingers than apes,[34] and they must have been able to grasp a stick effectively. In addition, digging sticks require little skill to select or modify, and making them is certainly within the capabilities of chimps, which modify sticks to fish for termites and spear small mammals and select stones to break open nuts.[35] Perhaps selection for digging with sticks set the stage for later selection to make and use stone tools.

Your Inner Australopith

Why should anyone today care about the australopiths? Apart from being upright walkers, they seem so very different from you and me. How can we relate to these long-extinct ancestors whose brains were little bigger than a chimp's and who spent their days foraging for an unimaginably tough and unpleasant diet?

I think there are two good reasons to pay attention to the australopiths. First, these distant ancestors were a key intermediate stage in human evolution. Evolution generally occurs through a long series of gradual changes, each of which is contingent on previous events. Just as the australopiths would not have evolved had not early hominins such as *Sahelanthropus* and *Ardipithecus* become bipeds of a sort, the genus *Homo* would not have evolved if *Australopithecus* had not become less arboreal, more habitually bipedal, and less dependent on fruit, setting the stage for subsequent evolution occasioned by yet more climate change. Even more important, there is a lot of australopith in all of us. Humans are odd apes because we spend little to no time in trees (were you arboreal today?), we walk a lot, and we don't eat just fruit for breakfast, dinner, and lunch. These trends might have begun when we initially split from the apes, but they intensified remarkably over the millions of years during which various species of australopiths evolved. Many traces of these evolutionary experiments persist in your body. Compared to a chimp, your cheek teeth are thick and big. Your big toe is short, stubby, and woefully unable to grasp branches. You have a long, flexible lower back, an arch in your foot, a waist, a big knee, and many other features that help make you an excellent long-distance walker. We take these features for granted as normal, but they are actually very unusual, present in our bodies only because of strong selection for gathering and eating fallback foods millions of years ago.

Nevertheless, you are not an australopith. Compared to Lucy and her kin, your brain is three times bigger, and you have long legs, short arms, and no snout. Instead of eating lots of low-quality food, you rely on very high quality food like meat, as well as tools, cooking, language, and culture. These and many other important differences evolved during the Ice Age, which began around two and a half million years ago.