On The Origin of Species, the greatest achievement in the history of biological thought, is remarkably silent on the evolution of one important species: Homo sapiens. Darwin was understandably reticent to speculate in The Origin on the role of natural selection in human evolution. One reason was tactical. To many of his readers, it was difficult enough to accept the idea that an agentless process, rather than divine creation, was responsible for the diversity of various plants and nonhuman animals. Going the next step to suggest that humans arose in a similar manner, rather than at the hand of the Divine Creator (and in His image), would have been far too radical. Another reason for Darwin’s silence on human evolution was ignorance. Although Darwin had amassed much information on variation and evolutionary change in all sorts of living things, he had very few facts at his disposal about what happened during the evolution of the human species. In 1859, it was clearly premature to address the topic directly.

By 1871, Darwin had changed his mind. His next book, The Descent of Man and Selection in Relation to Sex, grapples directly with many aspects of human evolution, notably evidence that humans are related to other mammals, the nature of human variation, and the evolution of intelligence and morality. The book is largely an effort to demonstrate that humans evolved through the same mechanisms as other animals, and little of The Descent addresses what events actually occurred in human evolution—and for good reason. By 1871, a few fossil Neanderthals had been discovered, as had stone tools associated with extinct mammals, but Darwin and his contemporaries knew almost nothing about the intermediate evolutionary stages between humans and nonhuman primates. In spite of this ignorance, Darwin made a number of prescient speculations. For one, following T. H. Huxley and others, he reasoned that humans evolved in Africa and were most closely related to the African great apes. In addition, Darwin also inferred that the origin of bipedal locomotion was a key initial event that set humans on a separate evolutionary trajectory from our ape cousins. In his words (Darwin, 1871:140–142):
Man alone has become a biped; and we can, I think, partly see how he has come to assume his erect attitude, which forms one of his most conspicuous characters. Man could not have attained his present dominant position in the world without the use of his hands, which are so admirably adapted to act in obedience to his will…. But the hands and arms could hardly have become perfect enough to have manufactured weapons, or to have hurled stones and spears with a true aim, as long as they were habitually used for locomotion and for supporting the whole weight of the body, or, as before remarked, so long as they were especially fitted for climbing trees…. If it be an advantage to man to stand firmly on his feet and to have his hands and arms free, of which, from his pre-eminent success in the battle of life, there can be no doubt, then I can see no reason why it should not have been advantageous to the progenitors of man to have become more and more erect or bipedal. They would thus have been better able to defend themselves with stones or clubs, to attack their prey, or otherwise to obtain food. The best built individuals would in the long run have succeeded best, and have survived in larger numbers.

In other words, contrary to what the animals in George Orwell’s Animal Farm initially proclaim, “Four legs good, two legs bad,” Darwin reasoned that, under the right circumstances, bipedalism could be a powerful force for evolutionary change by freeing up the hands, thus permitting natural selection to promote tool use and other special human characteristics. Put differently, “Four legs good, two legs fortuitous.”

Darwin was a famously cautious scientist, loathe to speculate without cause. When he did make unsubstantiated guesses, he was always careful to admit so openly and to provide some justification. So why did Darwin feel comfortable enough to guess, without much evidence, that bipedalism was a key initial driving force in human evolution?

There are several answers to this question, but I think the chief one is that any satisfying theory of human evolution must address not only what happened to make humans the way they are but also why humans are so special. It is one thing to speculate on the evolution of the giraffe’s long neck or the varied beaks of Galápagos finches, but it is a far taller order to speculate on the origin of human peculiarities. Every species is unique, but we humans tend to be keenly attuned to how our species is astonishingly different from other animals, and we want to understand why. Why, of all the earth’s species, do we
have such big brains, complex language and culture, the ability to make and use sophisticated tools, to grow food, to build cities, and to exercise dominion over all other creatures? To provide a compelling alternative to creationist myths, Darwin, in 1871, just like his successors today, needed to address how and why natural selection made humans so special. But explaining the evolutionary origin of human uniqueness poses a conundrum for evolutionary biologists. The essence of Darwin’s theory is that natural selection is an agentless process by which random, heritable mutations change their frequency from one generation to the next, depending on whether they increase or decrease an organism’s odds of reproducing successfully in particular circumstances. How and why did such chance events make humans so special?

