11

The Origins and Evolution of Early *Homo*

BIG QUESTIONS

1. What characteristics define the genus *Homo?*
2. What were the earliest members of the genus *Homo?*
3. What are the key evolutionary trends and other developments in early *Homo?*

Charles Darwin was struck by the great anatomical similarity of living humans and African apes. In 1871, writing about human origins without having seen a human fossil, he settled on Africa as the birthplace of the earliest hominins. But he was not the only leading scientist in the nineteenth century to think about human origins and where humans first evolved. Ernst Haeckel (1834–1919), Germany's preeminent anatomist and evolutionary biologist of the late nineteenth century, came up with an entirely different origins scenario. He reasoned that the Asian great ape, the orangutan, is more anatomically similar to humans than are the African great apes. Asia, not Africa, he concluded, must have been the hominins' ancestral homeland. In his extensive scholarly work about human origins and evolution, Haeckel went to great lengths to describe what the first hominin would have looked like. He even went so far as to propose a genus name for the ancestor: *Pithecanthropus,* meaning "ape-man."

　　Haeckel's books on early human evolution and its Asian origins profoundly inspired a precocious Dutch teenager, Eugène Dubois (1858–1940; **Figure 11.1**). Fascinated by Haeckel's ideas about

FIGURE 11.1

Eugène Dubois A Dutch anatomist and anthropologist, Dubois discovered the first early hominin remains found outside Europe.

evolution, Dubois devoured Darwin's *On the Origin of Species.* He enrolled in medical school at the University of Amsterdam at age 19 and received his medical degree at 26. In addition to being a well-trained physician, he was a superb scientist and was hired as a lecturer in the university's anatomy department. At the same time, his interests in evolution deepened. He became convinced that to truly *study* human origins, he had to *find* human fossils. Within a year of being promoted to lecturer he quit his job, gathered his resources, got hired as a physician for the Dutch colonial government, and moved with his wife and their baby to the Dutch East Indies (the modern country of Indonesia, which includes the islands of Sumatra and Borneo; **Figure 11.2**). His friends, neighbors, and associates thought he was reckless at best to risk his family's well-being as he looked for something that might never be found. Soon after landing in Sumatra in December 1887, Dubois assumed his new responsibilities as a physician at a military hospital, spending his money and free time in the pursuit of fossils. After trying to juggle medicine and fossil hunting, he talked the Dutch colonial government into letting him leave his day job to work for the Dutch as a full-time paleontologist. With the help of two civil engineers and a group of 50 convicts, he searched the island but found nothing. Meanwhile, he suffered from discomfort, fatigue, illness, and depression.

Desperate to avoid returning to Holland without having found fossils, Dubois pleaded with his superiors to let him shift his focus from Sumatra to nearby Java. The authorities accepted his assurances that Java would produce fossils. After his move to Java, Dubois heard about bones appearing out of the eroding banks of the Solo River, near the village of Trinil. Soon after commencing excavations in the late summer of 1891, he and his field crew discovered a human molar. Within a couple of months they found a partial skull, and later in the following year they found a complete femur (**Figure 11.3**). The skull was extraordinary. It was clearly not from *Homo sapiens*—it had a low and long braincase, no forehead to speak

FIGURE 11.2

Dutch East Indies On the island of Java, one of the southernmost islands of what is now Indonesia, Dubois discovered the hominin fossil later identified as *Homo erectus.*

of, and large browridges like apes'. Was it from an ape or a human or something between the two? By measuring the braincase's volume, he estimated that in life the brain had been about 1,000 cc, too big for a modern ape (a chimpanzee's brain is 400 cc) and too small for a modern human (the average human brain today is about 1,450 cc). He had found what he was looking for: the human ancestor. In fact, Dubois's anatomical study revealed that the femur was essentially identical to a modern human's—this primitive human ancestor was fully bipedal. Convinced that he had found what Haeckel had predicted, he called his fossil hominin **Pithecanthropus erectus,** meaning "upright-walking ape-man."

Dubois's ideas and the fossils he found met with mixed reactions, mostly negative. However, as the years went by, others found more hominin fossils in Java and elsewhere in Asia. It became clear to most anthropologists that Dubois's fossils from Java were early members of our genus but a different species, and these hominins are now called **Homo erectus.** Dubois's fossil turned out to be not from the earliest hominin or even from the earliest species of *Homo* (see chapter 10 and later in this chapter).

Dubois was wrong in thinking that evidence of the earliest human would be found in southeast Asia, but he was working in a scientific vacuum. Without today's fossil record to guide him, he drew the best possible conclusion from the evidence available and made crucially important discoveries about the genus *Homo*'s evolution. The only scientist of the time who set out a research plan to test a hypothesis about early human ancestors, he sought fossil evidence to establish evolutionary relationships. In contrast to the great evolutionists of the nineteenth century—Darwin, Haeckel, Huxley, and others—he endeavored to use fossils, not living animals' comparative anatomy, to test his hypothesis. This revolutionary development in anthropology set the stage for paleoanthropology, the study of early human evolution.
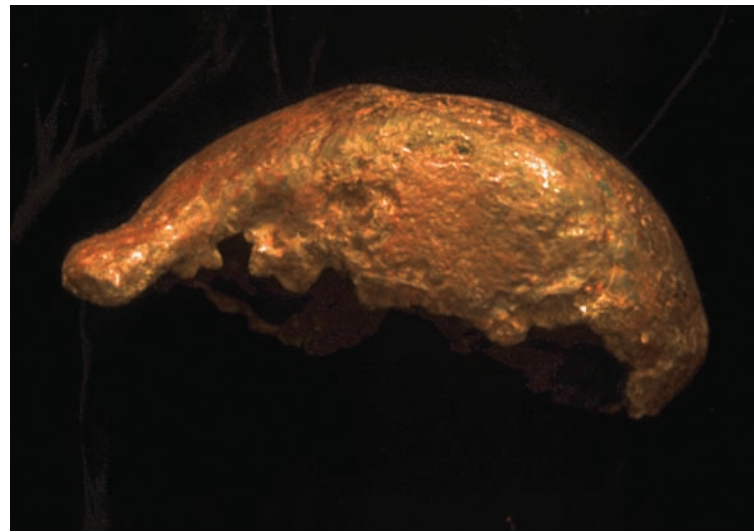
This chapter focuses on the earliest members of our genus: *Homo habilis* and *H. erectus*. These were the hominins that began to develop the characteristic behaviors that we see in living humans, that increasingly employed intelligence and displayed adaptive flexibility, and that first depended on material culture. During early *Homo*'s evolution, hominins began to colonize areas of the world outside Africa. The earliest fossil evidence, from around 2.5–1.0 mya, indicates that *H. habilis* and the earliest *H. erectus* lived at the same time as other hominins, the later australopithecines (discussed in chapter 10). Early *Homo,* however, adapted very differently from the australopithecines. These changes set the course for human evolution, the record of which is supported by abundant fossils.

FIGURE 11.3

Java Man Dubois originally named this hominin fossil *Pithecanthropus erectus,* though it was nicknamed "Java Man" after the island on which it was found. Dubois recovered hominin remains, including this partial cranium.

Pithecanthropus erectus The name first proposed by Ernst Haeckel for the oldest hominin; Dubois later used this name for his first fossil discovery, which later became known as *Homo erectus.*

Homo erectus An early species of *Homo* and the likely descendant of *H. habilis;* the first hominin species to move out of Africa into Asia and Europe.

11.1 *Homo habilis*: The First Species of the Genus *Homo*

The Path to Humanness: Bigger Brains, Tool Use, and Adaptive Flexibility

Modern humans are distinctive in having large brains and in depending on material culture for survival. Rather than relying on their bodies for the collection, processing, and eating of food, modern humans rely on tools and technology as part of their adaptive strategy. These attributes are what scientists looked for in the fossil record when they sought the first species of our genus. Which of the multiple hominin species in the late Pliocene and early Pleistocene show brain size expansion? Which of the hominins with brain size expansion likely depended on tools and material culture for promoting adaptive success and behavioral flexibility?

Soon after the discovery of the massively robust australopithecine *Australopithecus*
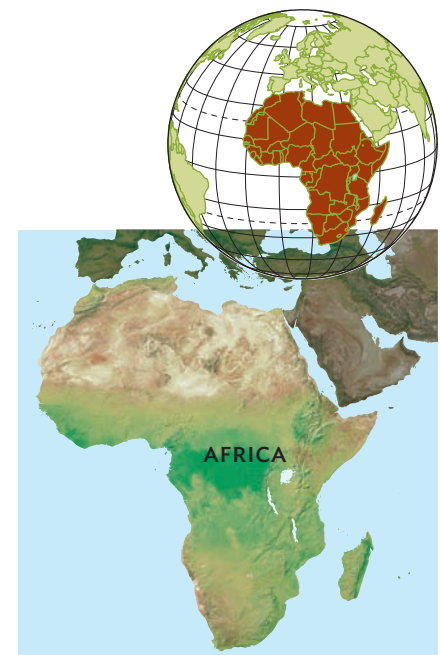

AFRICA

Lake Turkana

KENYA

boisei ("OH 5" from Olduvai Gorge; see chapter 10), remains of a hominin having jaws, teeth, and a face that were relatively smaller and a brain that was relatively larger were found, also in Olduvai Gorge. Its describers—Louis Leakey, Philip Tobias, and John Napier—recognized the significance of this combination of characteristics and named the new hominin *Homo habilis* (meaning "handy man"). *H. habilis* is now known from Tanzania, Kenya, Ethiopia, Malawi, and South Africa—the same geographic distribution as that of the contemporary australopithecines (**Figure 11.4**). *H. habilis* found on the eastern side of Kenya's Lake Turkana is sometimes called *Homo rudolfensis* (**Figure 11.5**). The major difference is that *H. rudolfensis* is somewhat bigger than *H. habilis*. Because they have the same general body plan and overall morphology (bigger brains, smaller faces), here the two species are discussed as *H. habilis*.

As Leakey and his associates recognized, *H. habilis* differs in its anatomy from the robust australopithecines dating to about the same time in East Africa and South Africa. *Au. boisei* had an enormous chewing complex—its back teeth, jaws, and face were very large—but it had a small brain. In sharp contrast, *H. habilis* had a smaller chewing complex and a larger brain. Combined, the reduced chewing complex and increased brain size gave *H. habilis*'s skull a more rounded, or globular, appearance. Most anthropologists agree these attributes indicate that *H. habilis* began the lineage leading to modern humans.

Still unconfirmed is the identity of *H. habilis*'s immediate ancestor. The anthropologist Tim White's morphological comparisons between *H. habilis* and the earlier australopithecines suggest that the ancestor was *Australopithecus garhi* because its face, jaws, and teeth are most similar to *H. habilis*'s. White suggests that the evolutionary transition took place sometime around 3.0–2.5 mya. Consistent with this interpretation is the discovery of hominin fossils that combine australopithecine and *Homo* morphological characteristics. For example, from the site of Ledi-Geraru in the Afar region of Ethiopia, a partial mandible dating to 2.8 mya combines large teeth (*Australopithecus*) with *Homo*-like morphology. The discovery of a hominin with australopithecine

(a) (b) (c)

FIGURE 11.4

Homo habilis Many fossils of this hominin species have been recovered from East Africa and South Africa. **(a)** This specimen, known as "OH 24" or "Twiggy," was discovered in Tanzania in 1968. Dating to 1.8 mya, Twiggy had a larger brain and a less protruding face than australopithecines. **(b)** Slightly younger than Twiggy, this lower jaw, known as "OH 7," was found in Tanzania in 1960 and dates to 1.75 mya. Given its small dental size, researchers estimated that the brain size would have been smaller than in other *H. habilis* fossils. **(c)** This cranium, "KNM-ER 1813," was discovered in Kenya in 1973 and dates to 1.9 mya. Its brain capacity is somewhat smaller than that of other, later *H. habilis* specimens. (Photo [a] © 1997 David L. Brill, humanoriginsphotos.com; photo [c] © 1985 David L. Brill, humanoriginsphotos.com)

characteristics meets the expectation of early *Homo*; that is, the hominins represented by the Ledi-Geraru mandible have only minor differences with the ancestral hominins.

Homo habilis and *Australopithecus:* Similar in Body Plan

For many years, *H. habilis* was known from just skulls and teeth. Anthropologists had no idea what the rest of the skeleton looked like. Excavations at Olduvai Gorge in the 1980s by Donald Johanson and his associates led to the discovery of a very fragmentary but important skeleton of *H. habilis,* known as "OH 62." The skeleton is from an individual that was short—about 1.1 m (3.5 ft)—like the australopithecines. Also like the australopithecines, this individual had short legs in comparison with the arms. Although *H. habilis* walked bipedally, these short legs would not have been involved in the kind of efficient striding performed by living people. The gait would have been shorter.

