

Insights and Advances

Locomotion of the Last Common Ancestor

Because African apes and humans differ so dramatically in their anatomical adaptations to locomotion, to identify our ancestors in the fossil record we look for the anatomical adaptations to bipedalism. However, scientists disagree as to the most logical precursor of bipedalism. Did the most recent common ancestor (MRCA) of African apes and humans knuckle-walk? Or were they adapted to life in the trees? Sir Arthur Keith (1923) raised the possibility that humans were descended from arboreal apes, not knuckle-walkers (Figure A).

Orangutans walk upright when on slender branches and use their arms to grab branches overhead for balance. New work suggests that such behavior in an early common ancestor would have been an appropriate precursor for bipedality as well as the knuckle-walking and fist-walking

practiced by the great apes (Thorpe et al., 2007). Alternatively, although a deeper arboreal ancestor is accepted, other researchers argue that the MRCA of chimpanzees and humans was a knuckle-walker (Gebo, 1996; Figure A, bottom). The two views have different implications for aspects of the postcranial anatomy of the early hominins since knuckle-walkers tend to have short, stiff backs and particular specializations of the wrist that might be expected to hold-over, at least in part in the earliest hominins, but longer backs are the norm for more arboreal forms.

The ape fossil record doesn't help matters much. As we saw, early "dental apes" possess a monkey-like arboreal quadrupedal skeleton with some species showing a mixture of some suspensory characters as well. Additionally, some fossil apes may have been arboreal quadrupeds (but not knuckle walkers). But we lack good candidates for the most recent common ancestor of African apes and humans.

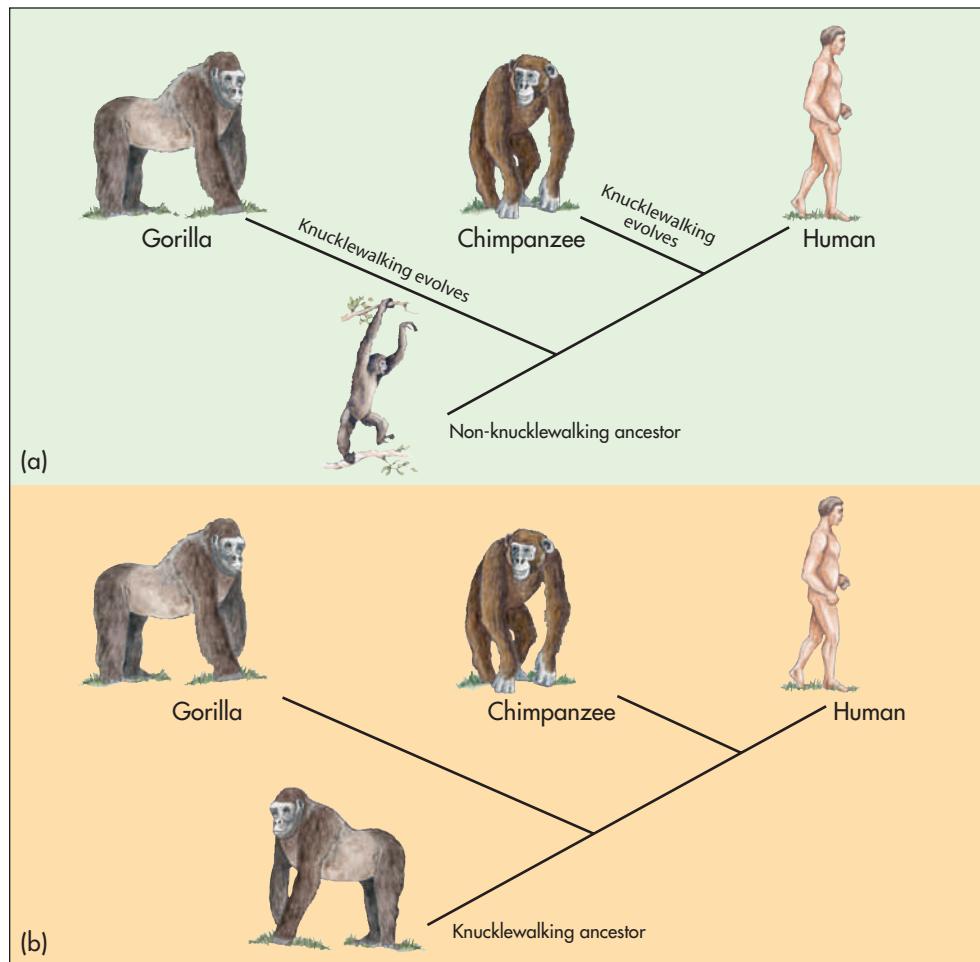


Figure A (a) If the last common ancestor of gorillas, chimpanzees, and humans was not a knuckle-walker, then knuckle-walking would have evolved independently in both the chimpanzee and gorilla lineages, and the ancestral condition for humans is not knuckle-walking. (b) Alternatively, if the last common ancestor of gorillas, chimpanzees, and humans was a knuckle-walker, then the ancestral condition for humans (and the other African apes) is knuckle-walking.

