5 HOMININ EVOLUTION

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The fossil record provides a clear record of the evolution of the human species from a small-brained bipedal ape over the past 10 million years. Some people mistakenly believe that paleoanthropologists are searching for the “missing link” between us and creatures such as the modern chimpanzee or gorilla. However, modern humans, chimpanzees, and other living primate species each lie at the end of their own, distinct evolutionary branches. Paleoanthropologists are also skeptical of the phrase “missing link” because it implies that evolution unfolded in a linear path with well-defined junctures. The reality of the fossil record demonstrates that evolution is much messier: Different branches evolved at varying rates, and new traits emerged as a result of populations both intermingling and diverging. Rather than a tree of life with distinctive branches showing common ancestors, the fossil record emerges more like a dense, tangled bush with overlapping lines of descent (Quammen 2018).

The evolution of primates in the Miocene and Pliocene epochs provides a backdrop for the emergence of our early human ancestors. By the Miocene epoch (23 million to 5.3 million years ago), varied primate species including the precursors of modern prosimians, monkeys, and apes proliferated in many geographic regions. Sometime in the late Miocene or early Pliocene, new and distinct forms of primates of the subfamily Homininae emerged. Classified as members of the tribe Hominini or hominins (see the box “What’s in a Name?” in Chapter 4, page 70), these varied species present a range of distinctive features in their teeth, jaws, and brains that represent adaptations to varying environments. However, they all share the structural anatomy needed for bipedalism, the ability to walk upright on two legs. It is this characteristic that separates the hominins from other primates and collectively identifies them as the species most directly related to modern humans.

Over the past century, paleoanthropologists have advanced numerous interpretations of hominin phylogeny—the evolutionary history of humans and their ancestors (Ayala and Conde 2017; Henke and Tattersall 2015; Stringer and Andrews 2012). Although opinions diverge on the naming and classification of individual fossil specimens, paleoanthropologists broadly agree that the human species evolved from a small-brained bipedal ape, the Hominini lineage branching off from the other Homininae primates between about 7 million and 10 million years ago (T. White et al. 2009). For the purposes of this discussion, we primarily focus on two genera of hominins: Australopithecus, which emerged first, and Homo. Both of these groups include a number of different species, some of which have at times been placed in different genera. Going back over 6 million years, the australopithecines are the older group, and they are only known from African fossil finds. The earliest representatives of the species are A. anamensis and A. afarensis. Australopithecine fossils date from roughly 4 million to 1 million years ago. After that, there is no trace of this genus in the fossil record, leading paleoanthropologists to conclude that the group became extinct at about that time.

Representatives of Homo, the genus that includes modern humans, first appear in the fossil record after 3 million years ago. There is a consensus among anthropologists that genus Homo evolved from the australopithecines, though interpretations vary as to which australopithecine species gave rise to the new genus. The earliest members of the Homo line to be identified in the fossil record are the species H. habilis and H. rudolfensis, dating between 2.4 million and 1.5 million years ago. What distinguishes the first representatives of genus Homo from the australopithecines is a trend toward larger brain size. Homo habilis is followed in the fossil record by Homo erectus (including finds sometimes designated Homo ergaster), which is known from finds in Africa dating just after 2 million
years ago. *Homo erectus*, in turn, evolved into *Homo sapiens*—modern humans—during the past 400,000 years. Members of genus *Homo* coexisted with some of the later australopithecine species between 2.2 million and 1 million years ago.

**TRENDS IN HOMININ EVOLUTION**

5.1 Explain the principal trends in hominin evolution and within genus *Homo*.

The hominins are members of the order Primates. As such, they share the basic primate characteristics discussed in Chapter 4, including a generalized skeleton, a high degree of manual dexterity, and prolonged infant dependency. But the hominins evolved with distinctive, derived characteristics. As noted, the first and most significant of these is bipedalism, a feature common to all hominins. Other distinctive features include the reduction of face, jaw, and anterior teeth and a trend toward increasing cranial capacity in genus *Homo*. Changes in these attributes are preserved in the fossil remains of early hominins, and the evolutionary relationships of different species are traced on the basis of the similarities and differences present in individual finds. These characteristics are exemplified in modern humans and least pronounced in earlier hominin species.

The evolution of some physical, social, and cultural characteristics of early hominins is difficult to trace because these characteristics are not preserved in the fossil record. For example, unlike other surviving primates, modern humans are not completely covered with hair. Loss of body hair, as well as characteristics such as skin color and the prevalence of sweat glands, might be a relatively recent phenomenon (see discussions in Chapter 6), but we can find no indication of these developments in fossilized remains. Other trends, such as degrees of social complexity and the origins of human culture, are also of great interest, but such features cannot be directly inferred from fossil remains. Rather, they are evaluated on the basis of early hominins’ tools, food remains, and living sites, topics examined in Chapter 7.

**Bipedalism**

Hominins are the only primates that are fully bipedal. As discussed in Chapter 4, although gorillas, chimpanzees, orangutans, and other primates can stand upright, they spend most of their time on all fours. As with other types of locomotion, bipedalism is reflected in skeletal structure, and so its evolution can be traced in the fossil record. For example, the hips and knees of hominins differ markedly from those of knuckle walkers like the chimpanzee. Paleoanthropologists also focus on the position of the *foramen magnum*, the opening in the base of the skull through which the spinal cord passes. In quadrupedal animals, this aperture is at the back of the skull, which allows the head to extend out in front of the body (Russo and Kirk 2013). In contrast, the *foramen magnum* in bipedal creatures is on the bottom of the skull, sitting squarely above the body. Structures of the skull associated with bipedalism are especially important because the postcranial bones of many fossil hominins have not been preserved.

Bipedalism stands as the earliest and most important trend in hominin evolution. However, the fossils of early hominin ancestors indicate skeletal features that would have been well suited for an *arboreal* lifestyle—that is, life in the trees (Senut 2012; S. Thorpe, McClomont, and Crompton 2014). In light of this evidence, many paleoanthropologists believed that the earliest hominins, the australopithecines, were not fully bipedal, perhaps moving with a swinging, slouched gait like that of chimpanzees or gorillas. These interpretations were based on limited fossil finds and have not been supported by more recent studies. Fossil remains of the oldest known hominins, in fact, indicate that these creatures walked as well as modern humans (see Figure 5.1). Our best scientific guess places the appearance of bipedalism in early hominin ancestors sometime between 10 million and 15 million years ago, a period of time that is unfortunately poorly represented in the fossil record.

**Why Bipedalism?**

Although bipedal posture can be clearly inferred on the basis of skeletal remains, it is more difficult to reconstruct the behavior of early hominins and thus evaluate how upright posture may have been beneficial. While walking upright would have freed the hands of early hominins for tasks other than locomotion, the adaptive aspects of bipedalism and how it may have enhanced the reproductive success of evolving hominin species are not immediately apparent. Bipedalism is a relatively slow means of locomotion. Nor does the skeletal and muscle structure needed for bipedalism provide the most effective way of climbing or moving through trees—it would have been a disadvantage in terms of avoiding predators. Upright posture also places added stress on the lower back, hips, and legs and makes it more difficult to supply the brain with blood. In light of these seeming drawbacks, there has been a great deal of debate regarding how this feature was adaptive, and why it was selected for in early hominins.

While there is ongoing debate about the origins of bipedalism, two overarching points can be made. First, bipedal locomotion probably evolved as a result of a confluence of factors rather than a single adaptive characteristic. As discussed in the next section, thermoregulation models may provide the most plausible explanation for the origins of bipedalism. Perspectives, however, vary, and researchers have suggested different views of how walking upright may have been adaptive. Second, bipedalism clearly had important social, as well as behavioral, consequences. Behaviors such as food gathering and food sharing may or may not have played a role in the emergence of bipedalism (G. Isaac 1978a; Lovejoy 1984; E. Smith and Winterhalder 2017). But there is no question that once developed, this type of locomotion served early hominins well by...
An interrelated aspect of the thermodynamic model also considers the possible benefits of sweat glands and the loss of body hair (Wheeler 1992, 1994). Sweat cools the body; less body hair and more exposed skin would have further facilitated cooling. Modern humans have substantially less body hair than other primates and also sweat more than any other animal. Modern apes such as the chimpanzees and gorillas sweat, though not as much as humans. Sweat glands and limited body hair would have provided an adaptive advantage under the hot equatorial sun, and so been selected for in early hominins. Early hominins may have been able to move during the hottest times of the day, times when predators such as lions rest.

As a consequence of these physical traits, bipedal hominins, while slower moving than some four-legged (quadrupedal) animals over short distances, would have moved more efficiently over longer distances, something that would have allowed them to travel greater distances in search of food. Humans are not simply able to walk upright; we excel at walking. Daniel Lieberman and Dennis Bramble (2007) have observed that with our steady pace, humans can outdistance almost all other mammals over long distances, particularly freeing their hands for these, as well as a variety of other tasks. These activities, in turn, would have facilitated a number of important social and cultural innovations.

**Thermoregulation**

Recent theories regarding the origins of bipedalism have considered the unique adaptive advantages that bipedal locomotion may have conferred in the environment in which early hominins evolved, possibly the semi-open savannas and mixed woodlands of East and Central Africa, regions that have produced many of the early hominin fossil finds (Wheeler 1991). Food resources in this mixed savanna–woodland environment would have been scattered, and selection would have favored endurance, rather than speed, in locomotion.

A combination of attributes in humans makes us very efficient at bipedal locomotion, particularly with regard to endurance running or jogging (Bramble and Lieberman 2004; D. E. Lieberman et al. 2007). Less heat is generated in the legs of bipeds. In addition, the ligaments in the legs and feet (the Achilles tendon, for example) allow humans to release energy like a spring as they move forward. Our flexible chests and anatomy also make for stable bipedal movement.

![Figure 5.1](Do not copy, post, or distribute)
when it is hot. Indeed, it has been noted that the modern San people of southern Africa sometimes employ persistence hunting, literally chasing animals until they collapse (Liebenberg 2006). These interrelated traits may have conferred important adaptive advantages on early hominins; their bipedal stature, combined with efficient vision, would also have facilitated their ability to identify food resources.

While these interpretations are plausible, and they may explain why bipedalism emerged, the movements of early hominins across the savanna and their behaviors are difficult, if not impossible, to assess on the basis of the archaeological record. Nor does the fossil provide a record of features such as body hair and sweat glands, so it is unknown how sweaty or hairy our early hominin ancestors might have been. It is, therefore, difficult to fully evaluate all of the variables and which ones played the most prominent roles in the development of bipedalism.

Reduction of the Face, Teeth, and Jaws

Evolving hominin lineages also present a series of interrelated changes associated with diet and food-processing requirements (Ciochon and Fleagle 2017). The oldest fossil hominins have a protruding, or prognathic, face, the jaw extending outward farther than in modern humans. In addition, the canine teeth of early hominins, while smaller than those of other apes, are large compared with those of modern humans. In this respect, early hominins can be seen as transitional between earlier ancestors and later humans. To accommodate these larger canines, which extend beyond the other teeth, there are gaps between the teeth of the opposing jaw. This feature, called diastema, is characteristic of the early hominins, as well as living apes and monkeys such as the gorilla and baboon, but absent in humans (see Figure 5.2). The teeth of early hominins are also arranged in a U-shaped pattern, and the teeth on opposite sides of the mouth are parallel. This arrangement is similar to that found in modern gorillas, orangutans, and chimps. In contrast, in the human jaw the teeth are not parallel, but flare away from each other at the back of the mouth.

Approximately 2 million years ago, fossil evidence indicates that these apelike characteristics started to become less pronounced in hominins, becoming more humanlike in dentition. Early primates, as well as living prosimians and anthropoids, had large canine and incisor teeth that are well suited to cutting and slicing. In contrast, the size of the canine teeth is greatly reduced in later hominin species. Early representatives of the genus Homo have smaller canines, and the gaps associated with larger canine teeth disappear. In modern humans, the canine teeth retain a distinctive shape, but they are almost the same size as the other teeth. Of all the hominins, the faces of modern humans are the least protruding.