Homo habilis's Adaptation: Intelligence and Tool Use Become Important

H. habilis's short legs indicate that the species retained a primitive form of bipedalism, more australopithecine than human. Much more telling about *H. habilis*'s adaptation and evolution are skull and teeth morphology and evidence of the making and use of stone tools. Fossil skulls and fossil teeth reveal that this hominin ancestor had a larger brain, smaller chewing muscles, and smaller teeth than did earlier and contemporary hominins, the australopithecines. Both the brain enlargement and the masticatory changes may be linked to the growing importance of tools. Anatomical evidence from the study of hand bones, such as the presence of muscles that would have provided the necessary precision grip, suggests that *H. habilis* and at least some of the australopithecines made and used tools. For several reasons, toolmaking and tool use were

Homo habilis: The First Member of Our Lineage

H. habilis was the first hominin to have anatomical and behavioral characteristics that foreshadowed the evolution of *Homo sapiens:* greater intelligence, reliance on tools, and dietary and behavioral flexibility.

(Photo © 1985 David L. Brill, humanoriginsphotos.com)

Location/Sites	Africa (Olduvai Gorge, Lake Turkana, Middle Awash, Omo, Uraha, Sterkfontein)
Chronology	2.5–1.8 mya

Biology and Culture (Compared with Australopithecines)

Feature	Evidence	Outcome
Tool use (Oldowan)	Skulls Teeth	Smaller face and smaller jaws Reduced size
Intelligence	Brain size	Increase (to 650 cc)
Diet (scavenging, plant collecting)	Plants available Body size	Perhaps more generalized No significant change
Locomotion	Leg length:arm length	No significant change

likely more important in *H. habilis*'s adaptation. First, stone tools are more common in *H. habilis* fossil sites than in *Australopithecus* fossil sites. Second, *H. habilis*'s expanding brain size indicates that it was smarter than *Australopithecus,* with a kind of cognitive advancement almost certainly linked to toolmaking and tool use. That is, *H. habilis* and the lineage it founded became reliant on intelligence, toolmaking, and tool use as central means of adaptation. In contrast, the australopithecines became increasingly specialized, focusing on a narrower range of foods that required heavy chewing. They may have made and used tools, but tools were not as fundamental to their survival and adaptation. *H. habilis*'s behavioral advances laid the foundation for later hominins' success, including their rapid spread out of Africa and to other areas of the globe.

Habitat Changes and Increasing Adaptive Flexibility

Environmental reconstruction of the East African and South African landscapes at 2.5 mya provides some insight into early *Homo*'s adaptive shifts. This reconstruction indicates a spread of warm-season (C_4) grasses, increasing habitat diversity, and increasing food resources for early hominins. Such information, along with skull and teeth morphology, suggests early *Homo*'s increasing dietary versatility. Tools may have played a central role in these early hominins' ability to exploit this increasingly diverse landscape. That is, stone tools were likely important for digging roots and tubers and for processing them for consumption. Such extremely primitive technology did not include

the kinds of tools associated with later hominins that were clearly social, predatory hunters (discussed later; see "Evolution of *Homo erectus:* Biological Change, Adaptation, and Improved Nutrition"). Still, tools increased these early hominins' *capability* of eating a greater range of food, most of it plants or small animals, the latter acquired by luck and opportunity and perhaps scavenging. This dietary shift may be what spelled adaptive success for early *Homo* and extinction for late *Australopithecus*.

Early *Homo* in South Africa: *Homo naledi*

The record of human evolution is filled with unexpected discoveries, and more so perhaps for the African continent than for any other continent. At Rising Star Cave, located within a mile or so of the iconic Swartkrans, Sterkfontein, and Kromdraai australopithecine sites in the Blaaubank River valley in the Republic of South Africa (see chapter 10), spelunkers (or "cavers") recruited by paleoanthropologist Lee Berger discovered a remarkable cache of early hominin remains in 2013. The deep and torturous cave system made recovery of the fossils highly challenging (see "How Do We Know: Underground Astronauts," p. 360–361). To date, some 1,550 cranial, dental, and postcranial hominin fossils representing at least 15 individuals of various ages and both sexes have been found and described by Berger and his team (**Figure 11.6**). The sheer volume and number of fossils make this assemblage one of the largest collections of early hominins found at any one site in Africa or anywhere else in the world for that matter.

The general morphology of the series is representative of early *Homo*, and the skull is closest to *Homo erectus* in overall shape. However, Berger and his research team gave the fossils a new species name—*Homo naledi*—owing to the presence of distinctive characteristics. Like some of the record from South Africa, these fossils from Rising Star Cave are not dated owing to the fact that they are associated with sedimentary rock, which is not datable via the kinds of absolute methods used in other hominin

(a)   **(b)**
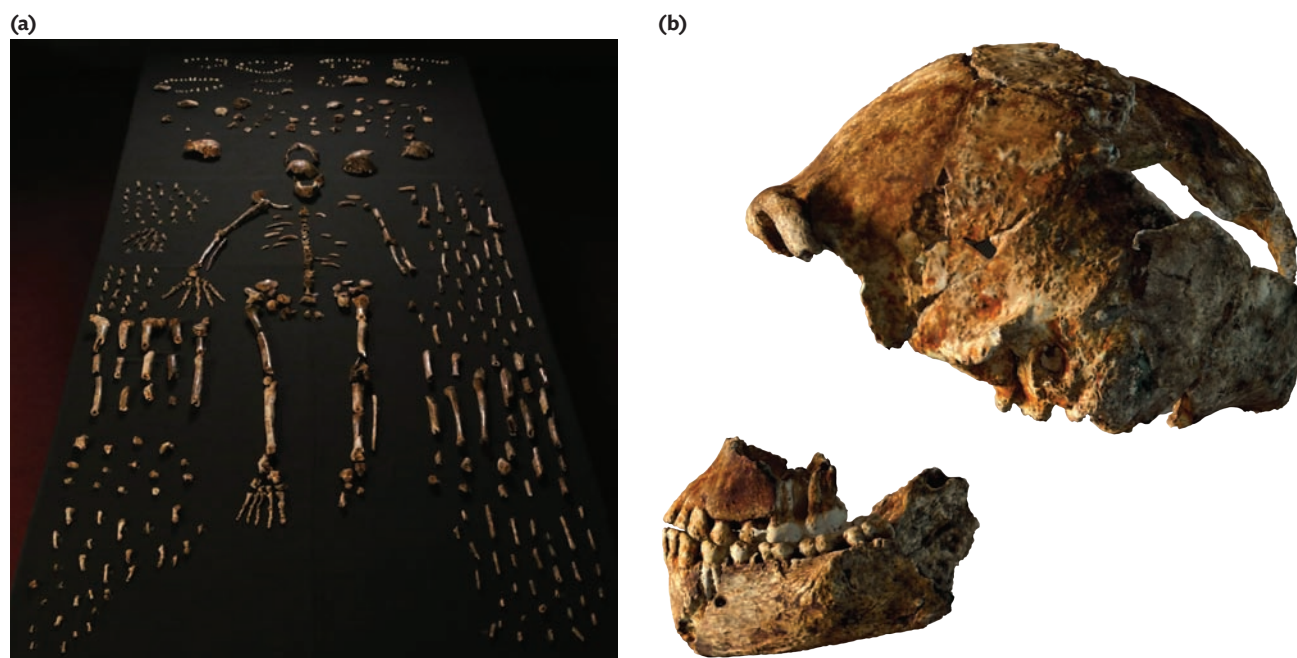
FIGURE 11.6

Homo naledi (a) The remarkable collection of *H. naledi* fossils representing at least 15 individuals reveals a hominin having a combination of primitive and derived characteristics. The hip region is australopithecine-like, but **(b)** the cranium is similar to *Homo erectus*'s protruding supraorbital torus and elongated cranial vault.

UNDERGROUND

FINDING EARLY *HOMO* IN SOUTH AFRICA

One of the central questions in human evolution is the timing and location of the origin of the early members of the genus *Homo*. The fossil record indicates that the earliest representative of *Homo* is from East Africa. Until recently, the record of early *Homo* in South Africa has been represented by very few fossils, with the most notable being a *Homo habilis* cranium from Swartkrans. That picture has dramatically changed with the 2013 discovery, and 2015 description, of an incredible cache of hominin fossils representing early *Homo* found in the Rising Star Cave in South Africa.

Paleoanthropologist Lee Berger, the discoverer of *Au. sediba* from nearby Malapa (see chapter 10), had long suspected that the old and complex cave systems in this region of the world held hidden fossils—a potentially richer trove than the iconic South African sites of Malapa, Swartkrans, Kromdraai, Sterkfontein, Makapansgat, and Taung worked by paleoanthropologists over the past century. Working on a hunch that fossils were waiting to be discovered, Berger recruited spelunkers ("cavers") to explore caverns and crevices in the Rising Star Cave. Within a remarkably short amount of time, their exploration of a previously unknown and deep chamber in the cave revealed a few bones. The pictures they took of the bones and subsequently showed to Berger sparked work at what turned out to be one of the most important hominin fossil sites in South Africa, Africa, and the world.

Soon after the initial discovery by the cavers, Berger enlisted a reconnaissance team to recover bones and teeth from the cave. All such field teams are special, but this one had to be particularly selective, as each of the crew members had to be able to fit into extraordinarily narrow cave shafts, just 7 inches wide in places. Berger recruited widely, noting he was looking for applicants that "…must be skinny and preferably small. They must not be claustrophobic, they must be fit, they should have some caving experience, climbing experience is
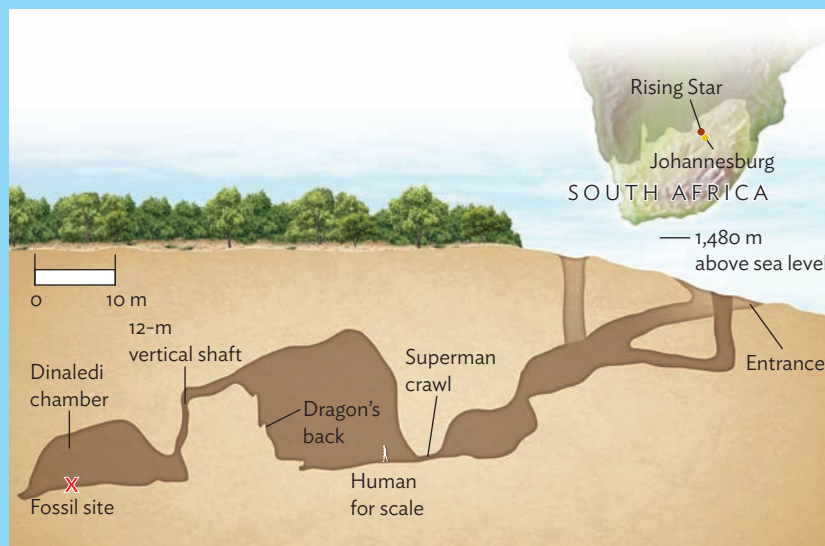
This diagram of Rising Star Cave illustrates the enormous physical difficulties confronting the excavation crew.

Rising Star

Johannesburg
SOUTH AFRICA

1,480 m above sea level

0   10 m

Dinaledi chamber

12-m vertical shaft

Dragon's back

Superman crawl

Entrance

Human for scale

X
Fossil site

ASTRONAUTS

a bonus." Berger identified six persons, nicknamed the "Underground Astronauts," who fit this narrow description. Each of the team members selected for the field project—all skilled women scientists—knew from the outset of the expedition that they were in for the challenge of their lifetimes, but they had no idea the extent of the challenge. Within a day after getting started, the crew discovered that there were not just a few bones and teeth at the bottom of Rising Star Cave. Rather, by week's end, the field team found and collected *1,550* fossils representing nearly all bones of a skeleton and at least 15 different individuals representing both sexes across a range of ages. Berger and colleagues soon determined that these fossils represented a new hominin species, which they named *Homo naledi.*

As with all fossils, understanding the context in which the Rising Star Cave fossils were found is crucial in their interpretation. Therefore, all members of the team had to be well trained in excavation and documentation methods under very tough field conditions. No matter the location, every anthropologist who excavates skeletons knows that difficult conditions are associated with virtually every field site. The most common challenges include maintaining awkward body postures for long hours and being subjected to high heat, humidity, insects, and far worse. But the conditions in Rising Star Cave were especially demanding, including the long descent and difficult climb using safety ropes and harnesses; working in a dark, claustrophobic setting; and maintaining difficult postures for six-hour stretches of time. So, another key requirement for each member of the excavation team was the willingness to work in and ignore awful working conditions.