Figure 10.8 Upper and lower jaws differ between chimpanzees (left), australopithecines (center), and humans (right). (a) Chimpanzees and other great apes have large incisors and projecting canines, a diastema, and U-shaped dental arcades caused by parallel rows of cheek teeth. (b) Early hominins like *Au. afarensis* have relatively smaller canines, little or no diastema, and a less U-shaped arcade with a still-shallow palate. (c) Modern humans have very small canines, no diastema, a deeper palate, and a parabolic dental arcade.



(a)

(b)

(c)

into a space or *diastema* in the tooth row of the lower jaw (the mandible) where they slide past the third premolar, hence the name CP_3 for the area. (This premolar is called P_3 , even though in primates it is the first premolar in the tooth row, because the first and second premolars were lost during evolution.) The back of the upper canine is sharpened, or honed, by the bladelike or sectorial P_3 . As canines shorten during evolution, the blade on P_3 disappears, and the tooth changes from having one cusp to having two. This reduction in canine size and honing is apparent in *Ardipithecus* and has been argued to be an important shift in early hominins. The very earliest **australopithecines** show some reduction of the canine, the absence or reduction of a diastema, and at least partial loss of the CP_3 honing complex, often including the presence of a two-cusped P_3 . The white outer coating, or enamel, of our teeth is also thicker than in the African apes—so this difference is sometimes used as well. But thick enamel evolved several times in Primates and doesn't guarantee you have a hominin.

Apes and humans also differ in brain size, cranial proportions, and cranial cresting. Although early hominins possessed essentially ape-sized brains, throughout hominin evolution brain size increases while facial size decreases. This change in proportions reflects both a de-emphasis of the masticatory (chewing) system and an emphasis on brain size and probably intelligence (see Chapter 14). In early hominins this de-emphasis results in the loss of **cranial crests** in one lineage and, as a result, a more rounded braincase. The decrease in facial size also reflects the change in the size and shape of the teeth described above.

australopithecines

The common name for members of the genus *Australopithecus*.

cranial crests

Bony ridges on the skull to which muscles attach.

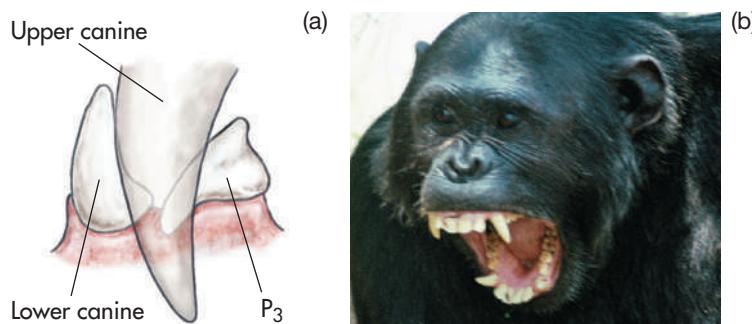


Figure 10.9 (a) A canine/premolar or CP_3 honing complex consists of a large, projecting upper canine passing across the bladelike edge of the lower premolar. Hominins lose this complex as the anterior teeth decrease in size. (b) Monkeys and apes such as this chimpanzee can be recognized in the fossil record by the anatomy of their teeth.

So fossil hominins, including human ancestors since the split from the chimpanzee lineage, can be recognized by anatomical characters related to bipedalism and by reduction of the canine teeth and CP₃ complex and changes in palate shape. However, the very earliest of the hominins show these features to only a very slight degree and therefore are often difficult to differentiate from fossil apes.

Ardipithecus and the First Hominins

10.3 Discuss the anatomical characteristics of *Ardipithecus* and the first hominins and the selective pressures that might have favored the origin of bipedalism.

The majority of the fossil evidence of the earliest hominins has come from the Great Rift Valley of East Africa, a broad expanse that runs roughly north to south from the Horn of Africa at the Red Sea southward to Zambia (Figure 10.10). The valley contains a series of ancient volcanoes and a string of lakes—Lake Victoria, Lake Turkana, Lake Tanganyika, and Lake Malawi, among others—that are often called the Great Lakes of Africa. The Rift Valley's tectonic history resulted in the creation and disappearance of lakes and streams during hominin evolution. These waterways provided likely habitats for species of early hominins, and the volcanic sediments allow radiometric estimates of the age of these fossil sites.

During the later Miocene (10–5.5 million years ago) and early Pliocene (5.5–4 million years ago) at least one lineage of apes made the adaptive shift to a terrestrial niche and became increasingly bipedal. The shift to bipedality came about partly in response to major climatic changes that were occurring in equatorial Africa in the late Miocene.