Some hominin species have teeth and cranial structures indicative of adaptations to specialized diets, distinct from those characteristic of genus Homo. In particular, the robust australopithecines (A. robustus, A. boisei, and A. aethiopicus, discussed later) developed massive chewing muscles and extremely large molars compared with those of modern humans. This strong dentition earned one species, Australopithecus boisei, the nickname “Nutcracker man.” Scientists believe that these features most likely evolved in response to a diet of coarse, fibrous vegetation. Paleoanthropologists cite several key skeletal structures in the jaw and the cranium as evidence of this creature’s powerful chewing capacity. Thick, enlarged jaws and cheekbones provided attachments for these huge muscles. Some australopithecine fossil specimens have a sagittal crest, a bony ridge along the top of the skull that grows larger as more chewing muscles reach up along the midline of the cranium.

In contrast to the australopithecines, evolving Homo species may have consumed a more varied, omnivorous diet based on gathering vegetation, hunting animals, and scavenging. This theory corresponds with the size and contour of their molars similar to those of modern humans and the absence of such features as sagittal crests, which accompany specialized chewing muscles.

Increase in Cranial Capacity

The defining characteristic of Homo, the genus of which modern humans are members, is a tendency toward increased cranial capacity and the complexity of the brain. Like the changes in dentition, growth in cranial capacity first appears in hominins dating from about 2 million years ago. Before that, the size and organization of the hominin brain underwent comparatively
little change. Early australopithecines such as *A. afarensis* (which lived some 3 million to 4 million years ago) had a cranium about the size of a softball, barely surpassing that of a modern chimpanzee. Hominin cranial capacity remained fairly constant at this size for 2 million years, averaging just over 400 cubic centimeters (cc). Then, after 2 million years, members of the genus *Homo* began to show a steady increase in cranial size. The cranial capacity of *H. habilis*, the first representative of the genus, was over 600 cc. The brain in *Homo erectus* averaged 1,000 cc, and the modern human brain measures, on average, 1,350 cc, a threefold increase from the australopithecines. Significantly, this constitutes an increase in both relative and absolute size. Even taking into account that modern humans are substantially larger than australopithecines, the relative size of the hominin brain more than doubled in the last 2 million years (Du et al. 2018; McHenry 1982).

Changes in the cranial capacity of early hominins undoubtedly influenced physical and social developments, which are less easily studied through fossil remains. For instance, increasing brain size almost certainly prompted numerous modifications in hominin diet, the use of tools, the evolution of language, and the intricacies of social organization. Greater sophistication in any of these areas may have improved early hominins’ chances of survival.

**FIGURE 5.3 Map of Early Hominin Fossil Finds**

In *On the Origin of Species* (1859), Charles Darwin devoted relatively little attention to human evolution, noting simply, “Much light will be thrown on the origin of man and his history.” In the mid-nineteenth century, when Darwin was writing his treatise, scientists had scant fossil evidence for hominin origins. Since Darwin’s time, however, thousands of hominin fossils have been recovered. The Hominid Vault of the Kenya National Museum alone contains hundreds of hominin specimens from Kenya and Tanzania, and thousands of other specimens have been recovered from other sites. Specimens range from isolated teeth to nearly complete skeletons. Although paleoanthropologists have uncovered many spectacular finds, some discoveries merit special attention because they prompted anthropologists to modify theories of human evolution. In this section, we examine several of the most important fossil finds, beginning with the earliest hominin ancestors. The locations of some of these key discoveries are illustrated in Figure 5.3.

In the following discussion of the fossil evidence for hominin evolution, the names designating specific genera and species
provide a simplified overview of some of the principal discoveries. The names used here are widely accepted apppellations used by paleoanthropologists, but they are not universally agreed on. Perspectives on hominin classification lie between two extremes. Some scientists, who can be called lumpers, argue that some species designations do not reflect all the species represented. For instance, some researchers have argued that the Australopithecus afarensis finds from Hadar constitute not a single species but at least two distinct species. Others contend that further divisions are called for within the gracile and robust australopithecines (Tattersall 1986, 1998). In fact, many researchers place the robust australopithecines (including A. aethiopicus, A. robustus, and A. boisei) into a separate genus from Australopithecus called Paranthropus. Some researchers have called for further divisions.

At the opposite extreme from the splitters are the lumpers, who maintain that current taxonomic designations place too much emphasis on differences among individuals and do not sufficiently consider the variation that might be expected within species. This position is best advocated by C. Loring Brace (1967, 1989). Brace asserts that the information available on Homo habilis, A. afarensis, and A. aethiopicus is insufficient to categorize each as a distinct species, and he advocates including them with other genera and species. For example, H. habilis might simply be included with Homo erectus.

Study of modern species, including humans, demonstrates that there is a great deal of variation within species in features such as cranial capacity, body size, and skeletal structure. For example, chimps from Tanzania’s Gombe National Park display an astonishing degree of variation in size and skeletal structure (Bower 1990). Modern humans are equally diverse in their physical characteristics. In interpreting fragmentary hominin fossils from widely separated localities, such natural variation within species must be considered.

At this point, it is useful to underscore that the different extremes represented by lumpers and splitters nonetheless include a great deal of consensus about the differences present in the individual fossil finds. The divergence in opinion is about what the differences in the fossil finds imply about taxonomic classification and the process of speciation. Unfortunately, the ultimate defining aspect of a species, the ability to interbreed, is not something that can be assessed on the basis of fossil evidence.

The Oldest Hominins

Fossil evidence for the evolution of the first hominins dates to the period between 6 million and 10 million years ago. The classification of these discoveries and their relationship to later species are uncertain, though some intriguing finds have been discovered. Among the most promising locales are a series of sites in Kenya, particularly the areas around Lake Turkana, Lake Baringo, and the Tuguen Hills in the Rift Valley region. The Middle Awash area of Ethiopia also has great potential. Geological deposits in each of these areas span the relevant time period, and well-preserved fossil deposits are represented. Notably, exciting discoveries have also been made in Chad in Central Africa, a region that had not previously produced hominin remains.

Sahelanthropus tchadensis

The Chad discoveries are especially notable because they occur some 1,500 miles farther west than any other early hominin find. This specimen, named Sahelanthropus tchadensis, consists of a complete, though distorted, cranium dated between 6 million and 7 million years ago, making it the oldest possible hominin (Brunet et al. 2002; Wolpoff et al. 2006). Some researchers have suggested that its age and physical characteristics may place it near the divergence of the hominin and chimpanzee lineages.

The dentition and cranium possess features that are a mixture of ape and hominin characteristics. In particular, the canine teeth are smaller than those of apes and do not extend below the other teeth, making it more comparable to later hominins. The limited information on the postcranial skeleton prevents the full assessment of how S. tchadensis may have moved. However, the shape and orientation of the foramen magnum suggests the ability to walk upright. Until more information becomes available, the evolutionary relationship of Sahelanthropus tchadensis to species will remain uncertain. Nevertheless, this fossil discovery from Chad has important implications regarding the evolution of the early hominins as it affords insight into the distribution and diversity of species present when hominin species were emerging.

Orrorin tugenensis

Fossil evidence for the early hominin ancestor Orrorin tugenensis consists of fossilized teeth and a few pieces of postcranial bone found from the Tuguen Hills in Kenya securely dated to between 5.7 million and 6.1 million years ago (Aiello and Collard 2001; Pickford et al. 2002; Wong 2003). The researchers who discovered these finds suggested that this species is an ancestor...
of later hominins. If recognized as a hominin, the Tugen Hills finds would indeed be those of *Orrorin*, which means “original man” in the local African language. In some respects, *Orrorin* presents features more similar to later human ancestors than australopithecine species (discussed later). *Orrorin*’s teeth, for example, are small like modern humans’. This has led some researchers to suggest this species as a more direct human ancestor, something that would move later australopithecine species to a side branch of human evolution (Reynolds and Gallagher 2012). However, because of the fragmentary nature of these fossils and the uncertainty of their classification, their hominin status remains uncertain.

**Ardipithecus ramidus**

Other potential hominin ancestors come from a series of fossil localities in the Middle Awash area of Ethiopia. This region, located at the intersection of the Great Rift Valley, the Red Sea, and the Gulf of Aden, has produced some of the most spectacular fossil finds, including Lucy and other examples of *Australopithecus afarensis* that will be discussed later. Fossil localities in the Middle Awash excavated by a number of researchers over the past two decades have produced a large number of fossil fragments that collectively represent some of the earliest potential hominin ancestors yet recovered.

**ANTHROPOLOGISTS AT WORK**

**DONALD JOHANSON, PALEOANTHROPOLOGIST**

In 1973, Johanson, in conjunction with French geologist Maurice Taieb, began research in an area known as Hadar in the Afar triangle of northeastern Ethiopia. At that time, the region had been largely unexplored by paleoanthropologists. Although the present climate is arid and inhospitable, the fossil record indicates that the region supported a variety of life-forms 4 million to 3 million years ago. In Hadar, Johanson and his fellow researchers (Johanson, Taieb, and Coppens 1982) uncovered many finds that cast light on early hominins and their environment.

Two spectacular finds in Hadar have received particular attention. The first, uncovered in 1974, was a strikingly complete (40 percent) skeleton of an early hominin affectionately referred to as “Lucy.” The second find, unearthed in 1975, consisted of a remarkable collection of hundreds of hominin bones, representing at least thirteen adults and children. Given the proximity of the finds, Johanson believes that all the creatures at the site may have died at the same time in a sudden catastrophic event like a flash flood. Both Lucy and additional fossil discoveries were representative of a previously undescribed species, which Johanson named *Australopithecus afarensis*.

In 1978, Johanson, in conjunction with paleoanthropologist Timothy White, reinterpreted the prevailing notions about hominin ancestry. They surveyed existing information and integrated it with Johanson’s finds from Hadar. Then, they restructured the hominin family tree, placing *A. afarensis* at the base, with two branches, one sprouting toward the genus *Australopithecus* and the other giving rise to the genus *Homo* (Johanson and White 1979). Some of Johanson’s interpretations are not without their critics. More recent discoveries have also led to an increasingly complex picture of hominin phylogeny. Nonetheless, researchers recognize *A. afarensis* as one of the earliest known hominins. As Johanson has aptly observed: “Frustrating as it is, the distantly tantalizing truths about our origins will probably not be revealed before we ourselves are buried under the earth” (Johanson and Shreeve 1989, 133).
They have been given their own genus, *Ardipithecus*, divided into two different species (T. White et al. 2009; T. White et al. 2015). The more recent of these, named *A. ramidus* ("ground ape at the root"), lived about 4.4 million years ago. The older of the two species, *A. kadabba*, has been dated to approximately 5.6 million years old (Haile-Selassie, Suwa, and White 2004). It is known from very fragmentary remains, and may be ancestral to *A. ramidus*. *A. ramidus* is of particular interest because it may have lived slightly after the divergence of the tribe Hominini and the African apes the gorilla (Gorillini) and the chimpanzee (Panini). In some respects, *A. ramidus* is quite different from both the African apes and later hominin species, such as the australopithecines. The cranial capacity of these Middle Awash creatures is quite small, as small as that of other early hominins, but the form of the cranium is also more apelike. The canine teeth in *A. ramidus* are larger than those in later hominins, and unlike other hominin species, this species also had a grasping big toe. This is a feature well adapted for locomotion in the trees found in nonhominin species such as the gorilla and chimpanzee. Yet, apart from these apelike features, the placement of the cranium over the spinal column, the shape of the pelvis, and the structure of the limb bones in *A. ramidus* are consistent with bipedal locomotion—the hallmark of the hominins (Lovejoy et al. 2009). This combination of features has led some researchers to argue that *Ardipithecus* should not be given hominin status (Stanford 2012).

**Australopithecus anamensis: Early Hominins From Lake Turkana**

The region around Lake Turkana in northern Kenya has also yielded a host of important fossil finds, including the discoveries of *Australopithecus aethiopicus*, *Homo habilis*, and *Homo erectus* (discussed subsequently). Some of the earliest widely recognized hominin remains are represented by a number of finds made over the past thirty years at Kanapoi, southwest of Lake Turkana, and Allia Bay, on the eastern side of Lake Turkana, including the remains of a species designated *Australopithecus anamensis* (M. G. Leakey et al. 1998; Wood and Leakey 2011).