How did this elite team of field workers accomplish the recovery of bones and teeth under these kinds of abysmal circumstances? The answer is pretty simple: Their passion for discovery and for a greater understanding of the evolution of our early ancestors motivated them to persevere under grueling conditions. Clearly, their passion paid off. This remarkable team recovered more hominin fossils in about a week than had been recovered from any other single locality in Africa, amassing a sample of hominin remains that will generate questions about the origins and evolution of *Homo* for decades to come.

Just when we think we have all the answers, Rising Star and other remarkable discoveries emerge, giving us new perspectives on the past. For this site, a huge part of the discovery and the subsequent knowledge gained was made possible by the six talented and committed individuals who compose the Underground Astronauts.

The "Underground Astronauts," Rising Star Cave.

Recording the fossils deep inside Rising Star Cave.
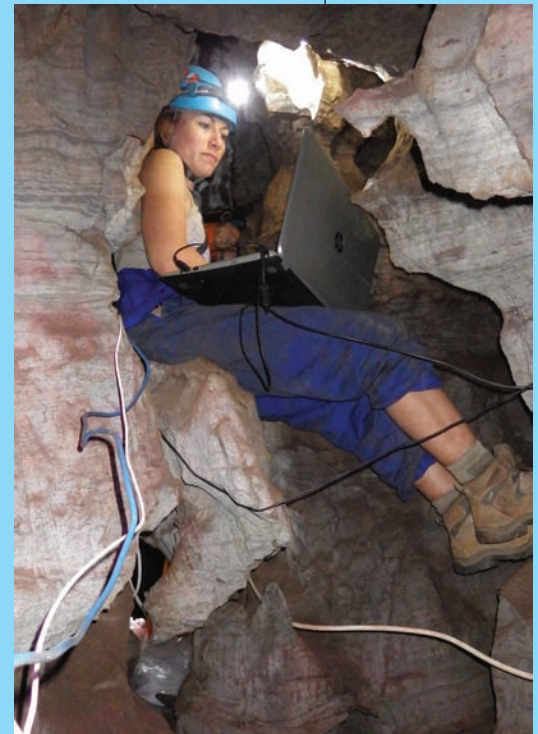
sagittal keel A slight ridge of bone found along the midline sagittal suture of the cranium, which is typically found on *H. erectus* skulls.

localities associated with volcanic rock (see chapter 8). Despite this, and although the overall morphology of the *H. naledi* remains are distinctive, the combination of primitive, australopithecine morphology and derived characteristics suggests where *H. naledi* might fall in the broad hominin chronology. For example, there are some anatomical features that are not present in the australopithecines but are associated with *Homo erectus*, including, for example, a **sagittal keel**, a large browridge, thick cranial bones, and reduced tooth size. However, the estimated brain size for *H. naledi* is quite small—560 cc and 475 cc for males and females, respectively. The small brain, therefore, is more like the australopithecines discussed in the past chapter and the early *H. erectus* from Dmanisi, Georgia (discussed later in this chapter; see p. 370). The overall suite of cranial and postcranial features are thus consistent with the notion that *H. naledi* may be an earlier rather than later taxa of the genus *Homo*.

11.2 *Homo erectus:* Early *Homo* Goes Global

Beginning around 1.8 mya, a new hominin appeared, *H. erectus,* which had anatomical characteristics that distinguished it from *H. habilis.* As discussed earlier, it was the only descendant taxon of *H. habilis* and was among the earliest fossil hominins described, having been found by Eugène Dubois at Trinil in Java.

In the century since Dubois began his work in Java, many fossils with the same general attributes as the Trinil skull—large browridges, long and low skull, and bigger
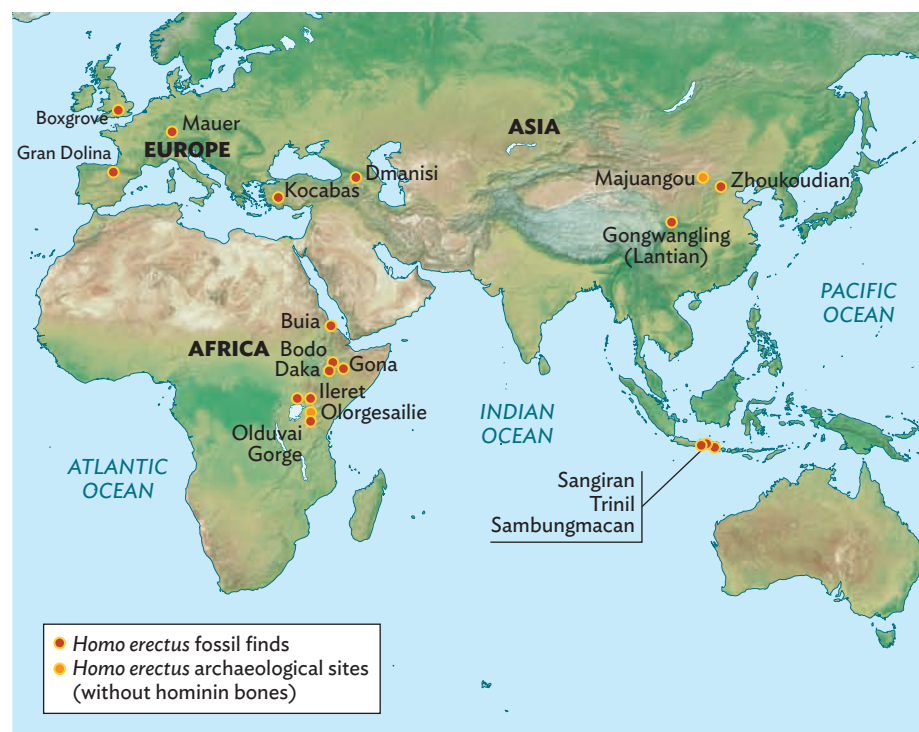

FIGURE 11.7

Homo erectus *Sites* Fossils of *H. erectus* have been discovered throughout Africa, Europe, and Asia.

brain—have been found in Europe, Asia, and Africa (**Figure 11.7**). These hominins collectively date to about 1.8 mya–300,000 yBP. During this fascinating and dynamic period of human evolution, hominins first left Africa, colonized vast areas of Asia and Europe, and underwent fundamental changes in culture and adaptation that shaped human biological variation.

Homo erectus in Africa (1.8–0.3 mya)

The earliest record of *H. erectus* comes from Africa, less than 2 mya. At that time, the last australopithecines were still around in East Africa and South Africa, and comparing the fossils of each reveals great differences in anatomy and adaptation between *H. erectus* and the last australopithecines (**Figure 11.8**). Among the earliest and the most spectacular of the *H. erectus* fossils is an 80% complete juvenile skeleton from Nariokotome, on the western side of Lake Turkana (**Figure 11.9**). This remarkably complete skeleton dates to about 1.6 mya. In contrast to *Australopithecus* and *H. habilis,* the Nariokotome hominin has several quintessentially modern anatomical features.
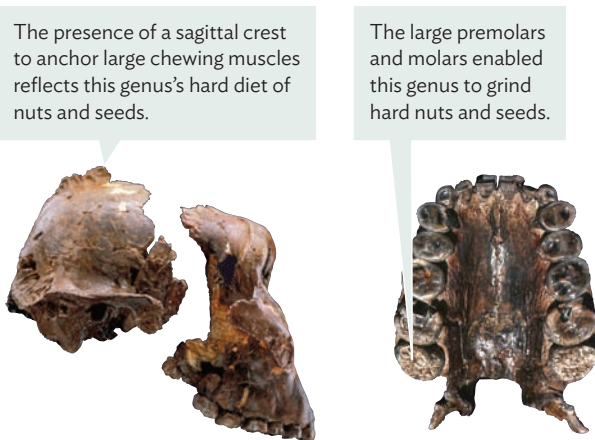
The presence of a sagittal crest to anchor large chewing muscles reflects this genus's hard diet of nuts and seeds.

The large premolars and molars enabled this genus to grind hard nuts and seeds.

Australopithecus boisei
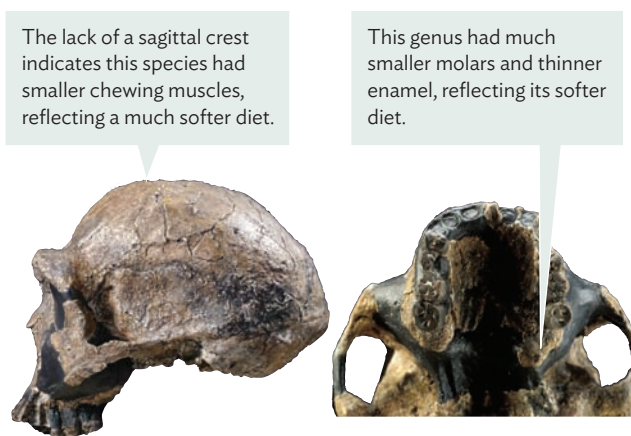
The lack of a sagittal crest indicates this species had smaller chewing muscles, reflecting a much softer diet.

This genus had much smaller molars and thinner enamel, reflecting its softer diet.

Homo erectus

FIGURE 11.8

Australopithecus boisei *versus* Homo erectus While both of these genera were contemporaneous for a period of time in Africa, there are important differences in their cranial and dental morphologies.

FIGURE 11.9

Nariokotome Researchers have debated the exact age of "Nariokotome Boy," also known as "Turkana Boy," but he was likely around 11 years old. Discovered in 1984, this *H. erectus* fossil is one of the most complete early hominin skeletons ever found.

One of the most striking modern characteristics is the combination of relatively short arms and long legs. That is, the *H. erectus* body plan is much more like that of a living human in its ratio of arm length to leg length. This change in limb proportions in *H. erectus* signals the beginning of a major alteration in the pattern of bipedal locomotion: *H. erectus* became completely committed to terrestrial life by adopting a fully modern stride. Life in the trees became a thing of the past.

Features of the pelvic bones and overall size indicate that the Nariokotome individual was likely a young adolescent male. He was quite tall, about 166 cm (66 in). Had he survived to adulthood, he would have grown to nearly 180 cm (71 in) in height. This change in height in comparison with *H. habilis* and the australopithecines indicates an enormous body size increase in this taxon. In addition, the Nariokotome boy's cranial capacity was about 900 cc (**Figure 11.10**). Even taking into account the body size increase (brain size and body size are roughly correlated), this expansion in brain size is large compared with similar changes in earlier hominins.
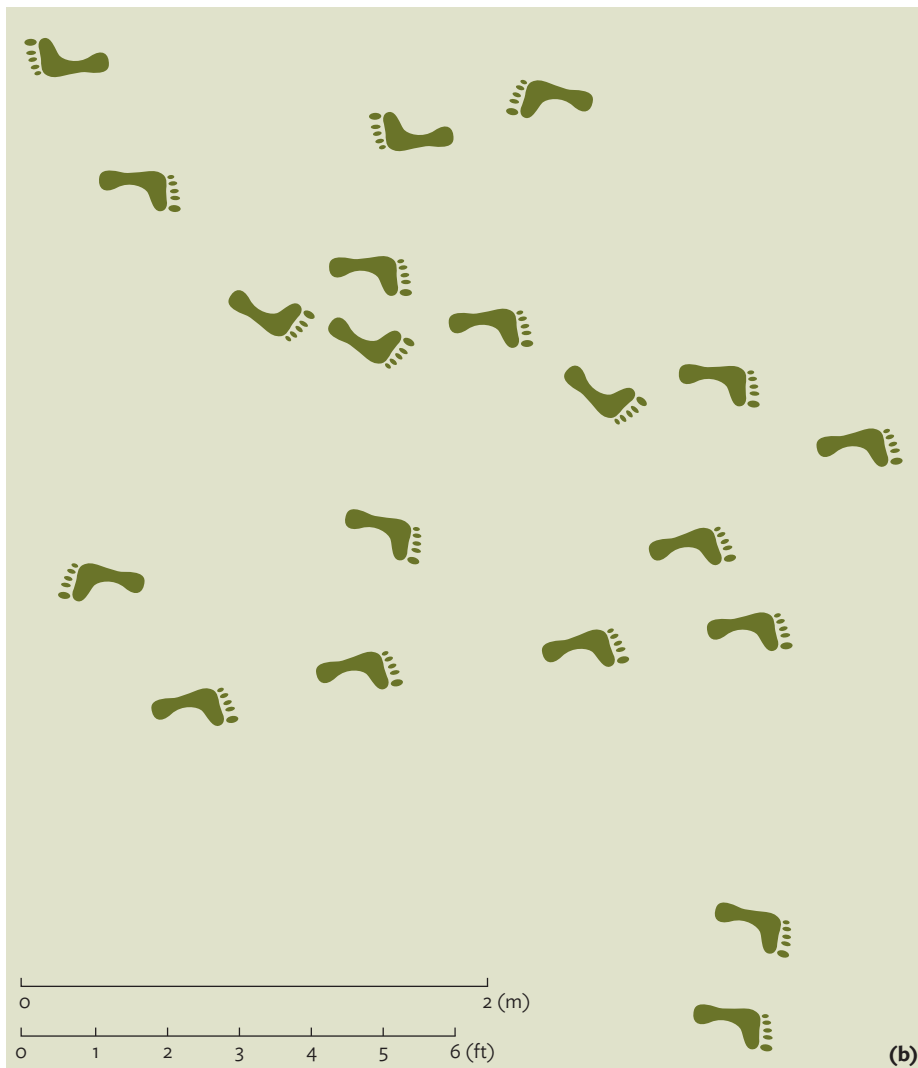
The Nariokotome skeleton is just one of many *H. erectus* fossils from East Africa.