Darwin’s hypothesis that bipedalism was an initial driving force in human evolution is a superb example of the critical role of contingency in evolution. One of Darwin’s key insights is that natural selection is a highly contingent process in which evolutionary changes are constrained and/or influenced by prior events. Species evolve differently not only because of their unique environmental circumstances but also because of their particular history. For example, fins evolved in fish to help them swim, but, by chance, they acted occasionally as weight-bearing appendages in certain fish, permitting natural selection to favor one lineage of fish with more limblike fins. Without fins, limbs might never have evolved. And so it was, thought Darwin, with bipedalism. At some point, natural selection favored an ape that stood upright, thus emancipating its hands to carry objects and to make tools. These capabilities, in turn, favored early humans that had larger brains, hence more advanced linguistic and cognitive abilities. In short, Darwin’s speculation was that, without bipedalism, humans might never have evolved.

When Did Hominins and Bipedalism First Arise?

It has taken more than 100 years to amass sufficient evidence to test Darwin’s hypothesis, and, until the last few years, most of the strongest clues about human origins have been genetic and comparative rather than fossil. Since Darwin’s day, anatomical studies have indicated that humans are most closely related to the African great apes (chimpanzees, bonobos, and gorillas). Given the many similarities between chimpanzees, bonobos, and gorillas, it was reasonable to infer that the great apes were more closely related to each other than to humans (as shown in Figure 1A). However, an avalanche of genetic evidence from the last 20 years has proven this tree to be wrong, with important consequences for thinking about human origins. We now know, as Figure 1B illustrates, that humans, chimpanzees, and bonobos are more closely related to
each other than any of those three species are to gorillas. Further, by calibrating the lengths of the tree’s branches against known fossil dates, we can estimate that the chimp and human lineages diverged sometime between 5 and 10 million years ago, and that gorillas diverged from the human–chimp lineage several million years before that.

Our closer relationship to the chimpanzees is profoundly important because it means that the last common ancestor (LCA) of humans and chimpanzees must have resembled the African great apes in many ways. The basis for this inference is that gorillas and chimpanzees are remarkably similar: they share a unique, distinctive mode of terrestrial locomotion (knuckle-walking), and they are very similar to each other both behaviorally and anatomically, with most of their differences deriving from the effects of size. If one enlarges a chimpanzee skeleton, preserving the scaling relationships between size and shape, then one gets something that looks very much like a gorilla. Given that the many similarities shared by chimpanzees and gorillas are unlikely to have evolved independently, we can reliably infer that the LCA of these two species must have resembled in terms of anatomy a chimpanzee or a gorilla (which amounts to much the same thing), and that the LCA of chimpanzees and humans must have been more or less the same. In other words, it is a good bet that the first hominins (defined as a species more closely related to humans than to chimpanzees) evolved from a knuckle-walking LCA that bore some morphological
resemblance to a chimpanzee. That said, it is unlikely the LCA was exactly like a chimpanzee.