The fossils of *A. anamensis* are fragmentary, including teeth and jaw fragments and some postcranial bones. The age of the finds is placed between 3.9 million and 4.2 million years ago. The leg bones are consistent with bipedal hominin posture, but the finds also present some distinctive attributes. Like *Ardipithecus*, the skull and the teeth are quite primitive. The external ear openings are also unlike more recent hominins. However, in contrast to the *Ardipithecus* remains, the molar enamel on the teeth of these specimens is thick and, thus, more analogous to more recent hominin species. Hence, the finds may represent a transitional link between species such as early *Ardipithecus* and the australopithecines. Because of their similarity to later finds, they have been placed in genus *Australopithecus* but have been assigned a new species designation, *A. anamensis*, in recognition of their distinctive attributes. The relationship of these finds to *Australopithecus afarensis* is still being evaluated, but most researchers place them near the base of the branches leading to genus *Homo* and the later australopithecines.

**Australopithecus afarensis**

Insights into *Australopithecus afarensis* have been provided by discoveries at fossil localities in Ethiopia and Tanzania dating 3 million to 4 million years ago. Finds include a series of spectacular fossils from the well-preserved geological beds near the Great Rift Valley in the Hadar area of the Afar region of Ethiopia (Bower 1991; Johanson, White, and Coppens 1978; Johanson, Taib, and Coppens 1982; see the box “Donald Johanson, Paleanthropologist”). This valley has experienced extensive mountain building and volcanic activity over the last several million years, and erosion has brought many fossils to the surface where they await discovery by researchers. Among the most spectacular *A. afarensis* finds recovered from Hadar is an almost 40 percent complete skeleton, one of the earliest and most complete fossil hominins recovered. Popularly known as “Lucy” (named after a Beatles song, “Lucy in the Sky With Diamonds”), the creature had a small cranium (440 cc) and large canine teeth. In fact, Lucy’s skull resembles that of a
modern chimpanzee. Lucy was fairly small, weighing approximately seventy-five pounds, and she stood about four feet tall.

Another fascinating find from Hadar is the popularly named “Dikika baby.” Excavated in 1999 at a site called Dikika, close to the site where the Lucy find was made (Alemseged et al. 2006). Like Lucy, the Dikika find is the well-preserved remains of an A. afarensis, but whereas Lucy was an adult, the Dikika fossil consists of an almost complete skull, the entire torso, and portions of the legs and arms of a three-year-old child. The young age and the completeness of the find afford unique insight into the growth and development of the species, as well as physical attributes, such as the shoulder blades, that have been poorly preserved in other A. afarensis finds. While just an infant, the Dikika baby possesses the definitive bipedal features that characterize adult examples such as Lucy. The arm sockets are, however, oriented upward, more like those of a gorilla than those of later hominids and humans.

A. afarensis is remarkably primitive in comparison to later australopithecines; from the neck up, including the cranium and jaw, the species is definitely apelike. The upper body also has features, such as curved figures, that would have made it well adapted for climbing and moving through an arboreal environment. However, the abundant lower limb bones and the pelvic orientation, as well as the position of the hips and knees, indicate that A. afarensis was a fully erect, bipedal creature (Lovejoy 1988). This mélange of postcranial features has led researchers to debate whether A. afarensis was ground dwelling or still spent a great deal of time in the trees (Kappelman et al. 2016). Such interpretive disagreements underscore the challenges researchers face in analyzing fragmentary remains of nonliving species.

The Laetoli Footprints

Australopithecus afarensis finds have also been excavated from the site of Laetoli, some thirty miles south of Olduvai Gorge in northern Tanzania. However, this site is best known for the remarkable discovery of fossilized footprints. Thousands of footprints of various animal species are preserved in an ancient layer of mud covered with volcanic ash. A remarkable finding in 1978 revealed footprints clearly left by fully bipedal creatures, provisionally identified as A. afarensis, dating to approximately 3.7 million years ago (depicted in the chapter opening photo) (M. D. Leakey and Hay 1979; Raichlen et al. 2010). The evidence consists of a trail more than seventy-five feet long made by three hominins. Studies of these footprints have revealed that the mode of locomotion for these early hominins was comparable to that of modern humans. The presence of bipedal species at this time period had already been well established on the basis of fossil evidence. However, the Laetoli footprints provided independent, and indisputable, evidence of the existence of a bipedal creature more than 3.5 million years ago.

Australopithecus africanus

Representatives of Australopithecus africanus are primarily known from fossil finds in Southern Africa dating between 2 million and 3 million years ago. The species lived after those discussed in the preceding sections. However, it possessed a smaller cranial capacity than more recent examples of genus Homo. An adult A. africanus had a cranial capacity that averaged around 450 cc, probably weighed between forty and sixty pounds, and was between 3.5 and 4.75 feet tall. Although the age of the South African finds are challenging to date, these gracile australopithecines are dated to between 2 million and 3 million years ago on the basis of fossils of extinct animals of known age found in the same deposits. Australopithecus africanus is memorable as the first described example of an australopithecine. The Taung child, found in 1924, was named Australopithecus africanus, the “southern ape of Africa,” by its discoverer (Dart 1925). The find was a remarkable combination of coincidence and luck. In 1924, Raymond Dart, an Australia-born anatomist living in South Africa, was given a box of fossils from the rubble of a limestone quarry near the town of Taung, South Africa. The rubble included the front of a skull, a jaw, and an endocranial cast of a bipedal creature that was clearly very different from modern humans. On the basis of the teeth, Dart judged the creature to have been quite young at death, and he called his discovery the “Taung child” (Dart 1925, 1967). Today, the individual is estimated to have been between three and four years old at the time of death.

Although A. africanus had certain apelike features, it also exhibited a number of unique characteristics. For example, the foramen magnum was farther forward in the Taung child than in modern apes, indicating that this creature’s head was balanced above the spine, indicative of the upright bipedal locomotion of the hominins. The brain of the Taung child was very small, hardly larger than that of a chimpanzee. Its structure, however, differed from that of apes and was more highly developed in some regions. The canine teeth were much closer in size to a human child’s than to an infant ape’s, and lacked the diastema found in apes’ teeth. Dart astounded the scientific world by announcing that the Taung child was
CRITICAL PERSPECTIVES

THE PILTDOWN FRAUD

One of the most bizarre stories in the history of paleoanthropology is the saga of “Piltdown Man.” Widely discussed and debated for decades, this fossil was eventually exposed as an elaborate fraud. Although it does not figure in current theories of hominin evolution, we examine the Piltdown Man controversy because the alleged specimen was accepted as a legitimate human ancestor during the early decades of the twentieth century and influenced some of the interpretations of human evolution prevalent at the time (Blinderman 1986; J. Weiner 1955). It is a cautionary tale that illustrates the efficiency of modern scientific techniques, but also serves as a warning about how scientists can be swayed in their interpretations by preconceived ideas.

Piltdown Man was “discovered” in 1912 in a gravel quarry near Sussex, England, by a lawyer and amateur archaeologist named Charles Dawson. The quarry had previously produced the bones of extinct animals dating to the early Pleistocene (approximately 1.8 million years ago). The supposed hominin remains uncovered consisted of the upper portion of the cranium and jaw. The skull was very large, with a cranial capacity of about 1,400 cc, which placed it within the range of modern humans. However, the lower jaw was apelike, the canine teeth large and pointed. This picture of early hominins mirrored popular early twentieth-century notions of the unique intellectual capabilities of humanity. Humans, so these interpretations went, evolved their large brains first, with other characteristics appearing later. In fact, fossil evidence pointed to just the opposite evolutionary pattern.

Piltdown Man was officially classified as *Eoanthropus dawsoni* (“Dawson’s dawn man”) and accepted by the scientific community as the earliest known representative of humans found in western Europe. A number of paleoanthropologists in France, Germany, and the United States remained skeptical about the findings, but they were unable to disprove the consensus of the English scientific community. As time went by, however, more hominin fossils were discovered, and none of them exhibited the combination of an apelike jaw and a large, hominlike cranium seen in the Piltdown find.

With contradictory evidence mounting, skepticism grew in the paleoanthropological community concerning the legitimacy of the Piltdown fossils. Finally, in the early 1950s, scientists completed a detailed reexamination of the Piltdown material. Using fluorine analysis (see Chapter 2), they discovered that the skull and jaw were of relatively recent vintage; the jaw, in fact, was younger than the skull. In reality, the Piltdown fossil consisted of a human skull from a grave a few thousand years old attached to the jaw of a recently deceased orangutan. The apelike teeth embedded in the jaw had been filed down to resemble human teeth. The place where the jaw joined the skull was also broken away so that it would not be immediately evident that the jaw and skull did not go together. To complete the ruse, the jaw was stained with a chemical to match the color of the skull.

By the time the fraud was unmasked, most of the people who could have been implicated had died. Clearly, whoever perpetrated the Piltdown hoax had some knowledge of paleoanthropology. Varied culprits have been suggested including prominent anthropologists and Sir Arthur Conan Doyle, creator of the famous fictional detective Sherlock Holmes. More recently, a strong case has been made that Charles Dawson, the discoverer of the Piltdown fossils, was the likely faker (Blinderman 1986; De Groote et al. 2016). Putting aside the question of who was responsible for the hoax, we now recognize that paleoanthropological research between 1912 and the 1950s was definitely harmed by the Piltdown find, because the scientific community pursued a false path in hominin research. The initial acceptance of the Piltdown fraud as legitimate may partially explain why the Taung child, one of the most startling hominin fossil discoveries of the early twentieth century, was relegated to relative obscurity for so many years.

Questions to Ponder

1. What lessons does the Piltdown fraud provide for the way paleoanthropological research should proceed and how findings should be validated?
2. The recovery methods and the limited information on the context of the find clearly contributed to the success of the Piltdown fraud. Contrast the details of the Piltdown discovery with more recent finds at Olduvai Gorge, Tanzania, or Hadar, Ethiopia.
3. Can you think of other cases in which researchers’ theoretical perspectives have affected their interpretation of the evidence?

...
human family tree. These include several species that have been collectively classed as robust australopithecines. They include at least three different species, *A. robustus*, *A. boisei*, and *A. aethiopicus*, dated between 2.7 million and 1 million years ago. Their specific taxonomic designations, however, have been widely debated, and an increasing number of researchers place them in a separate genus, *Paranthropus* (Day 1993; Stringer and Andrews 2005; Tattersall 1998). *Paranthropus* translates as “alongside humans,” a name that signals their distinct ancestry from modern humans. Nevertheless, while possessing a number of distinct features, they are also clearly bipedal and are, therefore, closely related to hominin species that were ancestral to humans.

Although not ancestral to genus *Homo*, the robust australopithecines merit attention as they underscore the diversity within the hominins and the increasingly complex picture that is emerging of hominin phylogeny; multiple species of hominins, some of them not ancestral to modern humans, roamed Africa at the same time. The fact that many of these species became extinct raises questions about the selective pressures that led to their demise and what adaptations and behaviors ensured the success of our human ancestors.

The first remains of robust australopithecine species were found in South Africa. In addition to examples of *Australopithecus africanus*, the South African cave sites yielded distinct hominin remains more recent in age, dating between 2 million and 1 million years ago. Although these hominins are referred to as “robust” australopithecines, in actuality, their body sizes may have been similar to those of *A. africanus* (McHenry 1988). Rather, the term *robust* refers to the distinctive features of the skull and heavy dentition of *A. robustus*. A particularly distinct feature found in *A. robustus* but absent in *A. africanus* is a sagittal crest, a bony ridge running along the top of the skull that is associated with the species’ massive chewing muscles. Collectively, these features indicate that *A. robustus* likely relied heavily on a diet of tough, fibrous foods. Because of these distinctive characteristics, researchers gave these discoveries species designations, placing them in the genus *Paranthropus*. Although differences of opinion still exist about their exact relationship to other species, for convenience they are here referred to as *Australopithecus robustus* to distinguish them from the more delicate, or gracile, *A. africanus*.