FIGURE 11.10

Nariokotome Skull The skull of the Nariokotome boy has been invaluable for relating brain size and overall body size in *H. erectus*. Why is that relationship important for us to know? (Photo © 1985 David L. Brill, humanoriginsphotos.com)

(a)

(b)

At Ileret, on the eastern side of Lake Turkana, the partial skull of a very small *H. erectus*—possibly a female—was found in geologic strata dating to about 1.6 mya. The skull's diminutive size and small browridges indicate the very high degree of variation in *H. erectus.* Some *H. erectus* individuals had very large and robust bones, whereas others—such as the hominin from Ileret—were quite gracile.

Just as significant as the Ileret fossil is the presence of multiple sets of footprints on an Ileret landscape dating to around 1.5 mya (**Figure 11.11**). Recall the footprints from Laetoli discussed in chapter 10, representing *Australopithecus afarensis* and dating to around 3.5 mya. These footprints provide a kind of fossilized picture of behavior: evidence of how early human ancestors walked. They reveal that the Ileret *H. erectus* walked just like a modern human. In fact, these prints provide the first solid evidence of fully modern walking. We know this because the footprints have all the fundamentals that we see in our feet, namely, the double arch (the long one extending from your heel to the base of your toes and the side-to-side one) and an adducted big toe (the big toe is close to the second toe), whereas in the Laetoli fossil the big toe and second toe are abducted (spread apart). Moreover, the prints are big, as would be expected given the great heights of *H. erectus* compared to earlier hominins. The pelvis and leg bones of *H. erectus* had strongly indicated the modern form of walking. The Ileret footprints
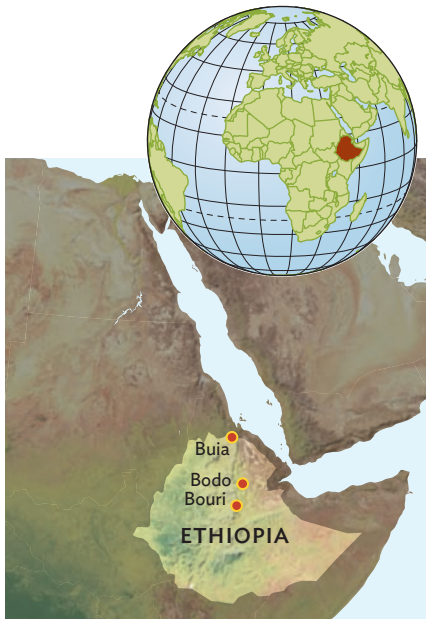
FIGURE 11.12

Daka Partial Cranium The Daka *H. erectus* fossil from the Middle Awash Valley, Ethiopia, has large browridges, a characteristic of many other *H. erectus* specimens in Africa and elsewhere. (Photo © 2001 David L. Brill, humanoriginsphotos.com)
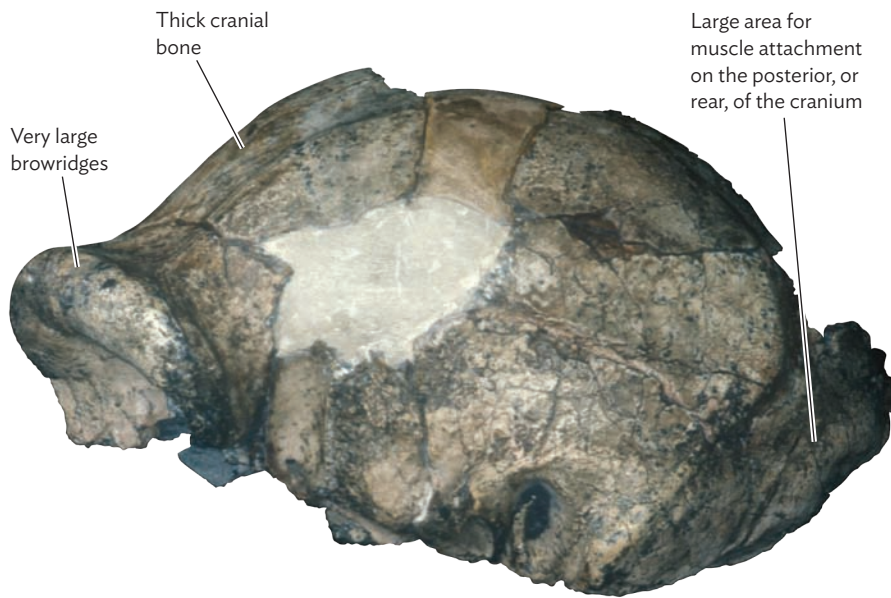
provide further proof that this hominin had a foot adapted for activities requiring travel, such as hunting and long-distance walking, behaviors likely first seen with *H. erectus*.

Other key *H. erectus* fossils from Africa include a partial cranium found in Olduvai Gorge and dating to about 1.2 mya, a partial cranium and postcrania found at Daka and dating to 1 mya (**Figure 11.12**), a partial cranium found at Buia and dating to about 1 mya, a pelvis found at Gona and dating to 1.2 mya, and a cranium found at Bodo and dating to about 600,000 yBP (**Figure 11.13**). The Daka and Bodo crania are from the

FIGURE 11.13

Bodo Cranium This *H. erectus* fossil has different cranial features from other specimens of this species. Note the large browridges and thick cranial bones.

Very large browridges

Thick cranial bone

Large area for muscle attachment on the posterior, or rear, of the cranium

FIGURE 11.15
Olduvai Cranium This *H. erectus* fossil, known as "OH 9," has the largest browridges of any hominin species.

Middle Awash Valley (**Figure 11.14**, pp. 368–369), and the Buia cranium is from Eritrea. In contrast to the Nariokotome boy's skull and the skull from Ileret, the skulls from Olduvai Gorge, Daka, Buia, and Bodo are very robust, having thick cranial bones and very large browridges. The Olduvai cranium's browridges are the largest of any known hominin, before or since (**Figure 11.15**). Only some of this greater size can be accounted for by the Nariokotome boy's immaturity because the other three hominins were fully mature adult males.

During the process of cleaning the facial bones of the Bodo skull, Tim White found a series of barely visible linear marks on the left cheek, around the left eye orbit and the nose, and elsewhere on the cranium (**Figure 11.16**). Microscopic analysis of the marks
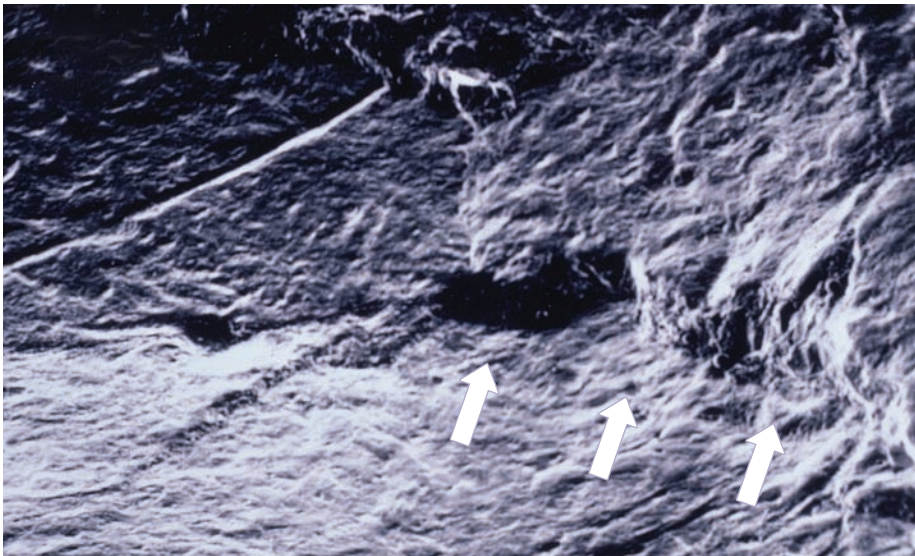
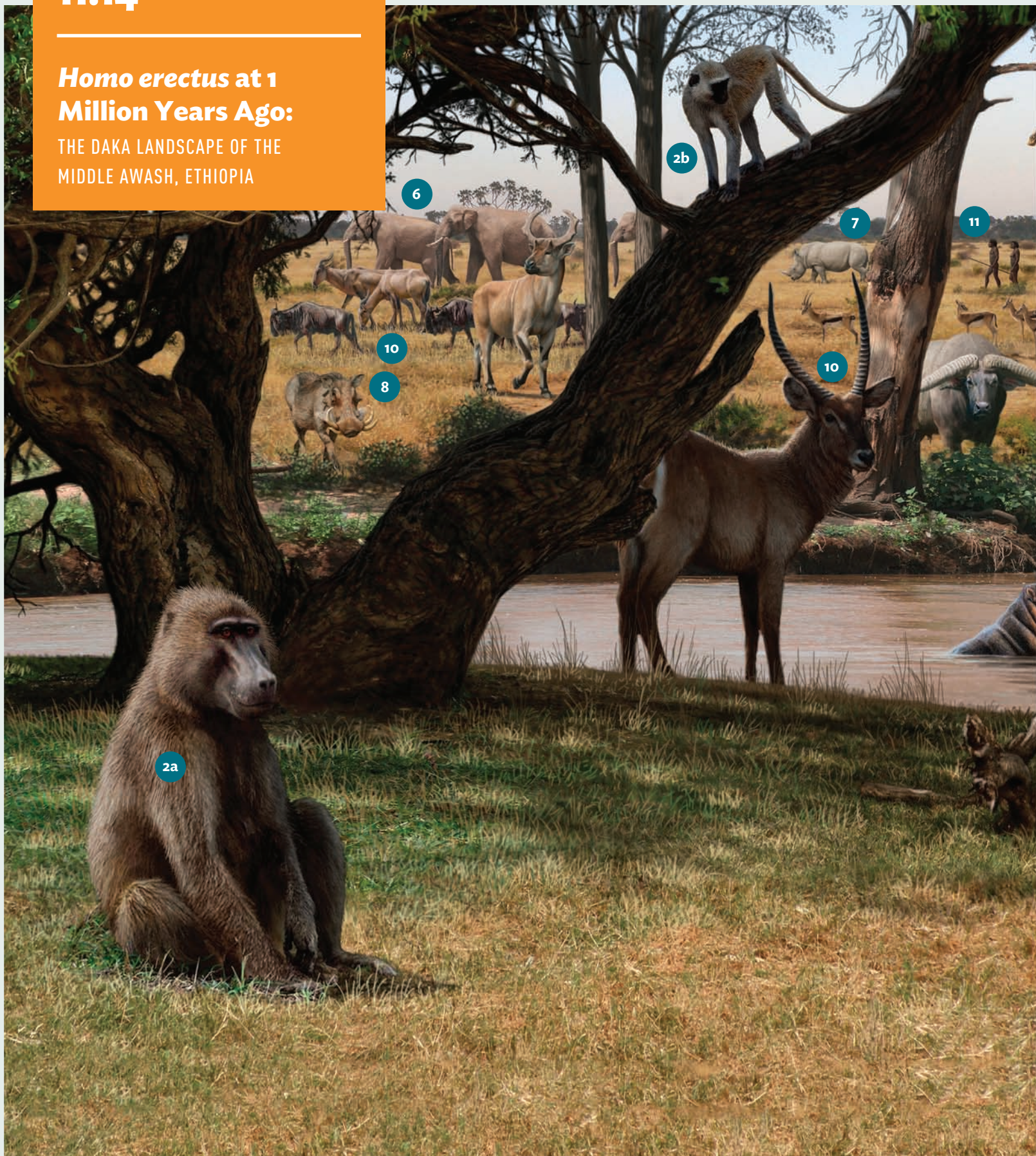**FIGURE 11.16**
Ritual Defleshing? Viewed through a scanning electron microscope, cutmarks such as this one (arrows) indicate that stone tools were used to remove flesh from the Bodo skull. The arrows point to the groove left by the stone tool.