Knowing something about the LCA permits us to ask how different the first hominins were from the LCA of humans and chimpanzees. Were these hominins bipedal or were they different in other ways? Efforts to answer this question have been controversial, in large part because of differences of opinion on how to interpret the fossil record of early hominins, particularly the australopiths. The first known species of *Australopithecus, A. africanus*, was discovered in 1924 in South Africa by Raymond Dart (Figure 2A). At the time, few scientists believed that *A. africanus* was a hominin because its small brain did not accord with the Piltdown forgery (Figure 2B). This infamous forgery (a partial orangutan jaw whose teeth were filed down, mixed with fragments of a human cranial vault that had been stained and broken to make them appear to be ancient) supplied Edwardian “experts” with just what they were looking for: evidence that big brains had evolved early in human evolution, and that humans had originated in England. However, Dart’s initial discovery was soon followed by many other fossil finds in Southern and Eastern Africa. By the 1970s we knew of at least four early hominin species, some more gracile, others more robust. The oldest and most primitive of these australopiths, *A. afarensis*
Four Legs Good, Two Legs Fortuitous (made famous by the partial skeleton known as Lucy), dates back to between three and four million years ago. Importantly, the australopiths were chimpanzee-like in many ways (they had big incisors, a long snout, and a small brain), but they also provided unambiguous evidence for habitual bipedalism. Key evidence for bipedalism (shown in Figure 3) included a lumbar curve that positions the upper body above, rather than in front of, the hips; femurs that angle inward so that the knees are more centrally positioned than the hips; hips that curve to the side, permitting the muscles along the side of the pelvis to stabilize the body’s center of gravity when one foot is on the ground; and humanlike feet with robust heels, a large big toe partly in line with the other toes, and a partial arch. Even more definitive evidence that australopiths were habitually

**Figure 3** Reconstruction of *Australopithecus afarensis* skeleton (from Bramble and Lieberman, 2004) highlighting several key adaptations for walking (w) and climbing (c).
bipedal came from the spectacular 3.6 million-year-old trackway of footprints that Mary Leakey discovered at Laetoli, Tanzania.

The chimpanzee-like nature of the australopiths, combined with evidence that they were bipedal, supported Darwin’s hypothesis that bipedalism came first in human evolution. There were two big problems, however, with this inference. First, the oldest australopiths known prior to the 1990s were all less than 4 million years old. If chimpanzees and hominins diverged between 5 and 10 million years ago, then approximately 2 million to 6 million years of evolution were still unaccounted for by the fossil record. In addition, reappraisal of australopith fossils suggested that, although these hominins were bipeds, they were bipedal in ways substantially different from modern humans, because they retained many primitive features that would have improved their ability to climb trees, some of which might have compromised their ability to walk efficiently. Among the many arboreal adaptations evident in such australopiths as Lucy were long, curved toes in both the hands and the feet; relatively short legs, combined with relatively long arms; somewhat more mobile ankles; and feet that had only a partial arch (Figure 3). To this day, a vigorous debate continues over whether australopiths walked with a slightly bent-hip and bent-knee gait, or more like you and me, with a long, striding gait.

Regardless of how, exactly, the australopiths walked and climbed, several exciting new discoveries from the last decade have pushed the hominin fossil record back much closer to the time of the LCA. Darwin, no doubt, would have been delighted by these finds, which include remains of four new species (currently assigned to three different genera): *Ardipithecus ramidus*, *Ardipithecus kadabba*, *Orrorin tugenensis*, and *Sahelanthropus tchadensis*. Of these, *Sahelanthropus tchadensis* is especially exciting (Figure 4). Discovered in Chad in 2001 by an intrepid team led by Michel Brunet, this species includes a nearly complete cranium (nicknamed Toumaï) along with some teeth and jaw fragments, dated to between 6 and 7.2 million years ago. *Sahelanthropus* thus falls within the predicted time range of the chimpanzee–human divergence. Not surprisingly, Toumaï’s cranium is ape-like in many ways, but it differs unmistakably from chimpanzee and gorilla crania in several features shared with other, later hominins: it has smaller canines; larger, thicker cheek teeth; and a somewhat forward-positioned foramen magnum oriented downward rather than backward. When Toumaï (which was a likely male) was looking forward—as animals typically do—his neck would have been vertical like a biped’s (see Figure 4). Not enough has yet been published about *Orrorin* (which dates from 6 million years ago in Kenya), but recently we have learned much more about *Ardipithecus ramidus*, a younger species dated to about 4.4 million years ago in Ethiopia. *Ardipithecus ramidus* has a cranium very much like *Sahelanthropus* with a downwardly pointing foramen magnum suggestive of bipedalism, along
with slightly smaller canines and somewhat bigger, thicker cheek teeth than chimpanzees. The rest of the skeleton of *Ardipithecus*, however, is very primitive, including an ape-like foot with long curved toes and a highly divergent big toe. Just what kind of biped it was remains to be seen.