**Australopithecus boisei: The “Nutcracker Man”**

One of the most interesting examples of the robust australopithecines is *Australopithecus boisei*, discovered in Olduvai Gorge, Tanzania, a thirty-mile canyon stretching across the Serengeti plain (page 96). The find was a robust australopithecine, but a species that was even more robust than the examples known from South Africa. The teeth of *A. boisei* were distinctly hominin in form, but they were massive, much larger than those of any other hominin species, a feature that earned *A. boisei* the nickname “Nutcracker man.”

At the time of its discovery in the 1950s, *A. boisei* was a particularly exciting find because it increased the range and number of potential human ancestors that had existed, revealing the complex history of hominin evolution. What also made the find especially notable was that it was the first early hominin find to be well dated using a numerical dating technique: potassium-argon (see dating methods in Chapter 2). The fossil deposits at Olduvai Gorge lie in undisturbed strata, occupying the same relative positions in which they were originally deposited. In addition, the area around Olduvai Gorge was volcanically active in the past. As a result, deposits of tuff, a porous rock formed from volcanic ash, created distinct layers within the Olduvai deposits. These volcanic layers can be dated by using the potassium-argon method. Potassium-argon dates on tuffs above and below the finds placed the fossils’ age at approximately 1.75 million years old. This date, and additional dates on other fossil finds, revolutionized paleoanthropology by providing numerical ages for specific fossil specimens.

**Australopithecus aethiopicus: The “Black Skull”**

The incomplete puzzle of hominin ancestry was filled in with one more piece in 1985, this one dug out of the fossil beds west of Lake Turkana, Kenya. The finds are of an australopithecine dating to approximately 2.5 million years ago. Because the fossil had been stained blue-black by manganese in the soil, it became known as the “Black Skull,” or, by its Kenya National Museum catalogue number, KNM-WT 17000 (A. R. Walker et al. 1986). Another example of the same species may be represented by more incomplete remains found earlier in the Omo River Valley of Ethiopia. The Black Skull is a robust australopithecine, but it has features distinct from both *A. robustus* and *A. boisei*, which are more recent in age. It also has some features resembling the older australopithecines, such as *A. afarensis*, but absent in more recent robust australopithecines. For example, the cranium of the Black Skull is small, comparable in size and shape to that of the older *A. afarensis* fossils. The movement of the *A. aethiopicus* jaw is also similar to that of *A. afarensis*. Yet the face is large, prognathic, and very robust, boasting massive teeth and a pronounced sagittal crest. Because of its distinctive combination of features, some researchers place it in a separate genus, *Paranthropus aethiopicus* (Stringer and Andrews 2005). These features suggest a different evolutionary lineage from the other robust australopithecines and, thus, may represent yet another branch on the hominin family tree.

**Australopithecus sediba**

*Australopithecus sediba* was defined based on six partial skeletons from the Malapa cave site, South Africa, dating to about 2 million years ago (L. Berger 2012; S. A. Williams, Desilva, and De Ruiter 2018). The two partial skeletons that have been analyzed, including 3-D scanning, show that *A. sediba* was a small creature weighing just seventy-seven pounds. But it has a unique combination of traits such as hands that were capable of precise manipulations and a powerful grip for climbing
Front and side views of the skull of *Homo habilis*, one of the oldest members of genus *Homo*.

trees. The shoulders and forelimbs are very primitive, but the pelvis and lower limbs indicate bipedalism.

The preservation at the Malapa site is remarkable, and the fossils of a variety of animal species are also represented, including saber-toothed cats and antelopes. The excellent condition of the fossils allowed for the recovery of plant phytoliths—microscopic siliceous plant—from the plaque on the hominins’ teeth (A. Henry et al. 2012). The phytoliths suggest that *Australopithecus sediba* may have lived in the open savanna grasslands but ate fruit and other foods that would have only been available in the forests. This mixed subsistence strategy is analogous to that of modern chimpanzees living in marginal savanna environments.

*A. sediba* represents one of the creatures evolving sometimet between *A. afarensis* and the emergence of the *Homo* line. In many respects, the species presents features that can be seen as transitional between *Australopithecus africanus* and *Homo habilis* and, thus, ancestral to modern humans.

**The Origins of Genus *Homo***

If the robust australopithecines are shutoff relations in the human family tree, what species present the most likely precursors of genus *Homo*. Our earliest ancestors are represented by a number of tantalizing finds that suggest the earliest members of our own species first emerged over 2 million years ago. The earliest known accepted representatives of the genus include two species, *Homo habilis* and *Homo rudolfensis*, distinguished from the australopithecines by their larger cranial capacity. The various *H. habilis* remains date from between 2.4 million and 1.4 million years ago, while the best dated example of *H. rudolfensis* dates to between 1.8 million and 1.9 million years ago. Hence, the temporal range of these hominins overlap with each other, as well as those of the robust australopithecines and the earliest *Homo erectus* finds, making it difficult to infer their evolutionary relationships. *Homo habilis* and *H. rudolfensis* may represent distinct evolutionary lineages separate from those leading to modern humans. Yet, their larger cranial capacity clearly separates them from the australopithecines.

The first representatives of these species came to light at Olduvai Gorge in the 1960s, with more recent discoveries coming from Koobi Fora, Kenya (M. G. Leakey et al. 2012; Simons 1989b). The discovery of *Australopithecus boisei* in 1959 and the revolutionary dating of the find using potassium-argon, sparked a flurry of excavations at Olduvai Gorge. Between 1960 and 1964, the paleoanthropologists Louis and Mary Leakey and their colleagues excavated the fragmentary remains of approximately twenty fossil hominins (Leakey 1961). Some were clearly *Homo erectus* (discussed later), while others were representative of *Australopithecus boisei*. However, still other finds pointed to the existence of a creature dating more than 2 million years old that was unlike any of the known australopithecines or more recent representatives of genus *Homo*. The distinguishing characteristic of the new species was its cranial capacity, which was estimated at close to 640 cc, significantly larger than that of any australopithecines, but still substantially smaller than that of *H. erectus*. Louis Leakey named *Homo habilis*, or the “handyman,” feeling that it was this species that must be responsible for the simple Oldowan stone tools that had been recovered at Olduvai Gorge (see Chapter 7).

Critics initially challenged the inclusion of *habilis* within genus *Homo*, maintaining that the fragmentary fossils fell within the normal cranial range of the australopithecines. However, more complete finds from Koobi Fora on the eastern shores of Lake Turkana, Kenya, confirmed *H. habilis*’s larger cranial capacity, so membership in genus *Homo* would seem justified. Oldowan tools have been found in contexts predating the appearance of *H. habilis* in the fossil record and also in association with other hominin species. Hence, these earliest known representatives of genus *Homo* cannot be credited with the earliest known use of stone tools. Nonetheless, *habilis* remains notable for its larger cranial capacity, the hallmark of genus *Homo*.

The Koobi Fora site also produced fragmentary fossil remains of *Homo rudolfensis*. Dated between 1.8 million and 1.9 million years ago, the fossil is known by its Kenya National Museum catalogue number, KNM-ER 1470. The skull has a cranial capacity of 775 cc, at the upper range of the known *habilis* fossils. It also possesses a flatter and broader face with thickly enameled cheek teeth, providing a very apelike appearance. On the basis of these differences, the 1470 skull and related finds have been designated as a different species from *H. habilis* (M. G. Leakey et al. 2012). Some researchers have, however, questioned this classification as the finds are limited and no reliable postcranial bones have been found. Thus, further evidence will be needed to determine the actual connection between *H. habilis* and *H. rudolfensis*.

**Homo erectus**

*Homo habilis* is followed in the fossil record by *Homo erectus* (including finds labeled *Homo ergaster*), which in turn is followed by *H. sapiens*, the species that encompasses all modern humans. The postcranial skeleton of *Homo erectus* is indistinguishable from those of modern humans, but the species skulls are small and flat,
with heavy brow ridges and a smaller cranial capacity compared to modern humans. Fossil localities that have produced H. erectus remains range from sub-Saharan and North Africa, to Europe, China, and Southeast Asia. Well-dated fossil finds identified as H. erectus range in age between 1.9 million and 140,000 years ago. However, dates obtained on H. erectus fossils and associated animal bones from the sites of Ngandong and Sambungmacan, Java, suggest that pockets of H. erectus populations may have existed as recently as 40,000 to 70,000 years ago, though the depositional histories of these fossil localities are uncertain and the direct dating of the fossils is problematic (Yokoyama et al. 2008).

Many of the discoveries now regarded as representatives of H. erectus were initially known by a variety of other genus and species names, including Pithecanthropus erectus and Sinanthropus pekinensis (Day 1993). However, more recent consensus has recognized the majority of the variation represented in the different finds as being within the range that occurs in a single species. Some of the examples of H. erectus share many similarities with modern humans, illustrating both the interrelatedness of the species with H. sapiens and the challenges of classification. Some researchers have argued that the earliest African finds, such as the Turkana boy (discussed as follows), should be designated by a separate species name, Homo ergaster. Conversely, other researchers have argued that some of the more recent H. erectus fossils should simply be regarded as archaic Homo sapiens.

The oldest remains of H. erectus have been found in Africa. One of the most complete finds, known as “Turkana boy,” was recovered at the Nariokotome site near Lake Turkana in Kenya. This discovery consists of the relatively complete skeleton of an eight-year-old boy about five feet tall. The skeleton indicates that, below the neck, Turkana boy was physically comparable to modern humans. The cranium has a brain capacity of about 900 cc, which falls into the range of other H. erectus finds (Stringer and Andrews 2005). More recently, fossils that may date from the same period as Nariokotome have been found outside Africa. For example, fossil evidence from Dmanisi in the southeastern European nation of Georgia has been dated at 1.7 million years ago (Balter and Gibbons 2000; Vekua et al. 2002). A relatively complete skull from Dmanisi indicates a brain size of only 600 cc and other characteristics that overlap with those of the earlier hominin species H. habilis. This suggests a possible transitional creature between earlier Homo and H. erectus.

Additional fossil finds classified as H. erectus have been recovered from Kenya, Tanzania, Zambia, Algeria, Morocco, Georgia in southeastern Europe, China, and Indonesia. Among the most notable finds came from Zhoukoudian, a cave system located southwest of Beijing, China (Beijing was spelled Peking in early English transliterations). The “Peking Man” finds captivated popular attention as some of the initial fossils were mysteriously lost at the outbreak of World War II. Initially excavated in the 1920s, the site and the materials recovered from it have been the focus of continued work. The Zhoukoudian contexts associated with Homo erectus have been dated from 670,000 to 470,000 years ago (Zhou, Lui, and Wang 2000). Aside from the recovery of hundreds of hominin fossils, the site has produced artifacts and features indicating occupation of the cave, including the possible manipulation of fire (Binford and Ho 1985; Boaz et al. 2004; S. Weiner et al. 1998).

Homo erectus was clearly a highly successful and widely dispersed species, having had the widest distribution of any hominin species with the exception of Homo sapiens. The wide geographic distribution of the species and the associated material culture set the stage for the emergence of Homo sapiens.

INTERPRETING THE FOSSIL RECORD

5.3 Discuss the challenges paleoanthropologists face in interpreting the fossil record and explain why their interpretations sometimes change.

Several sources of evidence indicate that the earliest human ancestors evolved in Africa. The oldest hominin species, as well as the earliest fossil evidence for anatomically modern humans, are from Africa. Climatic conditions on the African continent during the Pliocene and Pleistocene were warm, and they would have been well suited to evolving hominins. Our closest genetic relatives, the chimpanzee and gorilla, also come from Africa, indicating a large primate genetic pool. Finally, the earliest stone tools, represented by the Oldowan tradition, are also known to be from Africa. Although the recent discovery and dating of early representatives of genus Homo from Europe and Asia have raised questions concerning when hominins migrated out of Africa, the overwhelming evidence for hominin origins remains Africa. There is also consensus that humans evolved from a small-brained bipedal ape. In reviewing the fossil evidence, we can trace the increasing cranial capacity, changes in the shape and organization of the brain, and the development of other physical characteristics present in modern humans.