Homo erectus at 1 Million Years Ago:
THE DAKA LANDSCAPE OF THE MIDDLE AWASH, ETHIOPIA

The source of a continuous fossil record from before 6 mya to about 50,000 yBP, the Middle Awash Valley is among the most fossil-rich regions in the world. The Daka Member (*Daka* being an abbreviation of the place-name Dakanihylo and *Member* meaning part) is among the most interesting areas of the Middle Awash. The area's rich fossil record of plants and animals dates to around 1 mya, the time of *Homo erectus*, and thus provides us access to the habitat there during this period of human evolution.

The American paleoanthropologist Henry Gilbert and his team have studied the thousands of fossils, ranging from the tiny ancestors of mice to the large animals. The record indicates a savanna/grasslands setting with wooded areas, ample water, and floodplains, unlike the dry desert of the region today.

This reconstruction shows what the Daka landscape might have looked like a million years ago, when *Homo erectus* hunted and gathered there. The following animal taxa are represented.

1 *Felids* (ancestors of lions and domestic cats) are exclusively carnivorous. Their abundance indicates that the area included plenty of animals that served as prey for them.

2 *Cercopithecids* ([2a] *Theropithecus oswaldi* and [2b] *Cercopithecoides alemayehui*) suggest the presence of forests and permanent rivers with associated wetlands.

3 *Equids* (ancestors of asses) indicate a broad range of habitats.

4 *Giraffids* (ancestors of giraffes) indicate the presence of large acacia trees.

5 *Hippopotamids* (ancestors of hippopotamuses) indicate the continuous availability of deep water and adjacent grasslands.

6 *Elephantids* (ancestors of elephants) are grazers and browsers and occupy a wide range of habitats.

7 *Rhinocerids* (at least two genera, ancestors of rhinoceroses) are typically associated with standing water (ponds) and grasslands.

8 *Suids* (ancestors of pigs) indicate the availability of water but with sometimes semiarid conditions.

9 *Murids* (ancestors of grass mice or rats) are especially common today in grasslands and savannas.

10 *Bovids* (ancestors of today's impalas, gazelles, sheep, ibex, oryx, kudu, and other bovines of the African landscape) are very numerous and indicate the presence of woodlands and brush thickets, large streams, and water supply continuous throughout the year. The fossil record indicates that the grasslands would have been full of herds of different bovid species.

11 *Hominins* (ancestors of *Homo sapiens*) at this point in evolution are adaptable to a wide range of habitats, but are exclusively terrestrial.

GEORGIA
Dmanisi

bones—of an adult male dating to much later (about 500,000 yBP) in a rock quarry near the village of Kocabaş, in the Büyük Menderes, a large valley system in western Turkey. Like many other *H. erectus* specimens from Africa and from Asia, the Kocabaş specimen has massive browridges and a **sagittal keel.** According to the American paleoanthropologist John Kappelman and his colleagues, the cranium's internal surface appears to have had a bone infection very similar to that caused by tuberculosis. This hominin is doubly significant, first in being the only one found in this vast region of western Asia, and second in being the first one showing signs of tuberculosis.

Since Dubois completed his fieldwork in the 1890s, *H. erectus* fossils have been found in a number of sites in Indonesia, especially in Java. Some of these remains are nearly as old as the Dmanisi remains. The earlier fossils, from the Sangiran site, date to as early as 1.8–1.6 mya. This early date shows that *H. erectus* rapidly spread eastward from western Asia. Thus, once the taxon had first evolved, it colonized areas outside Africa at a rapid pace, perhaps within less than a few hundred thousand years. The emerging picture is of *H. erectus*'s rapid, widespread movement throughout Asia. This rapid spread illustrates the hominin's high degree of adaptive success, a factor likely related to increasing intelligence, increasing reliance for survival on both material culture and tools, and overall greater ability at acquiring food and other resources.

Dating to 800,000 yBP, the most complete skull from eastern Asia is the Sangiran 17 cranium from Sangiran, Indonesia. Like the African fossils, it has thick cranial bones and large browridges. Its cranial capacity is about 1,000 cc (**Figure 11.19**). A slight ridge, or "keel," runs along the sagittal suture atop the skull, and this sagittal keel appears on *H. erectus* skulls from Asia, Africa, and Europe.

Later *H. erectus* fossils from Java, dating to between 1 mya and 500,000 yBP, include fossil remains from Sangiran and Sambungmacan, plus the original Trinil skull found by Dubois. These fossils show many of the same physical characteristics as the earlier ones but also some changes, such as larger brains and smaller teeth. Some of the best information about the first hominins outside Africa comes from China. The earliest hominin fossil is a partial skull from Gongwangling, near the village of Lantian, Shaanxi Province. The skull dates to about 1.2 mya. Like the fossils from Java, this specimen has large, well-developed browridges and thick cranial bones. Its cranial

FIGURE 11.19

***Sangiran* Homo erectus** Excavations in Indonesia have uncovered many hominin fossils, including Dubois's Java Man and, shown here, the Sangiran 17 fossil. Note the long cranium, low forehead, and large browridges.

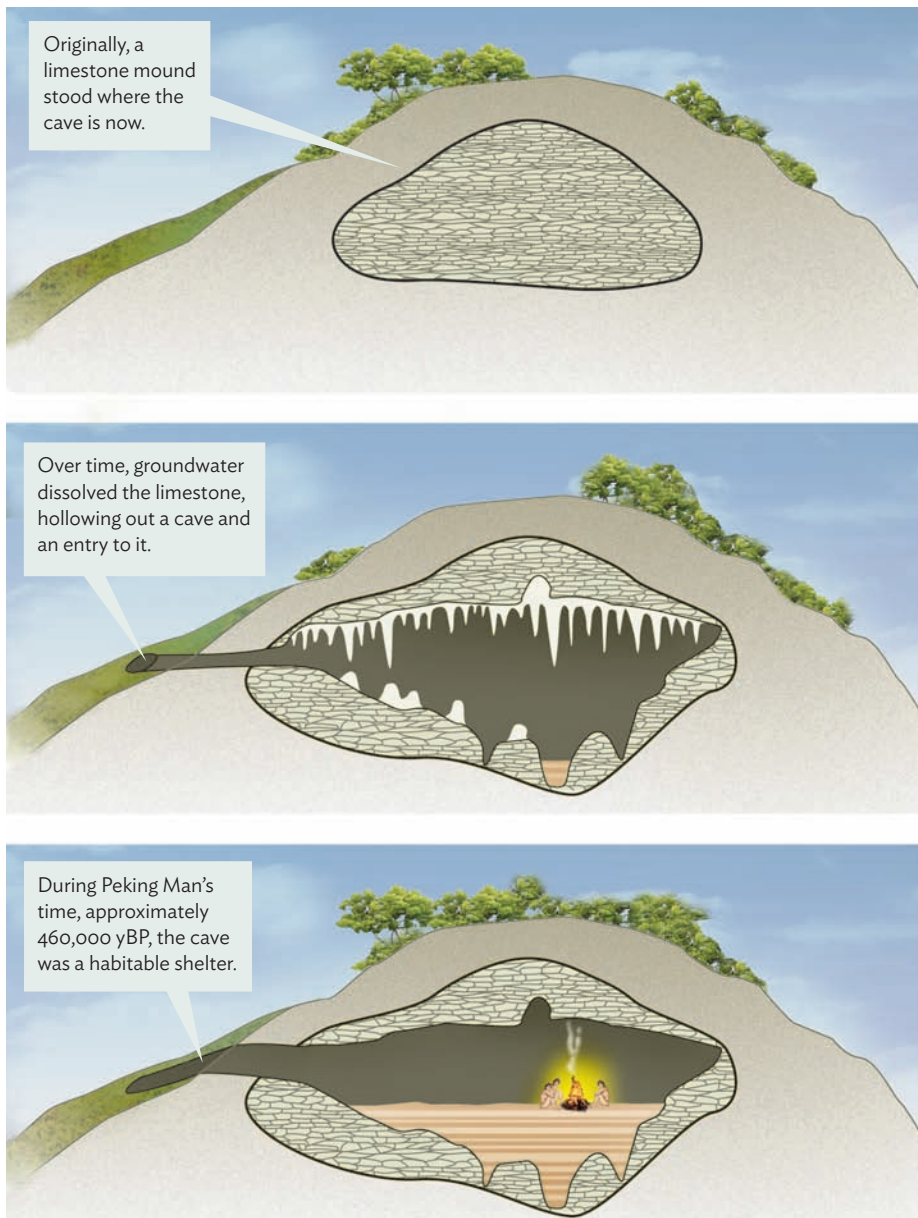capacity is about 800 cc. The skull postdates the earliest evidence of hominins in north China, from Majuangou, by nearly 500,000 years. Both the animal bones with butchery marks and the stone artifacts found by the Chinese geologist R. X. Zhu and his collaborators date to nearly 1.7 mya, making them the earliest specimens from Asia.

The site yielding the most impressive *H. erectus* remains in eastern Asia is the cave in Zhoukoudian, on Dragon Bone Hill, near the modern city of Beijing. After being discovered in the 1920s, the cave was excavated into the early 1940s (**Figure 11.20**). Deposits dating to 780,000–400,000 yBP contained, in fragments, the bones and teeth of 40–50 individuals, as well as many stone tools and food remains (**Figure 11.21**). Tragically, the entire collection of priceless bones was lost during World War II, late in 1941. Fortunately, shortly before the loss, the eminent German anatomist and anthropologist

Originally, a limestone mound stood where the cave is now.

Over time, groundwater dissolved the limestone, hollowing out a cave and an entry to it.

During Peking Man's time, approximately 460,000 yBP, the cave was a habitable shelter.

FIGURE 11.21

Cave at Zhoukoudian The cave in which Peking Man's remains were discovered took millions of years to form. In addition to the remains, stone tools were found there.

Franz Weidenreich (1873–1948) had thoroughly studied the bones and teeth, written detailed scientific reports, and made cast replicas, drawings, and photographs (**Figure 11.22**). This record has allowed scientists to continue studying the Zhoukoudian remains.

Homo erectus in Europe (1.2 Million–400,000 yBP)

The earliest presence and subsequent evolution of *H. erectus* were somewhat later in Europe than in Africa and Asia. The earliest fossil evidence of *H. erectus* in western Europe is from the Sierra de Atapuerca, northern Spain—at the cave sites of Sima del
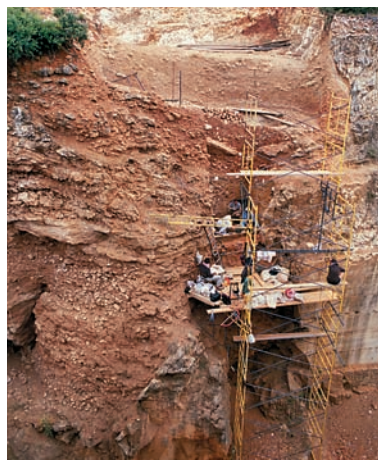

FIGURE 11.22

Peking Man Although the original remains of this *H. erectus* fossil are lost, excellent casts, such as this reconstructed skull, enable modern anthropologists to study this important hominin. (Photo © 1996 David L. Brill, humanoriginsphotos.com)

FIGURE 11.23

Gran Dolina In the mid-1990s, the excavation of this Spanish cave site uncovered fossil remains of at least six individual hominins along with hundreds of stone tools. In addition, ample evidence that both hominins and other animals were butchered there has led some researchers to suggest that these hominin ancestors practiced cannibalism. Like Zhoukoudian (see Figure 11.20), Gran Dolina is a UNESCO World Heritage Site.

FIGURE 11.24

Atapuerca 3 These remains, from Gran Dolina, are the subject of debate as some researchers believe that the juvenile they came from belonged not to *H. erectus* but to a new species of hominin, *Homo antecessor.* Others believe that despite its more modern appearance, this hominin belonged to *H. erectus.*

Elefante, dating to about 1.2 mya, and of Gran Dolina, dating to about 900,000 yBP. The earlier site is represented by a partial mandible and some teeth, along with animal bones showing cutmarks from butchering. The later site, excavated by the Spanish paleontologist Juan Luis Arsuaga and his colleagues, is among the most important in Europe, owing to the discovery of fragmentary bones and teeth of a half-dozen hominins, along with many stone tools and animal bones (**Figure 11.23**). Animal bones and hominin bones had been cut with stone tools and purposely broken. This evidence indicates that hominins processed and consumed animals and other hominins (these practices are discussed further in chapter 10).