**WHY BE BIPEDAL?**

As far as we can tell, the earliest known hominins resembled chimpanzees in many respects, and they differed in just a few ways, such as smaller canines; bigger, flatter, and thicker cheek teeth; and, crucially, being bipedal. These differences raise many questions, including why early hominins were bipedal and what the evolutionary consequences of becoming bipedal might have been. Again, contingency plays a central role in the answer to both questions because bipedalism appears to be a special solution to some particular problems posed by being a knuckle-walker.

Knuckle-walking, the manner in which chimpanzees and gorillas walk on the middle digits of their hands, is a classic example of the kinds of compromise solutions that evolution can favor, given the right conditions. Like their cousins, orangutans and gibbons, chimpanzees and gorillas evolved from frugivorous apes that were well adapted to hanging below the branches of trees—thanks to several specialized features, such as highly mobile shoulders, elongated arms, flexible wrists, and long, curved fingers. At some point, chimps and gorillas apparently re-evolved a unique form of quadrupedalism, knuckle-walking, which is really a way of walking on all four limbs.
while retaining features in their shoulders, forelimbs, and hands that are useful for climbing and hanging. Knuckle-walking enables chimps to be spectacular arboreal athletes while also permitting them to trek across the forest in search of areas with more plentiful food. But knuckle-walking has an energetic cost. Experiments that measure the cost of transport (the amount of oxygen consumed per unit of body mass to move a given distance) find that knuckle-walking by chimpanzees is about 75% more expensive than either normal quadrupedalism or bipedalism. This cost is not very significant to chimpanzees, who typically trek only 2 to 3 km per day, but it would have been very costly to apes that needed to travel longer distances. Under such circumstances, there probably would have been strong selection against knuckle-walking.

Which brings us back to bipedalism and the earliest hominins. We will never know precisely why the earliest bipeds stood up—perhaps they did so to feed on fruits on branches and in bushes—but we can guess that, at some point, a group of early hominins found themselves in a habitat that required them to travel longer distances but also to remain adept at climbing trees. Under these conditions, hominins with such features as lumbar spines that were more curved, hips that faced more laterally, and extended hips and knees that were better suited to a bipedal gait, would have had a selective advantage over hominins trying to trek long distances with a more ape-like anatomy. This scenario is difficult, perhaps impossible, to test definitively, but is supported by the few lines of evidence so far available. First, all of the earliest hominins (Sahelanthropus, Ardipithecus, and Orrorin) appear to have lived in woodland habitats that were apparently more open than the forests typically inhabited by chimpanzees and gorillas. In addition, selection for bipedal locomotion to forage efficiently for more widely dispersed foods accords with the derived dental characteristics of the first hominins. As noted above, early hominins also differ from chimps in having bigger, thicker cheek teeth as well as smaller canines. Studies of dental functional morphology show that bigger, thicker molars and premolars are useful for chewing harder, tougher foods that require more forceful grinding. Chimps have thinner, smaller molar teeth because they feed primarily on a diet of high-quality fruit. Chimps also have large canines, which are useful for fighting, but such canines restrict how much they can move their jaws from side to side when grinding food with their back teeth. Viewed together, all of the derived features evident in the earliest hominins point to a suite of adaptations for an ape-like animal that occasionally had to range more widely to find and to chew tougher, harder food than chimps typically eat.
Darwin was characteristically prescient when he speculated that upright locomotion evolved early in human evolution—but what of the rest of his theory, that emancipating the arms and hands from terrestrial locomotion set the stage for future developments? Darwin was well aware of the pitfalls of viewing evolution as a teleological process in which past events inevitably lead to present conditions. Bipedalism may have been a critical precursor to the evolution of big brains, tool-making, and other hallmark features of humankind, but these developments cannot have been inexorable consequences of an upright posture. Indeed, what little we know suggests that the early hominin way of life, once evolved, persisted with only minor variations for at least 4 million years. After *Sahelanthropus* and *Ardipithecus*, more than a half dozen species of different australopiths evolved, but the differences between them are not very extensive, and mostly reflect anatomical features involved in mastication. For the most part, the australopiths lived in woodland habitats and frequently ate fruits, but they probably also ventured out into more open habitats, either to travel long distances between patches of woods, or perhaps to dig up tubers and other foods unavailable in forest and woodland habitats.