While the broad picture of hominin origins may be clear, it is more challenging to chart the specific details of the hominin family tree. As illustrated in the preceding discussion of fossil finds, as paleoanthropologists have unearthed increasing numbers of early hominin fossils, their interpretations of hominin evolution have become increasingly complex. Initially, scientists drew a straight evolutionary line from Australopithecus africanus to Homo erectus and on to Homo sapiens. But the burgeoning number of finds clearly demonstrate that in several instances more than one hominin species roamed the Earth at the same time. How were these different species related, and how do they relate to the evolution of Homo sapiens? Fundamental to tracing hominin evolution is the question of which features should be used to classify genera and species. Because the size and complexity of the brain are the most distinctive physical characteristics of
however, the data from the fossil record cannot be obtained by laboratory experiments. Rather, paleoanthropologists must await the next unpredictable discovery. As new evidence is uncovered, new hypotheses are developed, and old ones are modified or discarded. As the number of fossil species represented has increased and our understanding of the fossil record has become more refined, the interpretations have had to account for these finds and models of hominin phylogeny revised (see Figure 5.5).

In the 1960s and 1970s, for example, a number of theories placed \textit{A. africanus} at the base of the hominin family tree, as illustrated in Figure 5.4(a). These interpretations suggested that the hominin developed along two main branches. As the oldest australopithecine then known, \textit{A. africanus} was considered the most likely to have given rise to the genus \textit{Homo} and modern humans, increasing cranial capacity is clearly an important feature in examining the evolution of genus \textit{Homo}. Yet, the range of cranial capacities overlaps among hominins, making it difficult to use this as the basis for distinguishing discrete species (Armelagos and van Gerven 2003; Tattersall 1986).

**Changing Views**

Many interpretations of hominin evolution have been advanced, some of which are illustrated in Figure 5.4. When they were proposed, they represented valid attempts to chart the evolutionary relationships of the known fossil species. Like all sciences, paleoanthropology proceeds by formulating hypotheses and then testing them against empirical data. In contrast to most sciences, however, the data from the fossil record cannot be obtained by laboratory experiments. Rather, paleoanthropologists must await the next unpredictable discovery. As new evidence is uncovered, new hypotheses are developed, and old ones are modified or discarded. As the number of fossil species represented has increased and our understanding of the fossil record has become more refined, the interpretations have had to account for these finds and models of hominin phylogeny revised (see Figure 5.5).

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Interpretations had to be further revised with a spate of new discoveries. With the discovery of the Black Skull in 1985, a relatively neat picture of human evolution grew more complex, as *A. aethiopicus* did not fit into earlier models. It has certain characteristics found in *A. boisei* but not in *A. africanus* and *robustus*, yet *A. aethiopicus* was as old as *A. africanus*. Scientists wishing to insert the Black Skull into the same phylogenic branch would be hard pressed to explain how certain features appeared in *A. aethiopicus*, disappeared in *A. africanus* and *A. robustus*, and then reappeared in *A. boisei* (Johanson and Shreeve 1989). A more logical interpretation placed *A. robustus* on its own branch and *A. boisei* and *A. aethiopicus* on another, with a third limb leading to genus *Homo*, as pictured in Figure 5.4(c).

**Current Perspectives**

Despite the seemingly confusing array of interpretations, the understanding of hominin phylogeny is becoming increasingly clear, even as new discoveries make the story of human origins more complex. While a number of possible hominin ancestors may be represented, the varied fossil finds are nonetheless...
consistent with a model of human phylogeny that traces the evolution of genus Homo from small-brained bipedal apes. No discoveries, for example, have revealed the presence of species with cranial capacities comparable to modern humans living 6 million years ago.

More recent discoveries have added new species, as well as extended the hominin family tree even further back in time (see Figure 5.5). New branches have also been added, making our family tree look increasingly bushlike (Quintyn 2009; T. White 1995; Wolpoff et al. 2006; Wood 2002). Current models of hominin evolution must take into account species like Australopithecus anamensis and Australopithecus sediba, as well as older, fragmentary finds such as Orrorin tugenensis and Ardipithecus ramidus.

While species such as Orrorin tugenensis and Ardipithecus ramidus may or may not be the ancestors of later australopithecines, they provide an indication of the types of features and range of species present 4 million to 6 million years ago, from which later species may have emerged. These early fossil species are followed by the earliest australopithecines, dating just over 4 million to 3 million years ago. They include A. afarensis (typified by Lucy) and A. anamensis.

The early australopithecines were clearly bipedal creatures, but have small brains and prognathic faces. Occurring more recently in the fossil record are more specialized, derived australopithecine species dating roughly between 2.5 million and 1 million years ago, known from finds in both eastern and southern Africa. These include the robust australopithecines, sometimes classified as Paranthropus. They have been divided into a number of species of which there are at least three: A. aethiopicus, A. robustus, and A. boisei. They are characterized by specialized features, such as broad faces, enormous teeth and jaws, and sagittal crests that are associated with massive chewing muscles. Importantly, they do not display an increase in cranial capacity compared to the earlier australopithecines. These features suggest that the robust australopithecines represent a specialized adaptation that makes them unlikely candidates for human ancestors.

Early representatives of the genus Homo appear in the fossil record at the same time as the robust australopithecines and, thus, coexisted with them. Most of the known specimens (Homo habilis and Homo rudolfensis) are from East Africa, but possible representatives have also been found in South Africa. This group of fossils has a number of important characteristics including larger cranial capacity, change in the shape of the cranium, and smaller teeth that place them as intermediaries between earlier australopithecines and the large-brained Homo erectus.

Missing Pieces in the Fossil Record

The preceding views of hominin evolution are based on excavated fossils. Part of the problem with these interpretations and the continuing need for revision lies in the fact that our perception of the fossil record is woefully incomplete. As impressive as the growing number of hominin fossils is, known fossils do not begin to represent the extent and diversity of extinct species. It has been estimated that less than 3 percent of the prime species that once roamed the Earth have been recognized in the fossil record (R. Martin 1990). Some scholars have long contended that australopithecines like Lucy emerged after the split between the Australopithecus and Homo lineages. In other words, the australopithecines represent a separate hominin branch, and the early part of the Homo lineage is still poorly known (Shipman 1986a). Given the fact that fossils of hominins dating earlier than 4 million years ago are fragmentary and their ancestry uncertain, any number of scenarios might be posited but cannot currently be evaluated because of the lack of fossil remains.

A tantalizing illustration of our inadequate knowledge of the fossil record is underscored by fossil finds such as Sahelanthropus tchadensis, discussed earlier. Until this discovery, early hominin fossils had only been recovered from sites in eastern and southern Africa, ranging from South Africa to Ethiopia. Consequently, models of hominin evolution focused on these finds and generally assumed that the hominins evolved in these areas. However, the distribution of hominins in Central and West Africa is poorly known. These regions lack the extensive,
and more thoroughly explored, exposures of Pliocene and Pleistocene deposits that have been studied in other parts of Africa. The presence of the Chad finds, far beyond what had been considered the geographic distribution of early hominins, highlights how much we do not know.

Future discoveries will continue to extend the human lineage further back in time and produce an increasingly “bushy” hominin family tree, and models of hominin lineages will continue to be revised. Further research will likely also lead the search for human ancestry in entirely new directions. In light of these observations, we might be tempted to put aside theories on hominin phylogeny until more information is at hand. But this is a somewhat unsatisfactory conclusion that lacks any explanatory value. Despite the limited information, the majority of paleoanthropologists prefer to speculate on the potential relationships of the known fossil species that allow us to think about how the human species may have emerged.

FROM HOMO ERECTUS TO HOMO SAPIENS

5.4 Compare the different models for the emergence of anatomically modern humans.

Scientists cannot pinpoint which selective pressures prompted the evolution of *Homo erectus* into *Homo sapiens*. Fossils of *H. erectus* (including finds designated *H. ergaster*) range in age from 1.9 million to less than 140,000 years old. The longevity of the species is a testament to how well *H. erectus* adapted to different environmental conditions, having ranged across the diverse climates from Africa to Europe and Asia. Presumably, *H. sapiens* must have had some adaptive advantages over earlier hominin species, but no consensus has emerged about what these may have been. Among the physical changes found in *H. sapiens* are a larger brain and the full mental and physical capabilities needed for speech, which undoubtedly sparked concomitant behavioral changes. As will be seen in Chapter 7, *H. erectus* made increasing use of socially learned technology to interact with and control the environment, a trend that intensifies in later *H. sapiens* populations.

Many hominin remains from the period between 700,000 and 200,000 years ago are difficult to classify because they exhibit physical traits characteristic of both *H. erectus* and *H. sapiens*. These hominins, which can be alternately viewed as either advanced *H. erectus* or early *H. sapiens*, can be referred to as transitional forms. Fossil finds with these ambiguous classificatory characteristics have been discovered throughout Europe, England, Africa, the Middle East, and Asia. The discovery of finds that do not fit neatly into taxonomic categories is not surprising. As we saw in Chapter 4, related species have many similar characteristics that reflect their close evolutionary relationships. Transitional forms illustrate these relationships and offer physical evidence of the process of speciation.

**Transitional Forms and Archaic Homo sapiens**

In examining the transition from *H. erectus* to *H. sapiens*, we need to critically consider the physical characteristics that distinguish the two species, as well as the objectives and limitations of classification. Although the classification of fossil finds into species facilitates comparison, these are nonetheless taxonomic boxes that cannot fully capture the variation that was likely present in living creatures and is often described on the basis of fragmentary skeletal material.

*Homo erectus* shares many physical features with modern humans. As will be examined more fully in the discussion of race in modern human populations in Chapter 6 (pages 126–130), the physical characteristics used to distinguish differences within and between populations generally do not fall into neatly bounded categories but rather exhibit a spectrum from one extreme to another. In the case of *H. erectus* and *H. sapiens*, the postcranial skeletons of the species are essentially the same, except for the often heavier, more massive structure of *H. erectus* bones. The major differences used to differentiate the species appear in the skull. The skulls of *Homo erectus* are low, flattened, and slightly wider at the base, resulting in a low, sloping forehead. The crania of *H. erectus* also exhibit postorbital constriction, meaning that the front portion of the skull narrows behind the eye sockets. The face of *H. erectus* is prognathic; the nose and teeth extend outward. This is an attribute of early hominins and many living, non-human primates that is not found in *H. sapiens*. The anterior teeth of *H. erectus* are relatively small compared to those of earlier *Homo* species, but large in comparison to those of modern humans. In contrast, the skulls of *Homo sapiens* are high and vaulted, providing a large cranial capacity. Anatomically modern *Homo sapiens* also have a pronounced forehead, the skull extending upward rather than back from the eyes. The teeth are also somewhat smaller, resulting in a more prominent chin.

While these characteristics are used by paleoanthropologists to differentiate the two species, many finds have various combinations of both *H. erectus* and *H. sapiens* features. Such transitional species have sometimes been assigned a confusing array of different genus and species designations depending on the criteria the individual researcher has used to define the species. The mosaic of physical characteristics found in some specimens often sparks debate over how to appropriately classify a find. These debates can be illustrated by the Petralona cranium, uncovered in eastern Greece in 1960 (Day 1993; Pouliaios 1981; F. Spencer 1997). Scientists have long debated the age of the find (assessments have ranged from 160,000 to 700,000 years old), with some consensus leaning toward an age of approximately 350,000 years old. The Petralona cranium exhibits many of the classic *H. erectus* characteristics, including thick bones, pronounced brow ridges, and a low cranial vault. However, the cranial capacity is estimated at approximately
1,200 cc, placing it at the uppermost limits of H. erectus and within the lower range of modern humans. The discoverer of the skull felt its distinctive features merited a separate species designation and named it *Archaeanthropus europaeus petraloniensis*. However, other researchers have generally classified it in existing taxonomic categories such as *Homo erectus*, *Homo heidelbergensis*, or *Homo neanderthalensis*.