The most complete skull from Gran Dolina is Atapuerca 3, consisting of the left facial bones, upper jaw, and teeth of a child. This specimen provides a rare glimpse at what juveniles looked like at this point in human evolution (**Figure 11.24**). Juvenile or not, the cranium indicates that Atapuerca 3 appeared more modern than other members of *H. erectus* but was clearly ancestral to later hominins in the Atapuerca region and elsewhere in Europe. Indeed, its bones and teeth are similar in a number of ways to those of hominins that lived in Europe later in the Pleistocene: *H. sapiens.* For example, like the later hominins, the Gran Dolina adults have a wide nasal aperture (opening for the nose).

The only other *H. erectus* remains in Europe are a partial cranium from Ceprano, Italy, dating to 800,000 yBP; the Mauer jaw—a mandible and most of its teeth—from near Heidelberg, Germany, dating to 500,000 yBP; and a tibia from Boxgrove, England, also dating to 500,000 yBP.
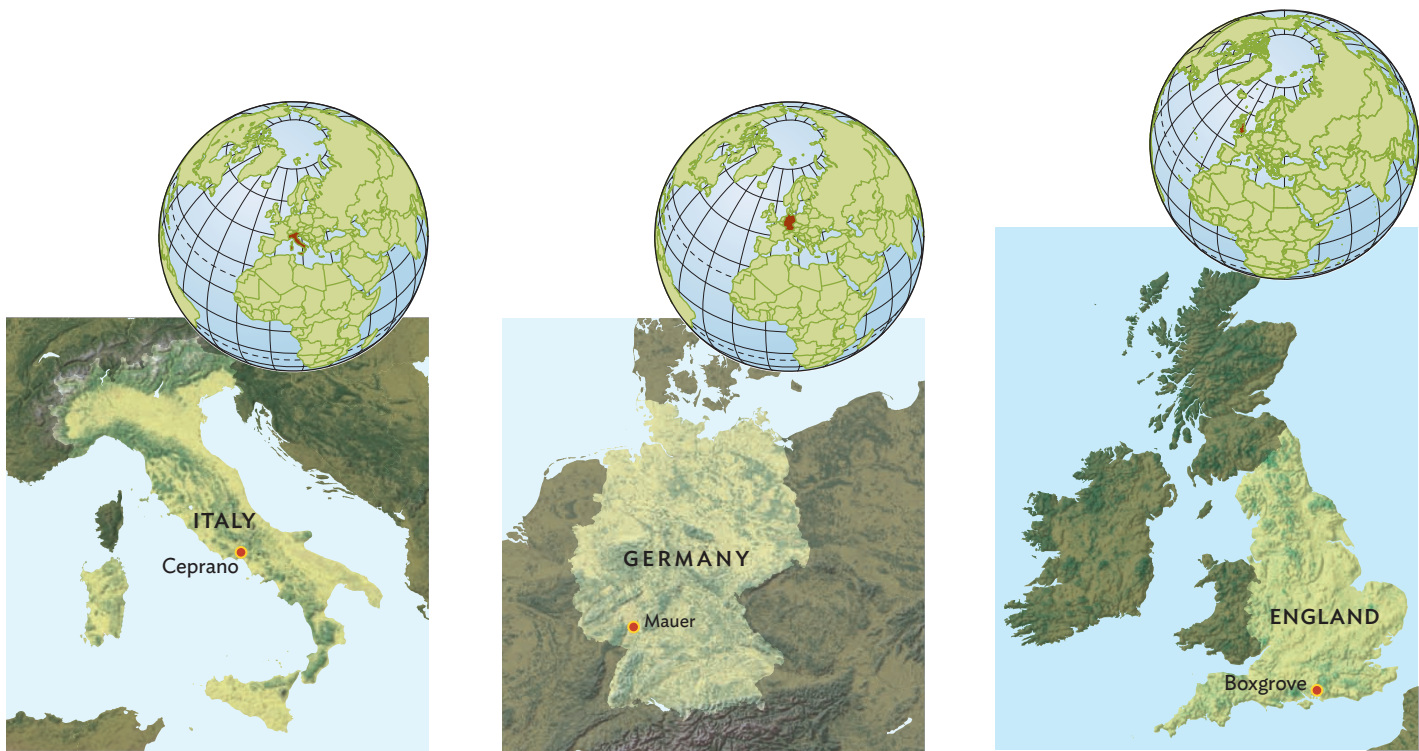
Evolution of *Homo erectus*: Biological Change, Adaptation, and Improved Nutrition

How did *H. erectus* differ from earlier *Homo* species, such as *H. habilis?* One of the most obvious differences is *H. erectus*'s remarkable body size and height. Moreover, the increase in body size occurred rapidly, perhaps in less than a few hundred thousand years. That is, at 1.8 mya *H. habilis* was about the size of an australopithecine, but by 1.6 mya another hominin, *H. erectus,* was considerably taller and heavier. The American physical anthropologists Henry McHenry and Katherine Coffing estimate that from *H. habilis* to *H. erectus,* males' heights increased by 33% (to 1.8 m, or 5.9 ft) and females' heights by 37% (to 1.6 m, or 5.3 ft). In other words, *H. habilis*—like the australopithecines—was quite short (typically less than 1.2 m, or 4 ft), but *H. erectus*

ITALY

Ceprano

GERMANY

Mauer

ENGLAND

Boxgrove

was considerably taller (more than 1.5 m, or 5 ft). Most of this increase took place 2.0–1.7 mya (**Table 11.1**).

What caused the rapid increase in body size from *H. habilis* to *H. erectus?* Various factors were likely involved, such as climate change and its impact on food supply. But the fundamental reason was likely increased access to animal food sources—protein—acquired from hunting. That some primitive stone tools date to 3.3 mya indicates that early hominins were able to cut meat and process it.

Cutmarks made with stone tools have been found on bones of animal prey in Kenya and Ethiopia, at the Olduvai Gorge and Bouri sites, respectively. Indeed, the pattern of cutmarks found at Bouri indicates that even some late australopithecines, ones that preceded *Homo,* were skilled in animal butchery.

As the American anthropologist Pat Shipman's work has shown, at Olduvai Gorge, stone-tool cutmarks overlay animal tooth marks. This finding suggests that at least some of the behavior involving butchering was scavenging—eating animals killed by other animals—and not hunting (**Figure 11.25**). Other evidence of meat eating has been documented in the bone chemistry of early hominins and in wear on their teeth.

Meat eating likely started long before *H. erectus* appeared, but the technology available to earlier hominins and the minimal record of hunting prior to *H. erectus* suggest that meat was a minor part of this hominin's diet. Two things had to happen for early hominins to routinely acquire meat. First, to kill game, hominins had to become able to manufacture the right tools, especially stone tools that could be thrown or thrust accurately, such as spears. Second, hominins had to develop the social structure whereby a group of individuals—older adolescent and adult males, primarily—could efficiently track and kill game. Both developments were part of the increase in hominin intelligence at this time, as recorded by brain size expansion and more complex technology. Once hominins had developed the technological and social means of accessing animal food sources daily, they likely had increased access to high-quality protein. This increased access to protein would in turn have produced *H. erectus*'s bump in height—these hominins were taller than their ancestors due to

Table 11.1 Trends from *Homo habilis* to *Homo erectus*

	H. habilis	→	*H. erectus*
Teeth		Reduction in size	
Face and jaws		Reduction in size relative to size of braincase	
Brain		Increase in size	
Browridge		Increase in size	
Cranial bone		Increase in thickness	
Body		Increase in size	
Arms		Reduction in length	
Legs		Increase in length	

(a)

(b)

FIGURE 11.25

Hunters or Scavengers? **(a)** The cutmarks on this bone were made by stone tools, while **(b)** animal tooth marks and cutmarks are visible on the shaft of this antelope humerus. Cutmarks that occurred after animal tooth marks indicate that *H. erectus* scavenged for meat at least some of the time. (Photos © David L. Brill, humanoriginsphotos.com)

improved nutrition that came about by acquiring food (especially protein) through hunting.

Such increasingly sophisticated technology and increased dependence on culture were important in human evolution generally. The culture associated with this period of evolution, beginning around 1.8 mya, is called the **Acheulian Complex.** Acheulian stone tools are more sophisticated than Oldowan tools, were produced from a wider variety of raw materials, and were fashioned into a greater range of tool types, with a greater range of functions. This diversity suggests increased familiarity with the necessary resources and with their availability. Within this diversity, the dominant tool is the **handaxe** (**Figure 11.26**). The handaxe's sharp edge was used in cutting, scraping, and other functions.

In addition, the tools became increasingly refined; better made than before, they clearly required a great deal of both learning and skill to produce. Acheulian tools are found in association with large animals, suggesting that these tools were used to kill large animals and butcher them. In Ethiopia's Middle Awash region, for example, tools are commonly associated with hippopotamus bones. In Olorgesailie, Kenya, the South African archaeologist Glynn Isaac recovered many baboon bones in addition to those

Acheulian Complex The culture associated with *H. erectus,* including handaxes and other types of stone tools; more refined than the earlier Oldowan tools.

handaxe The most dominant tool in the Acheulian Complex, characterized by a sharp edge for both cutting and scraping.

FIGURE 11.26

Olorgesailie **(a)** At this Acheulian site in Kenya, the remains of hundreds of butchered animals were found along with many handaxes and other tools. **(b)** This close-up shows the stone tools, with the handaxes in the middle.

(a)

(b)

KENYA

Olorgesailie

of hippopotamuses, elephants, and other animals. All these bones have cutmarks from stone tools. In addition, the tools from this and other Acheulian sites display microscopic patterns of wear that are the same as those seen in experimental studies where anthropologists have butchered animals. Clearly, *H. erectus* had killed, processed, and eaten the animals at these sites, well before 1 mya (**Figure 11.27**). This record, from Olorgesailie and sites like it, indicates that hunting was well in place by the Middle Pleistocene. If body size increase was tied to acquisition of animal protein via hunting, it was well in place by somewhat greater than 1.5 mya.

In addition to the increase in body size, a key difference between *H. habilis* and *H. erectus* is the latter's much larger brain. From *H. habilis* to *H. erectus,* brain volume increased by 33% (from 650 cc to 950 cc). Some of the enlargement in brain size was

due simply to the increase in body size generally. But even when accounting for the body size increase, there was still an increase in brain size. The increase in sophistication of technology and other cultural changes seen after 2 mya or so strongly suggests that this increase in brain size reflects an increase in intelligence and cognitive abilities generally. Simply, the adaptation of *H. erectus* placed an emphasis on intelligence, and there was likely a selective advantage for the cognitively advanced behaviors that characterized this hominin.

Anthropologists are keenly interested in the nature of the energy intake that would have been required to grow these very brainy ancestors. That is, the brain is an energetically "expensive" tissue. What did these hominins eat that "paid" the high energetic cost of a large brain? While a number of factors are likely to have operated, improved nutritional quality is central to understanding how the cost of increasing brain size was paid. Nutrition improved as a result of meat consumption and the rich source of protein that it provided. The British primatologist Richard Wrangham contends
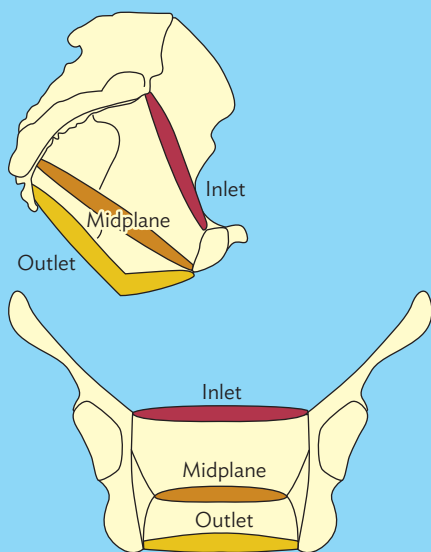

FIGURE 11.27

Butchering This artist's reconstruction shows how early *Homo* likely processed animals in groups, using a variety of stone tools. (© 1995 by Jay H. Matternes.)
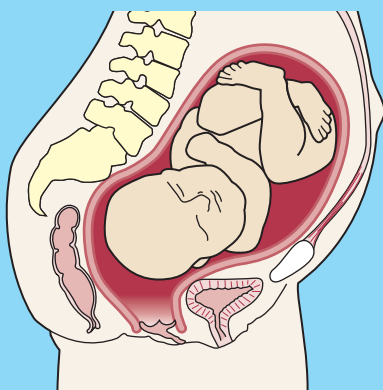
GIVING BIRTH TO BIG-

THE EVOLUTIONARY BENEFITS OF ROTATIONAL BIRTH

These side and frontal views of the human pelvis show the planes through which the infant passes.

In human birth, assistance generally is needed to ease the infant's large head out of the birth canal.

obstetric dilemma Hypothesis pertaining to hominin mothers giving birth to a large-brained, large-bodied infant: Owing to the large brain, the birth process requires a wide pelvis, but efficient bipedalism requires a narrow pelvis.