Unfortunately, the hominin fossil record is very poor between 3 million and 2 million years ago, but we do know that the genus *Homo* evolved sometime during this period. Many details remain obscure, but we can characterize the major features of this transformation by comparing *H. erectus*, which followed the transition, with earlier australopith species (see Figure 5). Australopiths vary to some extent, but they were generally the size of chimpanzees (25–50 kg in weight and 100–150 cm tall), with relatively long arms, short legs, and, as noted above, retaining many adaptations for climbing trees. Australopiths also had small brains, ranging from 400 to 550 cm$^3$, and they had big, thick, cheek teeth that were set in large, muscular faces well adapted for chewing hard, tough foods. *H. erectus* remains, which first appear 1.9 million years ago, vary considerably, but they generally have larger brains, ranging from 600 cm$^3$ to 900 cm$^3$, along with bigger bodies, with body masses ranging from 45 kg to 70 kg and heights ranging from 150 cm to 185 cm. In addition, *H. erectus* had smaller, thinner cheek teeth set in a vertical, less snoutlike face and a much more modern body with long legs and short arms poorly suited for climbing, but better suited for long-distance trekking and running. *H. erectus* was a long-enduring and widespread species that dispersed out of Africa and into Eurasia by 1.8 million years ago, and it persisted in Asia until quite recently, maybe less than 50,000 years ago. It is important to recognize, however, that the derived features evident in *H. erectus* did not evolve all at once, and the transformation from
Australopithecus to Homo was complex in nature. Early individuals of *H. erectus* were highly variable, and along with their likely ancestor, *H. habilis*, displayed a mixture of primitive australopith features, especially in its postcranium, as well as more derived cranial and dental features. The first appearance of the genus *Homo* corresponds very approximately to the first appearance of stone tools, around 2.6 million years ago.

No doubt many factors selected for the transition from *Australopithecus* to *Homo*, but changing environments probably played a major role. Gradual cooling over the last 5 million years was responsible for a general trend in Africa of shrinking forests and expanding savannas, but there is evidence that the pace of these changes increased after 3 million years ago. As more open habitats became more prevalent, the genus *Homo* apparently evolved a new way of life that was more energy intensive. Key evidence for this shift comes from the unusual combination of bigger bodies and bigger brains along with smaller...
teeth. As a rule, metabolic costs scale to body mass to the power of 0.75, which means that larger-bodied *H. erectus* individuals would have needed absolutely more calories per day than australopiths, although they would have needed relatively fewer calories per unit body mass. Bigger brains were also a major added cost because brain is one of the most expensive tissues in the body, consuming 20 kcal/kg/h, about 20 times the energy cost of muscle tissue. In practical terms, this means that the human brain consumes approximately 20–25% of an adult’s metabolism and as much as 50% of an infant’s. Increased energetic demands in *H. erectus* were especially onerous for reproducing females, who not only had to supply their own energetic needs but also the energetic needs of their infants. Daily energy requirements for gestating and lactating mothers increase by 25% and 50%, respectively. According to estimates by Aiello and Key (2002), a nursing *H. erectus* mother would have needed to eat about 2,500 kcal per day, about 800 kcal more than a nursing australopith. How did *H. erectus* mothers obtain this extra energy?