Similar classificatory ambiguities—and debates—characterize many finds dating to past 700,000 to 200,000 years. Fossils that exhibit a mix of characteristics seen in *H. erectus* and *H. sapiens*, but which have cranial capacities approaching or within the range of anatomically modern humans, are often referred to as *archaic Homo sapiens*—a term that suggests placement on the evolutionary lineage extending from *H. erectus* to modern *sapiens*. Among the oldest transitional forms discovered, first known from Heidelberg, Germany, are classified as *Homo heidelbergensis* and dated from about 700,000 to 200,000 years ago. *H. heidelbergensis* may be related to an even earlier species named *Homo antecessor*, found in Spain and dated at around 1.2 million to 800,000 years ago. These species may share an evolutionary history with both modern humans and the archaic *Homo sapiens neanderthalensis* (Bermúdez-de-Castro 2015; Bermúdez de Castro et al. 1997; Stringer 2012). Neandertal, or *Homo sapiens neanderthalensis*, a hominin population that lived in the Middle East and Europe, dates to between 430,000 and 30,000 years ago (Tattersall 1998; Trinkaus and Shipman 1994).

**The Evolution of *Homo sapiens***

Anatomically modern *Homo sapiens*—that is, people who physically looked like us—likely evolved from *Homo erectus* in Africa between 200,000 and 400,000 years ago. These populations were much the same as modern humans: Their fossilized skeletons do not have the heavy, thick bones; large teeth; and prominent brow ridges associated with *H. erectus*. The high, vaulted shape of their skull and its dimensions are similar to the skulls of modern-day humans (Stringer 2016). From the cold climates of northern Asia to the deserts of Africa, early humans shared similar characteristics as members of one species. However, like populations today, these early groups exhibited differences in physical traits, as a result of local environmental conditions and selective pressures.

Currently, the earliest fossil evidence of anatomically modern *Homo sapiens* comes from the Jebel Irhoud cave site in Morocco, dated to 315,000 years ago (Hublin et al. 2017; Richter et al. 2017). Although they were originally thought to be Neandertal remains, reassessment has classified the finds as *H. sapiens*. The cranial evidence indicates that the faces of these individuals were similar to our own, but the braincase is more elongated and slightly different from that of later *H. sapiens*.

Examples of anatomically modern humans have also been recovered from a number of fossil localities in sub-Saharan Africa. Among the oldest are two hominin skulls from Omo, Ethiopia, dated to 195,000 years ago. Other early, anatomically modern human fossils dating between 155,000 and 100,000 years ago have been found in Ethiopia, Tanzania, and South Africa (McDougall, Brown, and Fleagle 2005; Stringer 2016; Stringer and Andrews 1988, 2005; T. White et al. 2003).

These finds demonstrate the variation and diversity in evolving *Homo sapiens*, characteristics shaped by the various ecological and climatic conditions in Africa’s tropical rain forests and savannas (Sceri et al. 2018). They indicate that anatomically modern *H. sapiens* evolved within deeply rooted, widely dispersed African populations who were, nonetheless, intricately intertwined. Instead of showing a linear evolutionary tree of *H. sapiens* in Africa, a better metaphor is of braided rivulets with various streams weaving in and out, intermixing, and resulting in a modern human form (Ackermann, Mackay, and Arnold 2016).

The fossil evidence indicates that there were several migrations of *H. sapiens* out of Africa. Remains of teeth dated to 80,000 to 120,000 years ago in China and a *H. sapiens* jawbone in Israel dated at 200,000 years ago are indicative of these early migrations (Gibbons 2015; Herschkovitz et al. 2018). Further movement of *H. sapiens* out of Africa continued over the past 100,000 years. These populations migrated across the globe, adapting both physically and culturally to conditions in different regions.

Although researchers generally agree that *H. erectus* evolved into *H. sapiens*, there is substantial disagreement about how, where, and when this transition occurred. Early interpretations were based on limited information and often emphasized the uniqueness of individual finds. As noted, there is growing consensus that anatomically modern humans first evolved in Africa and then spread out to other world areas, but competing theories have been equally supported, and new interpretations continue to be evaluated. For the purposes of this discussion, two contrasting models are presented: the multiregional evolutionary model and the replacement model. A third set of interpretations, consisting of hybridization and assimilation models, attempts to reconcile these two opposing perspectives.

**Multiregional Evolutionary Model**

*Homo erectus* had the widest distribution of any hominin species other than modern humans. According to the multiregional evolutionary model of modern human origins, the gradual evolution of *H. erectus* into archaic *H. sapiens* and, finally, modern *H. sapiens* took place concurrently in various parts of Asia, Africa, and Europe over the past 2.5 million years (as illustrated in Figure 5.6a). In this view, the transition from *H. erectus* to *H. sapiens* was within a single human species. Through natural selective pressures and genetic differences,
Part II • Biological Anthropology

106

local *H. erectus* populations developed particular traits that varied regionally; consequently, the variation in physical characteristics seen in modern human populations is deeply rooted in the past (Wolpoff and Caspari 1997). Variations of this multiregional model, initially proposed in the early twentieth century, suggested the parallel evolution of *H. sapiens* in different regions. More recent perspectives, however, underscored that *gene flow*, the widespread sharing of genes through interbreeding between populations, across the different regions prevented genetic isolation. The emergence of *H. sapiens* was, therefore, a widespread phenomenon, although different regional populations continued to exhibit distinctive features.

Working from the multiregional evolutionary model, we would expect to see a great deal of regional physical and genetic continuity, meaning that the fossil finds from a particular geographic area should display similarities from the earliest representatives of *H. erectus* to those of modern populations. Supporters of this model argue that such continuities do indeed exist. For example, some of the skeletal characteristics of early *H. sapiens* from different regions of China, North Africa, and Europe resemble modern populations in those areas (Bednarik 2011; A. B. Smith 1984; Thorne and Wolpoff 1992; Wolpoff and Caspari 2002). Distinctive features have been identified in the cranium, dentition, jaws, and features of the postcranial skeleton. Researchers favoring this interpretation further note regional continuity in the archaeological records of different world areas.

**Replacement Model**

The *replacement model*, or the “recent African origin of modern humans model,” has increasingly garnered support among researchers (H. Liu et al. 2006; Stringer 1985; Stringer and Andrews 2005). It holds that *H. sapiens* evolved in one area of the world first (Africa) and migrated to other regions, as illustrated in Figure 5.6b. It is called the replacement model because it assumes that *H. sapiens* were contemporaries of the earlier *H. erectus* but eventually replaced them without significant interbreeding. According to the replacement hypothesis, *H. sapiens* populations all descended from a single common ancestral group. Thus, although the modern and earlier *H. erectus* populations overlapped temporally, they were highly distinctive, genetically different evolutionary lineages. Consequently, there is minimal diversity among modern humans, and the regional differences in modern populations are relatively recent developments.

Some researchers believe that fossil evidence supporting the replacement hypothesis may be found in the homeland of all hominins: Africa. As noted previously, the earliest known and the majority of examples of anatomically modern *Homo sapiens* come from African sites. In the replacement view, these
remains are evidence of the earliest representatives of modern *H. sapiens*, the species first evolving in Africa and then spreading out of Africa to other areas.

While the preceding scenario remains plausible, the evidence is not without limitations. The fossil evidence from Africa, as well as other world areas, remains fragmentary, and a fuller understanding of the distribution of early modern human populations is needed. Genetic data also provide challenges to this perspective. The replacement model garnered a great deal of support by studies of mitochondrial DNA in modern humans (examined in the following discussion), which suggested that the maternal line of all living women can be traced to a single female living in Africa about 150,000 years ago. This would clearly support a recent African origin of modern humans. While additional genetic data support an African origin, studies have also suggested that there was at least some interbreeding between anatomically modern *H. sapiens* and earlier archaic species, such as the Neandertals, affording a more complex picture of our genetic history. African fossil evidence has also provided dates for anatomically modern *Homo sapiens* that are substantially earlier than some of the genetic data seem to suggest.

**Hybridization and Assimilation Models**

Neither of the preceding models fully account for the fossil and genetic data at hand. The processes involved in the emergence of modern humans were more complex and encompassed more variables than can be neatly wrapped up in either of the two overarching perspectives (Gunz et al. 2009; Lahr and Foley 1994; Stringer 2001). Emergent human populations may have incorporated a great deal of physical diversity—as well as behavioral, social, and linguistic differences. Further, it is unlikely that migrations (out of Africa or elsewhere) were unidirectional affairs involving the movement of homogeneous populations. Many different migrations via different routes, recolonization of previously occupied territories, and gene flow with other populations are more probable. Understanding of such variables provides insight into not only the emergence of modern humans, but also the source of the diversity underlying present-day populations.

A number of more recent interpretations of modern human origins have attempted to reconcile the conflicting aspects of the multiregional and replacement models, as well as the varied factors noted earlier (Gibbons 2011). These have been referred to by a variety of names. The proposed interpretations can, however, be collectively referred to as hybridization and assimilation models in that they allow for varying degrees of gene flow between *H. sapiens* and earlier populations. Gene flow or genetic admixture between anatomically modern humans and indigenous premodern populations occurred as a result of population migrations and varying degrees of interbreeding with earlier populations.

As is the case with the replacement model, these perspectives generally accept the relatively recent African origin of anatomically modern humans. Thus, they can be differentiated from the multiregional model that assumes the emergence of modern humans in more than one world area. In these hybridization and assimilation scenarios, anatomically modern *H. sapiens* emerged in Africa first and then migrated outward into other regions. As a result of interbreeding, anatomically modern humans hybridized with earlier archaic populations, eventually replacing them. In fact, fossil evidence from the Near East, as well as Europe and East Asia, indicates that different hominin species overlapped in time and space, while fossils that seem to represent admixtures of *H. sapiens* and Neandertal features have also been identified (Soficaru Doboş, and Trinkaus 2006). Finally, genetic data indicate at least some interbreeding between modern human ancestors and archaic *Homo sapiens*. These interpretations underscore a greater amount of gene flow than the replacement model allows. Hence hybridization or assimilation models more correctly represent the complex and gradual nature of the processes represented.

**ARCHAIC AND ANATOMICALLY MODERN HOMO SAPIENS**

5.5 Summarize the theories regarding the relationship of *Homo sapiens neanderthalensis* and *Homo sapiens*.

Neandertals were noted in the preceding discussions as an example of a transitional form exhibiting a mix of characteristics seen in *H. erectus* and *H. sapiens*. Popularly known as “Neandertal man,” the species affords the best-known example of an archaic *Homo sapiens*. Yet the Neandertals also present a number of other distinctive characteristics unique to the species. Their evolutionary relationship to modern humans has been intensively debated since their initial discovery in the nineteenth century. Current consensus is to include them as a subspecies of *H. sapiens* (Tattersall 1998; Trinkaus and Shipman 1994).

Neandertal fossils dating between approximately 430,000 and 30,000 years ago have been discovered in broad swath from western Europe to Central Asia and the Middle East (Duarte et al. 1999; Higham et al. 2014; Pavlov, Roebroeks, and Svendsen 2004; Stringer 2012). This time frame substantially overlaps with fossils and archaeological sites associated with *H. sapiens*, and the Neandertals and anatomically modern humans clearly coexisted.

The Neandertal physique has become the quintessential image of “cave men” in popular culture. They have often been portrayed as second-rate hominins, swept to extinction by quicker-thinking modern humans (Brace 1964; for readable, fictional portrayals, see Auel 1981; Golding 1981). This depiction stems, in part, from an early find of a skeleton of
Neandertals and Modern Humans

Scientists have long pondered the links between Neandertals and modern humans. They have, alternatively, been seen as a transitional species between *Homo erectus* and modern humans; a distinct branch on the hominin family tree that ended in extinction; and a subspecies of anatomically modern humans—the last interpretation currently being favored (see Figure 5.8). Early interpretations that viewed Neandertals as an intermediate ancestor between *Homo erectus* and anatomically modern humans have been discarded (Figure 5.8a). Their restricted geographic range (Europe and Middle East) and distinctive physical characteristics make this scenario unlikely. As noted, Neandertals also appear to have coexisted with anatomically modern humans until the relatively recent past.