One of the most fundamental trends in human evolution is the remarkable increase in the size of the brain. Recall that the earliest hominins—the pre-australopithecines and australopithecines—had an average brain size of just 500 cc, give or take, and sometimes considerably less. By the time *Homo erectus* evolved, average cranial capacity had more than doubled. Today, our brains are on average three times the size of the brains of the earliest hominins. That expansion represents unprecedented neurological evolution in mammals. It reflects the fact that in our lineage the evolutionary priority was on intelligence, cognition, and behaviors associated with them.

The significant increases in brain size began with *Homo habilis,* some 3–2 mya. This increase must have had important implications for the birth process. While the hominin needed to remain fully efficient in bipedalism, its pelvis needed to be restructured to allow for the birth of big-brained (that is, large-headed) babies. Simply, an **obstetric dilemma** emerged for the *Homo* lineage once the brain began to expand in size: how to integrate brain-size increase in the infant with a bipedal skeleton

of the mother that accommodated in the past a relatively small brain. Scientists have been investigating this important evolutionary issue by studying the living record of primate and human birth and relating it to the fossil record.

What does the living record reveal about the evolution of birth? Owing to humans' big brains, broad shoulders, and big bodies, human birth is a complex and risky process that requires assistance by others. Today, this assistance normally is provided by health professionals and trained midwives, almost always in controlled settings such as modern hospitals. Primates have smaller brains, so primate birth is simpler, shorter, far less dramatic, and far less painful than human birth. In addition, the living record shows that throughout the birth process, the orientation of the primate infant's head and the path the head follows through the birth canal are different from those of the human infant's head.

The American physical anthropologists Karen Rosenberg and Wenda Trevathan have documented the orientation of the heads of living primates and humans in the various stages of birth. Throughout, as the primate infant travels from the pelvic inlet to the midplane to the pelvic outlet, for most births the primate infant's head remains in its front-to-back orientation with the face forward. In living humans, by contrast, in the inlet stage the head is oriented facing transversely so that one side of the head is against the back of the mother's pelvis and the other side is against the front of her pelvis. In the midplane and outlet stages, the head and shoulders nearly always rotate 90 degrees so that the front of the head and the shoulders face the back of the pelvis. The head has to rotate because the long axis of the inlet is perpendicular to the axis of the outlet. Moreover, the longest axis of the head and the broadest axis of the shoulders are at a 90-degree angle to each other. The head rotates externally when the baby is delivered so that the shoulders can follow its path. The generally contrasting patterns

BRAINED BABIES

in primate and human birth reflect the differences in brain (and head) size and the constraints placed on the pelvis by bipedalism. Rotational birth appears to be the key evolutionary solution for accommodating the birth of large-brained babies and maintaining efficient bipedalism.

What does the fossil record show? The American physical anthropologists Robert Tague and Owen Lovejoy have reconstructed the pelvic inlet, midplane, and outlet of the early australopithecine Lucy (*Australopithecus afarensis*) and found that, in contrast to those of living humans, the inlet and outlet axes are parallel. Therefore, the head would likely not have rotated during birth. While mothers of *Au. afarensis* infants such as Lucy would have felt discomfort while giving birth, they would not have experienced the excruciating pain and difficulty associated with the complex rotation that occurs in living humans, nor would they have required assistance during the birth process.

At what point in human evolution did the pelvic modifications develop that led to rotational birth? Most fossil hominin pelvises are not well preserved, but the two *H. erectus* pelvises present some interesting evidence. One is from Gona, in the Middle Awash Valley of Ethiopia, and the other is from Nariokotome, on the western side of Lake Turkana, Kenya. Both are somewhat broad relative to the front-to-back dimension. In this respect, they are australopithecine-like. Based on this important record, Scott Simpson suggests that rotational birth was likely not present 2.0–1.5 mya. Therefore, at this time in human evolution, the pelvis retained some primitive traits, relative

breadth especially. Later in human evolution, brain size reached modern levels, and rotational birth and the complex social behavior associated with it appeared. Perhaps the first rotational births were in the early members of our own species, *Homo sapiens.* They might have occurred as late as 100,000 yBP, when the brain reached its current size. By that time, our ancestral mothers definitely would have benefited from assistance, as human mothers do today.

In *Australopithecus afarensis*, the long axis of the head is oriented transversely, aligned along the long axis of the pelvic inlet throughout the entire birth process. In living humans, the long axis of the head starts in transverse position (inlet stage), but then rotates 90 degrees (midplane stage). This rotation likely evolved relatively late in human evolution.

Au. afarensis   *Homo*

Front

Back

Front

Back

Front

Back
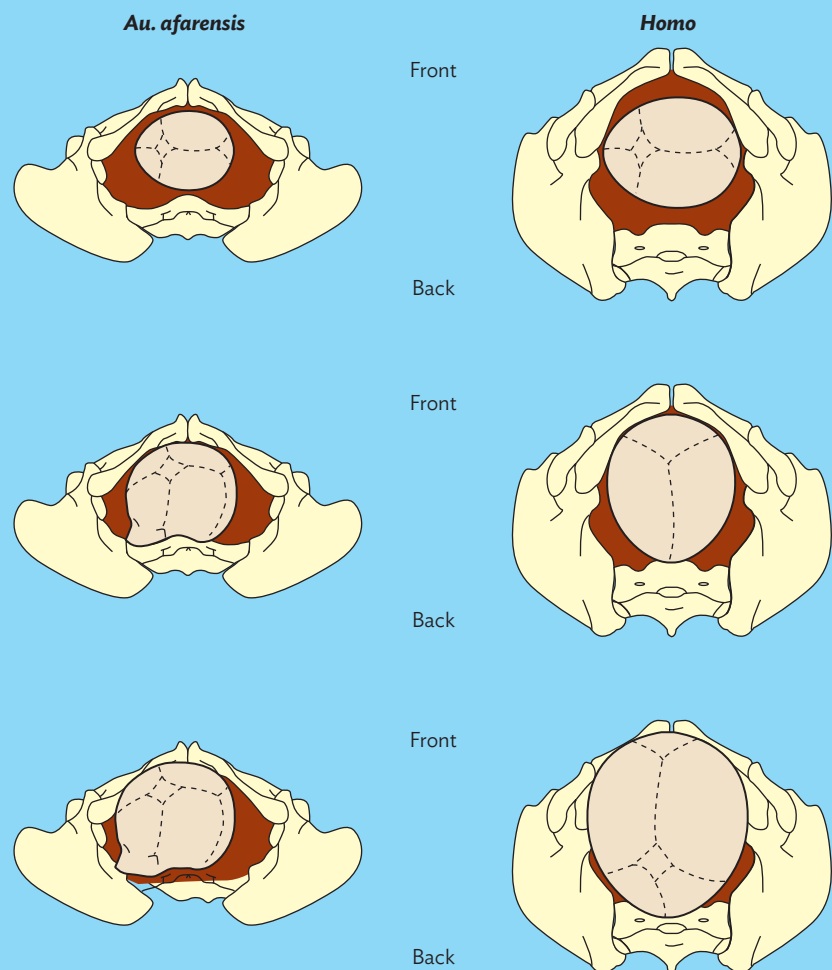
Wonderwerk Cave, South Africa This site may contain the earliest evidence for the controlled use of fire by early hominins.

that *H. erectus* was adapted to eating cooked meat and other cooked foods. These rich sources of energy would help explain the increases in brain size and body size. Cooking increases the digestibility of meat and other foods and improves the quality of the energy that it gives the eater.

Cooking would have required the ability to make and control fire. There are various claims for the early use of fire. By analyzing sediments from Wonderwerk Cave in South Africa, the Italian archaeologist Francesco Berna and his associates have determined that *H. erectus* made and used fire by 1 mya (**Figure 11.28**). The researchers' discovery of burned animal bones and plant remains in association with Acheulian tools indicates that these hominins used fire primarily for cooking. Fire may also have been used at Zhoukoudian, but the evidence from that locality is unclear and does not appear to have been made or controlled by human activity. That is, animal remains and stone tools are burned, but the type of burning is not associated with fire produced by hominins.

Fire also played a vital role in hominins' adaptation to regions of the globe where the temperature is cold much or all of the year. The controlled use of fire made possible a major expansion in where people could live and the manner in which they prepared their food. Thus, while there is not clear evidence for the use of fire at Zhoukoudian, hominins most likely had to have made and controlled fire in order to live there, especially during cold periods of the year.

Mostly important, however, *H. erectus* used fire to cook food. Before using fire, hominins ate plants and animals raw. But cooking these foods made them easier to chew and, as a result, made the very powerful jaws and large teeth of *H. erectus*'s predecessors less necessary. Indeed, the jaws and teeth of these Middle Pleistocene hominins were smaller than earlier hominins'. This size reduction was almost certainly related to the cultural innovations of the Middle Pleistocene, including both controlled use of fire and

more advanced tool technology. These cultural developments were the harbingers of increasing environmental control and improved adaptive success, both of which form an ongoing theme of human evolution.

Another potential means of improving dietary quality and energy intake is food sharing. In this case, males would have hunted for meat and subsequently shared it with females and dependent children. Indeed, an extensive ethnographic record for living societies shows that food sharing happened in this manner universally. It is likely that this kind of provisioning was an essential element of increased access to high-quality nutrition. Thus, food sharing, meat eating, and cooking help explain the increase in brain size in human evolution, beginning especially with *H. erectus*.

CONCEPT CHECK

Homo erectus: Beginning Globalization

Homo erectus was the first hominin to inhabit territory all over the Old World. After first evolving in Africa, it spread rapidly to Asia and then to Europe. Increased intelligence, increased dependence on technology and on material culture, social hunting, and access to more protein and to better nutrition contributed to this early hominin's remarkable adaptive success.

(Photo © 1985 David L. Brill, humanoriginsphotos.com)

Location/Sites	Africa (Olduvai Gorge, Lake Turkana, Ileret, Bouri, Buia, Bodo, Olorgesailie); Asia (Dmanisi, Kocabaş, Trinil, Sangiran, Sambungmacan, Gongwangling, Majuangou, Zhoukoudian); Europe (Gran Dolina, Mauer, Boxgrove)
Chronology	1.8 mya–300,000 yBP in Africa 1.8 mya–300,000 yBP in Asia 1.2–0.4 mya in Europe

Biology and Culture (Compared with *Homo habilis*)

Feature	Evidence	Outcome
Tool use (Acheulian)	Skulls Teeth	Smaller face and smaller jaws Reduced size
Fire and cooking	Ash in habitation sites	Smaller face and smaller jaws
Intelligence	Brain size	Increase (average 950 cc)
Hunting and increased meat protein	Butchered large animals	Increased body size
Possible cannibalism	Cutmarks	New ritual or dietary innovation
Growth	Enamel perikymata	Slower growth, but not modern
Locomotion	Leg length:arm length	No significant change

TRACKING HUMAN

Fossils Are the Record of Transition and Process

Outside the academic setting, anthropologists are often challenged by people who question the theory of evolution. The challenges to evolution come in a number of forms. For example, opponents argue that because one cannot actually see evolution operating, it cannot exist.

Anthropologists point out that evolution is happening all around us. When new life is conceived, with half the chromosomes coming from the father and half from the mother, the fertilized egg contains a unique mix of genes, one that had never existed before. This process is evolution operating at its simplest level.

A much more common challenge to the theory of evolution, however, targets the validity and scope of the fossil record. Such statements are also based on misconceptions about the fossil record. For example, challengers say that the human fossil record lacks intermediate forms. One of the most commonly cited examples is the apparent gap in the past between apes and humans. Simply, how could living apes and living humans share a common ancestor if these species are not connected by transitional forms? As discussed in chapter 9, the earliest hominins, the pre-australopithecines and early australopithecines, had both apelike and humanlike attributes. Indeed, the earliest hominin was essentially an ape that walked bipedally. The pre-australopithecines are important transitional fossils. The few specimens conform to expectations about what the earliest hominin would have looked like—they have primitive apelike skulls, for example.

In fact, the record of biological change throughout much of human evolution is now well defined. The fossil record is sufficient to support a number of conclusions about the evolution of early *Homo.* For example, brain size increased gradually in early *Homo* and was likely associated with both increasing intelligence and tool use. Body length increased rapidly within the same period, the late Pliocene, as the short *Homo habilis* became the relatively tall *Homo erectus.* This transition may have taken place within less than a few hundred thousand years.