Most animals cope with increasing energetic demands by taking advantage of scaling laws. Because basal metabolic rates scale to body mass to the power of 0.75, bigger animals have relatively slower rates of metabolism and can lengthen the time it takes for food to pass through their guts, thereby making use of fermentation processes in the gut to digest foods of lower quality and with a higher content of fiber. These principles account for why gorillas can eat a more fibrous and less fruit-rich diet than smaller-bodied chimpanzees. *H. erectus*, however, did not employ this strategy, as we can tell from its relatively smaller chewing muscles and the smaller, thinner teeth compared with *Australopithecus*. Instead of getting more energy by eating foods of lower quality, *H. erectus* appears to have been more reliant on foods of higher quality that required less energy to chew. Since fruits are not abundant in the savanna, and cooking was probably not invented until fire was first controlled by hominins less than 750,000 years ago, the major source of high-quality food was animal tissue: meat, marrow, and brains. The archaeological record provides corroborating evidence that *Homo* species became carnivores of sorts. By 2.6 million years ago, hominins were making simple stone tools, getting access to animal carcasses (perhaps initially by scavenging), and then extracting marrow and cutting meat off bones. By 1.8 million years ago, *H. erectus* was able to hunt big animals, such as wildebeest and kudu.

**B R A I N S , B R A W N , A N D E N D U R A N C E R U N N I N G**

The problem of how early *Homo* species become hunters brings us back to the topic of bipedal locomotion. In particular, it is useful to consider some of the constraints and opportunities of being a carnivorous, bipedal primate. Most
carnivores hunt using a mixture of stealth and power, ultimately relying on speed, agility, and force to overcome their prey. In this respect, having only two legs would have posed a problem for an unprepossessing early hominin hunter. Bipedal walking and running may be less costly than knuckle-walking, but bipeds cannot gallop and thus can run only comparatively slowly. Today, the world’s fastest humans can sprint approximately 10 meters per second for only about 20 to 30 seconds, not nearly fast enough or long enough to keep up with most quadrupeds, most of whom can easily run faster than 15 meters per second for several minutes. In addition, bipeds are much less stable and less maneuverable than quadrupeds (as anyone who has tried to chase a dog well knows). Because of these constraints, most paleoanthropologists have assumed that bipedal hominin hunters were able to compensate for these deficiencies by using tools and having the ability to throw. Until recently, human hunters relied on such technologies as the bow and arrow, nets, and the spear thrower. And, as Darwin (1871) argued in *The Descent of Man and Selection in Relation to Sex*, such adaptations were probably contingent upon bipedalism, which freed up the hands and arms from a role in locomotion, permitting natural selection to modify them for other uses.

But there is one problem with this deeply entrenched idea: it turns out that effective projectile weapons were invented only fairly recently. The bow and arrow and the spear thrower first appear less than 100,000 years ago, and the first stone spearheads were invented between 200,000 and 300,000 years ago. According to the archaeological record, the most lethal technology available to a *H. erectus* hunter 2 million years ago was a club or a sharpened wooden stick. To those of us who forage in supermarkets (hunting at most for bargains), this fact may seem unremarkable, but untipped spears pose several challenges that make them unsuitable weapons for even the most foolhardy and desperate of hunters. Untipped wooden spears have a limited ability to penetrate an animal’s hide when thrown, and, even if they do penetrate the hide, they seldom cause death because, unlike spearheads, untipped spears rarely cause lacerations and internal bleeding. Thus, early hominin hunters who wished to kill large animals with untipped spears probably would have had to get up very close to the animals and risk being gored or kicked by their prey. No experienced modern hunter is so foolhardy, and one can easily imagine that such risky behaviors would dramatically lower any early *Homo* hunter’s fitness, quickly selecting against them.

So to answer the question, “How did early hominins hunt?”, we need to return to the issue of contingency and the power of natural selection to favor novel solutions using whatever variations are at its disposal. As noted above, once hominins became bipedal, they gave up speed in order to be more economical. Indeed, the obvious fact that humans lack speed and power when
compared with most animals is deeply rooted in our psyche. Many creation myths tell stories about how we humans have triumphed over nature, red in tooth and claw, by using our superior wits. Darwin (1871, p. 157) also believed in this idea: “The slight corporeal strength of man, his little speed, his want of natural weapons, etc, are more than counterbalanced, firstly by his intellectual powers, through which he has, whilst remaining in a barbarous state, formed for himself weapons and tools, etc, and secondly by his social qualities which lead him to give aid to his fellow-men and to receive it in return.” Put simply, by becoming bipedal, hominins were set on a trajectory that favored brains over brawn.