A growing consensus among anthropologists holds that Neandertals had distinctive physical features that separate them from anatomically modern *H. sapiens*, but no one has come up with a cogent, widely accepted theory to explain which selective pressures produced these features (Endicott, Ho, and Stringer 2010; Trinkaus 2006). Researchers tend to favor the hypothesis that a “pre-Neandertal” population, possibly originating in another region and migrating to the classic Neandertal area, underwent severe natural selection in response to the cold environment of Ice Age Europe. Fossil finds interpreted as reflecting Neandertal characteristics have been found dating back over 400,000 years. In this view, natural selection and lack of gene flow with other archaic *H. sapiens* populations produced the distinctive Neandertal characteristics.

The transitional species *Homo heidelbergensis*, first known from fossil remains discovered in Heidelberg, Germany, has been interpreted by some researchers as an early form of Neandertal. Some paleoanthropologists have further hypothesized that this species gave rise to the Neandertals in Europe and to modern *Homo sapiens* in Africa (Stringer and Andrews 2005). *H. heidelbergensis* has smaller teeth and jaws and a very large brain (1,300 cc) and so notably differs from *H. erectus*. Yet the species also displays larger teeth, a larger jaw, a prognathic face, and a prominent large brow ridge that make this hominin very different in appearance from *Homo sapiens* (Rightmire 1997).

The site of Atapuerca in northern Spain has also been important in understanding Neandertal origins (Bermúdez de Castro et al. 2004). The Atapuerca site is deep within an extensive cave system that has yielded over 2,500 hominin...
interbreeding with another, unknown human lineage distinct from both the Neandertals and modern humans (Hawks 2013; Pennisi 2013). Recently, a new discovery of a Denisovan jaw-bone on the Tibetan Plateau in a cave in Gansu, China, dated at 160,000 years ago indicates that this hominin was also in Asia (Chen et al. 2019).

New Branches on the Hominin Family Tree

Two other discoveries—H. floresiensis and H. naledi—have further revealed the “bushy” nature of the Homo lineage. Fossils of H. floresiensis were first discovered in Liang Bua cave on the island of Flores in Indonesia in 2003. The find garnered a great deal of popular attention because of its diminutive height, estimated at about three and a half feet. The creature, nicknamed “the Hobbit” because of its small body size, had a cranial capacity under 380 cc, in the range of chimpanzees or early australopithecines. Skeletal remains of nine individuals have now been recovered, including one complete skull. The remains at Liang Bua cave are dated at 86,000 years ago, but at another site on Flores, fossils are dated at 700,000 years ago. Following fifteen years of research based on comparisons of skeletal material from both Africa and Asia, paleoanthropologists have concluded that H. floresiensis is a late survivor of H. habilis or its close descendants, indicating an early migration from Africa to Asia (Argue et al. 2017).

Denisovans or the Denisova Hominins

The intricate picture of the emergence of modern humans and their relationship to archaic human populations has been made all the more complex by the fossil and archaeological evidence that is emerging on the Denisovans, or the Denisova hominins, a previously unknown hominin species or subspecies that was contemporaneous with modern humans and Neandertals.

The site from which hominin remains are known is in the Denisova cave in Siberia, Russia. Archaeological data suggest that the site was occupied from over 125,000 years ago up until modern times (Dalton 2010; Hawks 2013; Krause et al. 2010). Archaeological excavations suggest possible occupation by both Neandertals and modern humans. The site is consequently of interest in tracing Neandertal and modern human interactions. The most tantalizing information, however, was provided by genetic data recovered from bones recovered from the site dating to between 30,000 and 48,000 years ago. Mitochondrial DNA (discussed in more detail later in this chapter) extracted from the bones revealed a pattern unlike that found in modern humans or Neandertals. The mtDNA signature has been described as the “Denisova hominin,” apparently an extinct hominin species or subspecies. Additional study of the nuclear genome suggests that the Denisovans share a common origin with Neandertals, and that they interbred with the ancestors of modern-day Melanesians and Australian Aborigines. Additional study of the genomic data suggests interbreeding with another, unknown human lineage distinct from both the Neandertals and modern humans (Hawks 2013; Pennisi 2013). Recently, a new discovery of a Denisovan jaw-bone on the Tibetan Plateau in a cave in Gansu, China, dated at 160,000 years ago indicates that this hominin was also in Asia (Chen et al. 2019).
This fossil evidence suggests a small brain for *H. naledi* ranging from 460 cc to 565 cc (L. Berger and Hawks 2017; L. Berger et al. 2015; Holloway et al. 2018). The cranial, dental, and postcranial remains consist of both humanlike characteristics and australopithecine traits. However, surprisingly, following sophisticated dating techniques, the fossil assemblage was dated between 236,000 and 335,000 years ago. This means that *H. naledi* existed at the same time as other later hominins including early forms of *Homo sapiens*. One other intriguing aspect debated by paleoanthropologists and archaeologists regarding *H. naledi* is that although there were no tool artifacts found, it may be one of the first intentional burials deep within this South African cave.

Discoveries such as the Denisova hominins, *H. floresiensis*, and *H. naledi* and the story of the Neandertals further underscore the complex history of human interactions and complexity of hominin phylogeny. They push us to reevaluate how we think about the evolutionary processes that led to modern humans and our unique place in hominin phylogeny.

### GENETIC DATA AND HOMININ PHYLGENY

**5.6 Indicate how new genomic research and molecular dating have helped anthropologists interpret human evolution.**

The preceding discussion of hominin phylogeny has focused on information gleaned from the fossil record, the actual traces of early hominins recovered from the ground. During the past several decades, some researchers have increasingly approached the study of human evolution from a completely different direction. As discussed in Chapter 4 with regard to the tracing of primate ancestry, researchers have brought biochemical techniques to bear on the question of hominin evolution and modern human origins (see the Chapter 4 box “What’s in a Name?” on page 70).

Scientists have studied the similarities and differences in chromosomes and DNA sequencing of living primates and determined the genetic relatedness of individual species (see discussion of DNA in Chapter 3). Drawing on the genetic data from living primates, including humans, researchers have gone a step further and attempted to infer the amount of time it took for evolution to produce the amount of genetic distance between various species. This is based on determining the rate at which mutation—and, ultimately, the process of speciation—takes place. Genetic research suggests the separation of the human and chimpanzee lineages approximately 5 million to 7 million years ago (Kumar et al. 2005; Yang 2002). The genetic information, therefore, would appear to potentially complement the fossil evidence, which provides evidence of species that lived near the time of the divergence of chimpanzees and humans (*Ardipithecus ramidus* and *A. kadabba*).

Researchers have also used DNA to examine the origins of modern humans and their dispersal out of Africa, as well as the relationship of Neandertals to modern humans. The genetic makeup of modern humans provides a record of the genetic history of our species. When individuals from different groups interbreed, the offspring’s DNA is provided by each of the parents. This admixture of DNA is subsequently passed down through the following generations, all the way to modern humans. The genetic data obtained have increasingly proven consistent with an African origin of *H. sapiens* (Deshpande et al. 2009). Yet in some cases, different kinds of genetic data have been seen as consistent with both the replacement and multi-regional models (Ayala 1995; Frayer et al. 1993; Harding et al. 1997; E. Harris and Hey 1999).

Human genetic variation reflects geographical origins: Two individuals from one region will, generally, be more genetically similar than two individuals from distant regions (see the box “Race and Genetics: The Human Genome Project” in Chapter 6, page 128). Yet, the study of the genetic makeup of modern humans, as well as the study of DNA extracted from the fossilized bones of archaic humans such as the Neandertals and Denisovans, also provides a record of the complexity of gene flow in ancient populations; populations were never “pure” in a genetic sense. Study of genetic material has also provided clues to gene flow over the more recent past. For example, it may provide a record of Arab and trans-Atlantic slave trades (Hellenthal et al. 2014). Two specific types of genetic markers have been examined with specific regard to the emergence of modern humans: mitochondrial DNA and Y-chromosomal DNA. These are notable in reflecting, respectively, female and male genetic ancestry.

#### Mitochondrial DNA

Among the genetic studies that have garnered the most popular media attention is the use of mitochondrial DNA (mtDNA) from modern humans to understand human origins. Working at the University of California–Berkeley in the 1980s, a team of researchers studied the mitochondrial DNA of modern women (Cann, Stoneking, and Wilson 1987; A. Wilson and Cann 1992). The original study by the Berkeley team focused on the mtDNA of 147 women from Africa, Asia, Europe, Australia, and New Guinea. If the mutation rate of mtDNA is constant, the age of a common ancestor can be calculated. On the basis of the studies, which were widely publicized, these researchers argued that modern humanity could be traced back to a single African female who lived between 200,000 and 130,000 years ago (popularly referred to in the media as “Eve”). More recent studies have traced this to circa 150,000 years (Poznik et al. 2013).

The accumulation of random mutations in the different populations displayed distinctive patterns. Significantly, the mtDNA of the African women tended to be more diverse, or
heterogeneous, suggesting that mutations present had a long time to accumulate. In other populations, the mtDNA was more uniform, or homogeneous, a sign that they had not had as much time to accumulate mutations. Further linking these data to the replacement model of human origins, the Berkeley research and subsequent studies suggest that these anatomically modern humans moved out of Africa, replacing the earlier *H. erectus* populations throughout the world.

This method provided important insights, but interpretation of the data is challenging and remains a source of debate. The strength of the technique lies in the distinctive characteristics of mtDNA. This type of DNA is located in the portion of the cell that helps convert cellular material into the energy needed for cellular activity. In contrast to the DNA in other cells, mtDNA is not carried by the (male) sperm when it fertilizes the egg. The genetic code embedded in mtDNA, therefore, is passed on only through the female. Thus, individuals’ mtDNA is not altered by recombination during reproduction. Each of us inherits this type of DNA from our mother, our mother’s mother, and so on, along a single, maternal genealogical line. The variation present in human female mtDNA is the result of accumulated mutations that have occurred. By determining the rate at which mutations have occurred, the time at which the human lineage diverged from that of earlier human ancestors can be determined. The greater the amount of mutations present, the greater the amount of time needed for them to accumulate.

Mitochondrial DNA studies provide tantalizing clues to modern human origins. There is still, however, debate about the methods used and the interpretation of the results obtained (Cyrano and Kimmel 2010; Mountain 1998; Templeton 1993, 2002). Some research has suggested that mutation rates across the mitochondrial genome vary and that the mutation rate has varied through time (B. Henn et al. 2009; Ho et al. 2005; Howell et al. 2003; Soares et al. 2009). Additional studies have, however, generally been consistent with the initial age assessments (Fu et al. 2013; Poznik et al. 2013). The mtDNA data are consistent with the replacement model, with Africa as the ultimate place of origin of later anatomically modern populations. These methodical concerns aside, the mtDNA studies only refer to descendants through females; it does not necessarily reflect the origin of a new species. Indeed, fossil evidence suggests the presence of anatomically modern humans in North Africa by 300,000 years ago. Here, again, the likely complexity of the movement of early human populations out of Africa, and their interactions with early hominin populations, needs to be underscored.

**Paternal Genetic Ancestry**

Researchers have also studied paternal genetic ancestry through information encoded on the Y chromosome. Humans have two types of sex chromosomes: X and Y. Females have two X chromosomes, while males have an X and a Y. A child’s gender depends on whether a father’s sperm contains an X or a Y chromosome, which combines with an X chromosome from the mother during reproduction (see Chapter 3). Consequently, studies of Y chromosomes provide a genetic record of paternal ancestry. As in the case of mtDNA, the mutation rate of Y chromosomes calculated on the basis of genetic data from modern humans has been used to infer the time when modern humans emerged as well as the relatedness of different human populations.

Y-chromosomal Adam is the popular name given to the most recent common patrilineal ancestor of all living men (Hammer et al. 1998; Hammer and Zegura 2002). The mutation rate in Y chromosomes is quite high, making assessment of the age of this patrilineal ancestor more challenging than in the case of mtDNA data. Estimates have varied in different studies, some contrasting with the estimates reached in mtDNA studies. However, more recent calibrations of both the mtDNA data and the Y-chromosome data have yielded relatively consistent results (Elhaik et al. 2014; Poznik 2013). Although the estimates of Y-chromosomal Adam range from 100,000 to 200,000 years old, the studies are consistent with the mtDNA data that suggest a relatively recent, African origin for modern humans. However, the data also suggest movement back into Africa following the initial expansion of modern humans out of Africa.