All fossils, like the genera and species they come from, represent transitions. Tens of thousands of hominin fossils now provide a remarkably diverse and comprehensive record of human transitions, or evolution. As the dating methods described in chapter 8 have shown, these fossils are anatomically and chronologically between modern humans and our earliest ancestors, who lived 6–5 mya. The record is compelling, and the unearthing of more and more fossils will help support the ideas behind evolution and more fully describe its processes.

In addition to the fundamental importance of fossils for documenting the phylogenetic record of human

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ancestry, fossils tell us about specific adaptations over the last six million years of hominin evolution. As you have learned throughout this book, the history of humans—and all primates—is one of dynamic change. For example, there have been periods dominated by cold temperatures. Paleoanthropologists have documented patterns of morphology that may reflect adaptations to cold. For example, European Neandertals—a form of archaic *Homo sapiens* that you will read about in the next chapter—have remarkably wide openings for the nose (and see Figure 12.22, p. 408). These wide nasal apertures are suggestive of adaptation to cold environments. That is, a large, wide nose provides the hominin with greater interior surface area than a small, narrow nose. This is important because this larger surface area allows a more efficient means of warming and moistening the cold, dry air being inhaled. Some physical anthropologists suggest that this nasal morphology may have been important for maintaining relatively normal temperatures for the brain, a very temperature-sensitive element of the nervous system. However, other populations living in cold climates lack large, wide noses. This suggests that either the nasal morphology is not linked to environmental change, especially cold climates, or it may have been an adaptive solution for European Neandertals. Indeed, local adaptive solutions in some settings but not others are a record seen in many places and many times. Regardless of how this morphology is interpreted, it gives us a point of discussion of the remarkable amount of variation in our hominin ancestors and its importance for documenting our evolutionary past.

These and other hominin fossils have enabled researchers to draw conclusions about hominin evolution and human ancestry.

Patterns of Evolution in *Homo erectus*

Comparisons of all the *H. erectus* fossils from Africa, Asia, and Europe reveal important information about this early *Homo* species, both in general similarities across these continents and in the individual forms' evolution. *H. erectus* skulls are long, low, and wide at the base, and they have thick bone and large browridges. The African *H. erectus* tends to be the most robust, with the largest and thickest cranial bones. The Dmanisi and African forms are strongly similar—the sagittal keel, for example, is missing in Dmanisi and present only rarely in the African representatives. Morphological variations are likely related to differences in time and in geography, but the degree of variability is far smaller than that in other mammals.

Some authorities have interpreted the general similarity of *H. erectus* across Africa, Asia, and Europe and through time as representing evolutionary stasis. However, various morphological attributes show significant evolution in *H. erectus,* with earlier forms having considerably smaller brains than later forms. For example, the average Dmanisi skull is 650 cc, while the average Zhoukoudian skull is 1,200 cc. Overall, *H. erectus*'s brain size increased by some 30%. The American physical anthropologist Milford Wolpoff has also documented decreases in cranial bone thickness and browridge size. These characteristics indicate a decline in skull robusticity. Accompanying these changes is a reduction in tooth size, caused by the decreased demand on the face and jaws due to the increasing importance of technology and of cooking.

Hominins' increasing reliance on tools profoundly affected human biology. As tools began to perform the functions of the face and jaws in preparing food for consumption—that is, in cutting up, cooking, and processing meat and other food—there was a commensurate decline in the robusticity of these body parts, the anatomical area associated with mastication. In terms of both culture and biology, *H. erectus* evolved the contextual behavior—hunting, successful dispersal across large territory, adaptive success, and increasing dependence on and effective use of culture as a means of survival. The increased dependence on culture and the dominance of behaviors requiring technology in acquiring and processing food increased the diversity of environments occupied by *H. erectus.* The expansion of resources acquired and habitats occupied, coupled with the high degree of mobility, laid the basis for a high level of gene flow and the presence of a limited number of species—most likely, one species. The next chapter tracks and interprets the evolution of that species: *H. sapiens*.

After *Homo erectus*: Expect the Unexpected in Hominin Evolution

As we have seen in this chapter, the evolution of *H. erectus* is critically important, including adding to our understanding of biological variation, changing patterns of diet and adaptation, and identifying patterns of variation that characterize this taxon. In general, the emerging picture of human evolution from 1.5 mya to 0.5 mya ago or so shows the presence a hominin evolving over a period of a million years. The record shows generally increasing size of the body, brain, and masticatory complex. The patterns described in this chapter provide an essential adaptive platform for interpreting the process and outcome of the evolution of *H. erectus* and the origins and evolution of *H. sapiens* discussed in the upcoming chapters. But, there are lots of surprises in human evolution, one of which is *H. naledi*. The discovery of a hominin having a unique suite of anatomical characteristics found deep in a cave in South Africa demonstrates that paleoanthropologists have to be ready for the surprises that do not necessarily meet the consensus of the time. That is one of the exciting things about science—the twists, the turns, and the surprises of discovery.

Indeed, it is not just the early end of the evolution of the genus *Homo* that is turning

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Flores

up surprises, but also the later evolution. Simply, new discoveries in this discovery-rich discipline are revealing that there is a considerable amount of variation that does not fit the consensus. One of the most remarkable of these discoveries was made in 2014 on Flores Island, Indonesia, by paleontologists excavating deposits at the Mata Menge site, a site that dates to 700,000 yBP. Expecting to find the remains of *H. erectus*—at a time during which *H. erectus* was ubiquitous throughout Africa, Asia, and Europe— paleontologist Gerrit van den Bergh and fellow discoverers found something very new and very different. It was exciting enough to find hominin fossils—a partial adult mandible and six isolated teeth representing at least two children. But, quite unlike all hominins from Indonesia, and the rest of Asia and Africa and Europe dating to the Middle Pleistocene, the Mata Menge mandible (and, by inference, the rest of the skeleton) is *extraordinarily* small, perhaps representing an adult having half the body size of other contemporary hominins. The morphology of the teeth is similar in some respects to the much later, but also remarkably small, *Homo floresiensis* ("Hobbit"), also from Flores Island and dating between 100,000 yBP and 60,000 yBP (see chapter 12). The extremely small body size of the Mata Menge hominin and the much later *H. floresiensis* is unique in this region. The presence of an earlier and a later dwarf hominin suggests the presence of a dwarf lineage of hominins, specific to Flores Island.

The Mata Menge hominins are likely not *H. erectus*, but rather represent descendants of *H. erectus* that had settled on Flores Island in the Middle Pleistocene. At least for now, van den Bergh ascribes the Mata Menge fossils to *H. floresiensis*, owing to the resemblance in the teeth with the later hominin from Flores Island and its very small body size.

Importantly, the Mata Menge mandible and teeth add to the growing body of evidence showing considerable anatomical variation in the Middle Pleistocene, ranging from very small body size (Flores Island) to relatively large body size (just about everywhere else *except* Flores Island). Although the taxonomic identity of the Mata Menge hominin is preliminary, it nevertheless underscores the important point made earlier in this chapter and in this textbook in general regarding the remarkable adaptability of humans and their ancestors. For Mata Menge and the later hominin from Flores Island, the very small body size may have been due to their having lived on an island with limited food resources. We know that many species of animals living in island settings worldwide have reduced body size, owing to limited food resources. Simply, stunted size requires less caloric intake. Therefore, it would seem that small body size would have a selective advantage in these circumstances. But, this remains a point of speculation. What is not speculation, however, is that it is this remarkable variation that lays the groundwork for the evolution of modern people.

CHAPTER 11 REVIEW

ANSWERING THE BIG QUESTIONS

1. **What characteristics define the genus *Homo*?**
   - The genus *Homo* is defined by physical and behavioral attributes, including a relatively large brain, small face and jaws, and dependence on material culture for survival.

2. **What were the earliest members of the genus *Homo*?**
   - The earliest members of the genus *Homo* were *Homo habilis* and *Homo erectus*.
   - Fossils of *H. habilis* have been found in East Africa and South Africa and date to about 2.5–1.8 mya.
   - *H. erectus,* a geographically and morphologically diverse species, dates to about 1.8 mya–300,000 yBP. Its fossil record is represented in Africa, Asia, and Europe.

3. **What are the key evolutionary trends and other developments in early *Homo*?**
   - Compared to the australopithecines, early *H. habilis* experienced an enlargement of the brain and a general gracilization of the chewing complex (face, jaws, and teeth). These developments were linked with increases in tool production and use, dietary diversity, and intelligence.

   - Compared with *H. habilis, H. erectus* experienced a continued reduction in size of the chewing complex, increased brain and body size, and the first evidence of modern limb proportions.
   - *H. erectus* developed an increasingly innovative and complex technology, including more elaborate tools, organized social hunting, and controlled use of fire. These developments facilitated greater access to protein and improved nutrition, which likely explains the rapid increase in body and brain size around 2.0–1.7 mya. This increasing adaptive flexibility is a central theme of human evolution.
   - *Homo* increasingly became a predator genus in the early Pleistocene, and this change at least partly explains its remarkable and rapid geographic expansion. Successful predation was largely from hunting, but early *Homo* likely acquired food through hunting *and* scavenging.
   - The increased intelligence and full commitment to material culture as an adaptive strategy of *H. erectus* set the stage for the emergence and evolution of *Homo sapiens.*
   - Discoveries of dwarf hominins from Southeast Asia reveal new variation in Middle and Late Pleistocene hominins.

KEY TERMS

Acheulian Complex
handaxe
Homo erectus
obstetric dilemma
*Pithecanthropus
   erectus*
sagittal keel

STUDY QUIZ

1. **What anatomical feature did *Homo habilis* share with earlier australopithecine species?**
   a. a small brain
   b. a large chewing complex
   c. a large face and large jaws
   d. short legs relative to arms

2. **Where does *Homo naledi* most likely fit into the human lineage?**
   a. an early taxon of genus *Homo*
   b. a late taxon of genus *Homo*
   c. a descendant of *Homo erectus*
   d. actually an australopithecine

3. **Which of the following represents skeletal adaptation of *Homo erectus* contributed to its fully modern walking?**
   a. longer legs and shorter arms
   b. a more abducted big toe

   c. loss of arches of the foot
   d. decreased body height

4. **Which of the following is *not* a *H. erectus* behavioral innovation?**
   a. long-distance hunting and walking
   b. controlled use of fire for cooking
   c. production of symbolic material culture
   d. migration outside of Africa to Asia and Europe

5. **The rapid increases in *H. erectus* body and brain size are most likely linked to which diets?**
   a. a high-fiber diet of fruits and vegetables
   b. a high-fiber diet of grasses and seeds
   c. a high-protein diet of raw meat
   d. a high-protein diet of cooked meat

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THE ORIGINS OF *HOMO*

Synopsis The earliest members of our genus, *Homo,* arose nearly 2.5 mya and were characterized by an increase in brain size and a stronger reliance on material culture for survival. Key anatomical changes in *Homo habilis*—such as a larger brain, a less robust jaw, and smaller teeth—highlight the growing importance of tool use and dietary diversity as adaptations in the genus *Homo. Homo erectus* became the first hominin species to spread out of Africa to Europe and Asia, a global dispersal made possible by anatomical and cultural adaptations, including increased brain size, larger body size, more complex tool technology, use of fire for cooking, and emergence of hunting behaviors. The first members of *Homo* exhibited a series of evolutionary trends that set the stage for the ongoing evolution of the genus and the eventual emergence of our own species, *Homo sapiens.*

Q1. Name the three features outlined in this chapter that set the earliest member of our genus, *H. habilis,* apart from the australopithecines and that are defining characteristics of the genus *Homo.*

Q2. In some ways, the differences between *H. erectus* and *H. habilis* are more pronounced than those between *H. habilis* and the latest australopithecines. Provide three examples of anatomical characteristics in *H. erectus* that differ substantially from those observed in *H. habilis.* What are the evolutionary trends in these characteristics that are seen between these two species?

Q3. What are some of the roles that tool use and climate change may have played in shaping the adaptive flexibility (and evolutionary success) of *H. habilis* relative to the species of australopithecines living at the same time?

Hint Climate change in the early Pleistocene led to the spread of a grassland environment and increased habitat and resource diversity.

Q4. *H. erectus* is characterized by substantial changes in body size, brain size, material culture, and dietary and behavioral flexibility compared to earlier hominin species. Rather than being unidirectional (for example, increased brain size leads to complex material culture but not the other way around), how might all of these changes be part of an evolutionary feedback loop driven by biocultural adaptation?

Hint Consider the ways that certain behaviors emerging in *H. erectus* may have had anatomical, physiological, and nutritional effects, as well as the ways in which these effects may have further influenced behavioral flexibility.

Q5. *H. erectus* was the first hominin species to spread out of Africa to other areas of the globe. Use specific biological and cultural features and the concepts of survival, reproduction, and migration to explain why *H. erectus* was the first species capable of such a widespread existence.

ADDITIONAL READINGS

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