I am loathe to disagree with Darwin, but I think the notion that humans became hunters through the triumph of brains over brawn is partly wrong for several reasons. The first is that large brains and sophisticated weapons did not evolve until later in human evolution. Brain size in early Homo species is a little bigger than in Australopithecus species, but so is body size, keeping the ratio of brain to body size about the same in early H. erectus and Australopithecus. In addition, although humans are slow and lack power compared with most mammals, humans are actually remarkable endurance athletes, particularly when running long distances in high heat. Such endurance athleticism is actually quite rare in the animal world. Most mammals, even dogs and horses, can trot for long distances, but they cannot gallop for long because quadrupeds cannot pant while galloping. Unless it is very cold, galloping quadrupeds overheat rapidly. In contrast, humans are able to run under aerobic capacity in the heat for hours on end at speeds up to 6 m/s, well above the trot-to-gallop transition speed of most mammals, even large quadrupeds weighing as much as 500 kg. Humans can actually outrun horses over long distances, such as the marathon (42 km), especially in hot weather.

The superb endurance running capabilities of humans are hardly a fluke, but, instead, derive from a suite of novel features. Many of these features are such musculoskeletal adaptations as long legs, a large gluteus maximus muscle, and long tendons in our legs that help us to run with a bounding, springy gait that is the biomechanical basis for energy exchange during running. (When running, we use our legs as springs, first storing and then releasing elastic energy in the tendons and muscles of our legs.) As my colleague Dennis Bramble and I have argued, many of these features first appear in Homo erectus and play no role in walking, which uses a different, pendular form of mechanics. In addition, humans are unique among mammals in being able to thermoregulate effectively by sweating. We are the champion sweaters of the animal world, thanks to our absence of fur and a many-fold increase in the number of eccrine glands (2 to 5 million) that we have all over our bodies. We do not yet know
when sweating and furlessness evolved, but my prediction is that it occurred at least 2 million years ago.

The evolution of running capabilities in humans in combination with the origins of meat eating raises the hypothesis that *H. erectus* evolved endurance capabilities—brawn of a special sort—in order to compete with other carnivores and, thus, to pay for bigger bodies and bigger brains. The hypothesis is that, long before the invention of the bow and arrow, *H. erectus* became the first diurnal, endurance-running carnivore by practicing a special form of predation called persistence hunting. During persistence hunts, hunters chase an animal above its trot-to-gallop transition speed during the middle of the day when it is hot. Because the prey cannot pant while galloping, it quickly overheats as it runs from the hunter. Like the tortoise chasing the hare, the hunter keeps coming, tracking the animal whenever it hides. And the faster the hunter can track his prey, the less time the animal has in which to cool itself down between bouts of galloping. Eventually, usually in 10 to 15 km, the exhausted prey collapses from hyperthermia and the hunter can kill it safely with nothing more than a simple spear or a club. All a *H. erectus* hunter would have needed was a good drink of water before (and after) he started running, and a hot, open habitat in which to chase his prey. Further, persistence hunting is not very costly when compared with its potential returns. The cost of transport (kcal/kg/km) for running at endurance speeds is only about 30–40% higher than walking, so chasing an animal for 15 km costs a hunter only about 1,100 kcal, about 300 more kcal than walking the same distance. According to ethnographic accounts by Louis Liebenberg, persistence hunting is remarkably effective (50% of persistence hunts by Bushmen in the Kalahari desert are successful) and was practiced until recently by hunter-gatherers in many hot, arid parts of the world, such as Africa, America, and Australia. Persistence hunting is rare today not because it is ineffective but because it has been rendered unnecessary by such recently invented technologies as the bow and arrow, nets, hunting dogs, and guns. Why run 10–15 km to kill an animal when you can shoot it or buy it shrink-wrapped at the butcher’s shop?