**Neandertal DNA and Modern Humans**

Genomic data have also provided new insights into Neandertals’ relatedness to modern humans. Generally, ancient bones contain little, if any, organic material. However, genetic material may survive in some settings and in bones of more recent age. Increasingly sophisticated analytic techniques have also afforded increased chances of recovering genetic material from ancient bones. Molecular testing of genetic material extracted from Neandertal bones indicates substantial differences between the Neandertals and modern humans, while estimates of the separation of the Neandertal and modern human lineages range from 370,000 to 500,000 years ago, the genetic data again seeming to complement the fossil record (R. Green et al. 2010; Hawks 2013; Noonan 2006). While these data must be regarded as tentative, they clearly suggest significant genetic distance between humans and Neandertals. Yet, initial findings that indicated Neandertals did not contribute to the mtDNA pool of modern populations (Krings et al. 1997) have been reevaluated in light of the recent work that suggests interbreeding between the two different populations about 50,000 years ago (Sankararaman et al. 2012). Neandertal DNA in modern, non-African European populations may range from 1.5 to 4 percent (R. Green et al. 2010; Hawks 2013). Neandertal DNA may have provided immunity from regional
pathogens and diseases in modern humans, and Neandertal genes may influence health conditions ranging from allergies to risks of depression (Hawks 2017; Simonti et al. 2016). Analysis of mtDNA from a Neandertal tooth discovered in Belgium has further shown that the Neandertals made up a very diverse population (Hawks 2013; Hodgson, Bergy, and Disotell 2010; Orlando et al. 2006). The perceived variation in Neandertal DNA and the inclusion of Neandertal DNA in some modern human populations is particularly significant in light of the previous discussion of hybridization and assimilation models in the emergence of modern humans.

Genetic data have also been brought to bear on the Denisova hominin from Siberia, Russia. As noted, archaeological data suggest that the site was occupied from over 125,000 years ago up until modern times, with possible occupation by both Neandertals and modern humans (Dalton 2010; Hawks 2017; Krause et al. 2010). Genetic data gleaned from bones recovered from the site dating to between 30,000 and 48,000 years ago suggests that the Denisovans share a common origin with Neandertals and that they interbred with both Neanderthals and anatomically modern humans. As noted earlier, additional study of the genomic data suggests interbreeding with another, unknown human lineage distinct from the Neandertals and modern humans (Hawks 2013; Pennisi 2013).

**Modern Human Variation**

Genetic research has provided important insights into human origins. It also stands as a good example of the degree of scrutiny and debate that new theories attract and the importance of relying on different sources of data in interpretation (Relethford 2003). Yet, genetic data provide no clues to how ancestral hominins adapted to different environments, their feeding habits, their geographic range, their lifeways, or any of the myriad other questions that concern paleoanthropology. Clues to human origins, therefore, will continue to also depend on discoveries pried from the fossil record.

An underlying theme in the preceding discussions is the degree to which the history of human evolution is expressed in modern humans. As well illustrated in the discussions of Neandertals, Denisovans, and the emergence of *Homo sapiens*, our evolutionary past is very much still with us in our skeletal structures, facial features, and genetic makeup. The outline of hominin phylogeny outlined sets the stage for the discussion of modern humans.

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**SUMMARY AND REVIEW OF LEARNING OBJECTIVES**

5.1 **Explain the principal trends in hominin evolution and within genus *Homo***.

Hominini (the hominins) is the tribe of order Primates that includes modern humans and their immediate ancestors. Although hominin species share certain general features with all primates, they also evince several distinct characteristics. Changes in these attributes are preserved in hominin fossils, and the evolutionary relationships of different species are traced on the basis of the similarities and differences present in individual finds. Bipedalism, the ability to walk upright, is the most important trend in hominin evolution. Hominins are the only primates that are fully bipedal. Fossil evidence indicates that bipedalism is the earliest hominin trait, evolving sometime between 10 million and 15 million years ago. Although bipedal posture can be inferred on the basis of skeletal remains, it is more difficult to evaluate why it was selected for in early hominin species. Other trends include a tendency toward the reduction of face, jaw, and anterior teeth and, within genus *Homo*, a trend toward increasing cranial capacity. These features appear more recently, primarily during the past 2 million years. These characteristics are exemplified in modern humans and least pronounced in earlier hominin species. Sweat glands and reduction in body hair may also have been selected for in early hominins. However, while these traits are readily apparent in modern humans, they are impossible to assess on the basis of fossil evidence. Some hominin species have teeth and cranial structures that suggest adaptations to specialized diets. In particular, the robust australopithecines developed massive chewing muscles and extremely large molars compared with those of modern humans, suggesting a distinct evolutionary history from more direct human ancestors.

5.2 **Describe the fossil evidence for early hominin evolution**.

Thousands of hominin fossils have been recovered; all of the earliest remains came from Africa. There is debate regarding the classification and evolutionary relationships of individual fossil finds. However, the fossil record is consistent with the evolution of the human species from a small-brained bipedal ape, the Hominini lineage branching off from the other Homininae primates approximately 6 million to 10 million years ago. Intriguing finds that may represent the oldest hominins have been discovered in Kenya, Ethiopia, and Chad.

However, these remains are incomplete, and their relationships to later species are still being debated. This discussion has focused on two genera: *Australopithecus*, which includes
species that may be ancestral to humans as well as extinct side branches, and *Homo*, which includes modern humans and their closest ancestors. Paleoanthropologists believe that *A. anamensis* may be a species that lived close to the base of the hominin family tree, with at least three branches: two branches leading to later australopithecine species, and one to genus *Homo* and modern humans. The first representatives of *Homo*, the genus that includes modern humans, appear in the fossil record just over 2 million years ago. The earliest members of genus *Homo* to be identified in the fossil record are the species *H. habilis* and *H. rudolfensis*, dating between 2.3 million and 1.4 million years ago. Consequently, members of genus *Homo* coexisted with some of the later australopithecine species between 2.2 million and 1 million years ago. What distinguishes the first representatives of genus *Homo* from the australopithecines is a trend toward larger brain size. *Homo habilis* is followed in the fossil record by *H. erectus*, known from finds in Africa dating 1.8 million years old. *Homo erectus*, in turn, evolved into *H. sapiens*, the species that encompasses modern humans, during the past 400,000 years.

5.3 Discuss the challenges paleoanthropologists face in interpreting the fossil record and explain why their interpretations sometimes change.

Like all sciences, paleoanthropology proceeds by formulating hypotheses and then testing them against empirical data. In contrast to most sciences, however, the data from the fossil record cannot be obtained by laboratory experiments. Rather, paleoanthropologists must await the next unpredictable fossil find. As new evidence is uncovered, new hypotheses are developed, and old ones are modified or discarded. As the number of fossil species represented has increased and our understanding of the fossil record has become more refined, interpretations have had to account for more variation and thus have become increasingly complex.

Initially, scientists drew a straight evolutionary line from the earliest known human ancestors to modern humans. A number of finds, however, clearly demonstrate that in several instances more than one species of hominin roamed the Earth at the same time. To account for these discoveries, new branches have been added, making our family tree look increasingly bushlike. New discoveries have also extended the hominin family tree even further back in time. Researchers sometimes disagree about the classifications of individual finds. Splitters argue that some species designations do not reflect all the species represented. At the opposite extreme, lumpers maintain that current taxonomic designations place too much emphasis on differences among individuals and do not sufficiently consider variation within species. To complicate things further, current models of hominin evolution must also be reconciled with increasing information provided by genetic data. Despite this seemingly confusing array of interpretations, the diversity of finds uncovered provides insight into human origins. While a number of possible hominin ancestors may be represented, the varied fossil finds are nonetheless consistent with a model of human phylogeny that traces the evolution of genus *Homo* from small-brained bipedal apes. Future discoveries will continue to extend the human lineage further back in time, and models of specific hominin lineages will continue to be revised.

5.4 Compare the different models for the emergence of anatomically modern humans.

Although researchers agree that *H. erectus* evolved into *H. sapiens*, there is substantial disagreement about how, where, and when this transition occurred. Early interpretations were based on limited information and often emphasized the uniqueness of individual finds. Currently, there is growing consensus that anatomically modern humans first evolved in Africa and then spread out to other world areas. A variety of competing interpretations continue to be evaluated of exactly how this took place. These include two contrasting perspectives referred to as the multiregional evolutionary model and the replacement model. A third set of interpretations, consisting of hybridization and assimilation models that attempt to reconcile the two opposing extremes in various ways, has also been presented. Supporting evidence for each of these perspectives has been presented, and each have their supporters.

5.5 Summarize the theories regarding the relationship of *Homo sapiens neanderthalensis* and *Homo sapiens*.

*Homo sapiens neanderthalensis*, popularly known as “Neandertal man,” is the best-known example of an archaic *sapiens*. Neandertal fossils dating between 200,000 and 30,000 years ago have been discovered in Europe and the Middle East. Ever since their initial discovery, scientists have pondered the links between Neandertals and modern humans. Neandertals have, alternatively, been seen as a transitional species between *Homo erectus* and modern humans, a distinct branch on the hominin family tree that ended in extinction, and a subspecies of anatomically modern humans. Early interpretations that viewed Neandertals as an intermediate ancestor between *Homo erectus* and anatomically modern humans have been discarded. The restricted geographic range of the Neandertals (Europe and Middle East) and their distinctive physical characteristics make this scenario unlikely. As noted, Neandertals also appear to have coexisted with anatomically modern humans until the relatively recent past. Current consensus tends to regard Neandertals as an archaic subspecies of *H. sapiens* that disappeared as a result of intensive selective pressures and genetic drift. Some additional clues to the Neandertals’
relatedness to modern humans come from genetic material extracted from Neandertal bones. This indicates substantial differences between the Neandertals and modern humans, while estimates of the separation of the Neandertal and modern human lineages range from 370,000 to 500,000 years ago. Yet research also indicates some interbreeding took place between Neandertals and anatomically modern humans. Estimates of Neandertal DNA in non-African modern European populations range from 1 percent to 4 percent. The inclusion of Neandertal DNA in some modern human populations is particularly significant in light of hybridization and assimilation models of the emergence of modern humans: Although the distinctiveness of the Neandertal genetic makeup is clear, the evidence for some Neandertal DNA in modern humans suggests some interbreeding.

5.6 Indicate how new genomic research and molecular dating have helped anthropologists interpret hominin evolution.

Researchers have increasingly approached the study of human evolution by studying the similarities and differences in the chromosomes and DNA sequencing of living primates and modern humans, as well as genetic material recovered from fossils. The genetic data from living primates led to a reassessment of the way in which both living and fossil species are classified, as illustrated by the change in subfamily Homininae to include chimpanzees, gorillas, and humans (respectively referred to as the tribes Panini, Gorillini, and Hominini). Researchers have further attempted to infer the amount of time it took for evolution to produce the amount of genetic distance between various species. Genetic research into mutation rates suggests the separation of the human and chimpanzee lineages approximately 5 million to 6 million years ago. Genetic research has also focused on more recent human ancestry. Two specific types of genetic markers have been examined with specific regard to the emergence of modern humans: mitochondrial DNA and Y-chromosomal DNA. These are notable in reflecting, respectively, female and male genetic ancestry. While they remain the focus of a great deal of debate, the genetic data obtained have increasingly proven consistent with an African origin of *H. sapiens*. The study of the genetic makeup of modern humans, as well as the study of DNA extracted from the fossilized bones of archaic humans such as the Neandertals and Denisovans, also provides a record of the complexity of gene flow in ancient populations.

**KEY TERMS**

anatomically modern *Homo sapiens*, p. 105
archaic *Homo sapiens*, p. 105
bipedalism, p. 88
hominins, p. 88
hybridization and assimilation models, p. 107
multiregional evolutionary model, p. 105
replacement model, p. 106
transitional forms, p. 104

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