In short, walking was initially very important in human evolution, but, at some point, running also became important by enabling hominins to become carnivores. Although traces of our history as walkers and runners are abundant in our physiology and anatomy, many aspects of the endurance-running hypothesis are difficult to test. Although a number of musculoskeletal features that would have enabled hominins to run long distances were first evident in fossil remains attributed to *Homo erectus*, many key adaptations, such as greater tendon length or the elaboration of sweat glands, are hard to assess from fossil evidence. Therefore, we do not know if *H. erectus* was as good at endurance running, hence persistence hunting, as modern humans. In addition, although
archaeological traces suggest that *H. erectus* hunters were able to kill medium-to large-sized animals, we don’t actually know how those animals were hunted. That said, the endurance-running hypothesis not only explains how early hominins could have hunted such big animals as wildebeest armed with nothing more lethal than a sharpened wooden stick or a club, but it also accounts for why humans apparently evolved the ability to run long distances in the midday sun. In addition, the hypothesis also explains another important fact—namely, that the increase in brain size in human evolution occurred well after hominids became proficient hunters. The first individuals of *H. erectus* had brains between 600 cm$^3$ and 900 cm$^3$, but, by a million years ago, *H. erectus* brains were larger than 1000 cm$^3$. It is reasonable to speculate that the evolution of endurance-running capabilities, which permitted persistence hunting, released a constraint on the size of the brain, a costly organ to grow and to maintain. In turn, bigger brains set the stage for the evolution of our own species, *H. sapiens*, in Africa sometime in the last 300,000 years. But that’s another story.

**FINAL THOUGHTS AND FUTURE DIRECTIONS**

To some, the idea of evolution is most threatening because it leads one to realize that the world around us is really the result of innumerable chance events, many of them contingent upon previous chance events. It follows that, although we humans are indeed a special species with dozens of unusual features and traits that make us unique in myriad ways, those qualities evolved for no particular reason, other than through the cold calculus of natural selection. Further, the characteristics that make us human and have given us some measure of dominion over the other animals and plants of the Earth derive from a long chain of fortuitous occurrences, each of which set up conditions that made subsequent changes either possible or impossible.

After 150 years of concerted research, we know far more than Darwin did about how, when, and why humans evolved, but much of our species’ evolutionary history remains unknown or in dispute. The hypothesis recounted above just scratches the surface of what we know and need to explain about human evolution. I have not touched upon the evolution of language, aggression, moral sense, concealed ovulation, and other important aspects of human biology and behavior that make us special. That said, Darwin made some pretty good guesses in *The Descent of Man*, including the hypothesis that becoming bipedal was one of the first major shifts that helped set our first hominin ancestors off on a new path from the apes. Being bipedal had some advantages over knuckle-walking, reducing costs and freeing up the hands, but upright locomotion also constrained our ancestors to be slow and awkward creatures. Hence, selection for walking in the earliest hominins appears to have set the stage for
selection for endurance running, which helped species of the genus *Homo* to become carnivores of sorts, gaining access to high-quality food as the savannas expanded sometime about 2.5 million years ago. Thus, as Darwin speculated, becoming bipedal was one of those chance events that made possible a suite of later shifts, including tool-making, hunting, bigger brains, language, and the ability to run a marathon.

Paradoxically, humans have become essentially sedentary today, in part because the evolution of walking and running helped us to evolve large, complex brains that freed us from the need to walk or run much anymore. Today, many humans walk very little, and few people run except to keep fit. Should civilization collapse tomorrow, few of us would know how to hunt or gather. If and when this collapse occurs, and if our species does not go extinct, then perhaps natural selection will go to work again, this time constrained by a new set of contingencies, many of which will trace back to some knuckle-walking apes about 6 million years ago that could walk better than their cousins.

**SUGGESTED READINGS**