Molecular evidence suggests that the first signs of hominization should appear in lineages of late Miocene apes. Unfortunately, between 10 and 6 million years ago, the fossil record for the roots of our lineage is poorly represented. Between 7 and 4.4 million years ago, we have several candidates for the site of the earliest hominin remains, but all or some of them may represent fossil apes rather than hominins. Some of these sites (Lothagam, Tabarin, Djurab, and Tugen Hills) have produced evidence too fragmentary for an unambiguous answer. The others (Aramis and several Middle Awash sites) have produced a plethora of remains, which have just recently been published (Table 10.1). Two recently discovered fossils from 7 to 6 million years ago may be the very earliest hominin remains known. However, both have generated much debate, and whether they are primitive hominins or fossil apes remains to be determined.

Sahelanthropus tchadensis (7.0–6.0 MYA)

In the sands of the Djurab Desert of northern Chad in 2001, a French expedition led by Michel Brunet discovered a fossilized skull, which they nicknamed “Toumai” (“hope of life”; Brunet et al., 2002) (Figure 10.11 on page 302). Formally named *Sahelanthropus tchadensis* (“the Sahara hominin from Chad”), the fossil was estimated to be between 5.2 and 7 million years old based on biostratigraphic correlations with East African sites, with 6–7 million years considered most likely by Brunet. This age would make it the oldest member of the Homininae. Toumai would also be the oldest hominin found west of the Great Rift Valley of East Africa; a jaw fragment assigned to *Australopithecus bahrelghazali*, also found by Brunet, dates to about 3 million years ago and is the only other hominin from Chad. The site where Toumai was found was a dry, lightly forested area near a lakeshore in the late Miocene, when *S. tchadensis* lived.

The Toumai fossil consists of a fairly complete skull, mandibular fragments, and isolated teeth. Surprisingly, the face is less prognathic than expected for an early hominin. Other characters that argue for Toumai being a hominin are a large browridge, somewhat smaller canine teeth, a nonfunctional CP₃ honing complex, no diastema, a horizontal nuchal plane, and possibly an anteriorly placed foramen magnum, which may indicate bipedality. However, Toumai also exhibits a number of ape-like characters,



Figure 10.10 Geographic distribution of early hominins. Hominins are limited to the continent of Africa until about 1.8 million years ago. Some of the important sites for australopithecine and other early hominin fossils are located on the map. Although most known sites are in eastern and southern Africa, *Australopithecus* likely inhabited most of the African continent.

Table 10.1 Candidates for the Earliest Hominin

| Site | MYA* | Species |
|------------------------|---------|----------------------------------|
| Toros-Menalla, Chad | 7.0–5.2 | <i>Sahelanthropus tchadensis</i> |
| Tugen Hills, Kenya | 6.0 | <i>Orrorin tugenensis</i> |
| Middle Awash, Ethiopia | 5.8–5.2 | <i>Ardipithecus kadabba</i> |
| Lothagam, Kenya | 5.8 | ?? |
| Tabarin, Kenya | 5.0 | ?? |
| Aramis, Ethiopia | 4.4 | <i>Ardipithecus ramidus</i> |

*MYA = millions of years ago

including small brain size (cranial capacity is 320–380 cc), a U-shaped dental arcade, and somewhat thin enamel (but intermediate between chimps and *Australopithecus*). Milford Wolpoff, Brigitte Senut, and Martin Pickford (2002) argue that Toumai is nothing more than a fossil ape that was deformed after burial. They point out that large female apes (such as gorillas) can have small canine teeth. Alternatively, some of those who accept Toumai as a hominin prefer to place it in the genus *Ardipithecus*, thus making it closely related to the somewhat later hominins from Ethiopia. In either case, Toumai is profoundly important because it fills key gaps in the fossil record of 6 to 7 million years ago and pushes the distribution of fossil homininae far to the west of the Rift Valley.

Figure 10.11 The skull of *Sahelanthropus tchadensis* is argued to be the earliest of the hominins and one of only two species known from western Africa. The significance of the specimen is still hotly debated.



Figure 10.12 *Orrorin tugenensis* may be among the oldest of the hominins, although its taxonomic position is still debated.



megadontia
Enlarged teeth.

Orrorin tugenensis (6.0 MYA)

Also in 2001, Martin Pickford and Brigitte Senut announced the discovery of "Millennium Man" (Pickford & Senut, 2001), so named because the discovery was made in the year 2000. The approximately 6-million-year-old fossils were found in the Lukeino Formation of the Tugen Hills of Kenya and consist of fragmentary cranial and postcranial remains, most importantly multiple femoral (thigh bone) fragments (Figure 10.12). Pickford and Senut thought that the new fossils were so different from other known hominins that they chose a new genus name, *Orrorin tugenensis* ("hominin from the Tugen Hills"). They argue that *Orrorin* is a hominin because of a suite of postcranial characters that indicate it was a biped, but the anatomy of the femur and the arm are not conclusive indicators of bipedality. The remains do indeed indicate a larger body size than expected for a late Miocene ape and internal femur anatomy may support bipedality (Galik et al., 2004). Also linking *Orrorin* to the hominins is the fact that its small teeth possess thick enamel. However, the upper canine is large and a bit more ape-like. Because we typically define hominins based on anatomy related to bipedality, more fossilized remains will be needed before we can make a final determination about the place of *Orrorin tugenensis* in the hominid family tree.

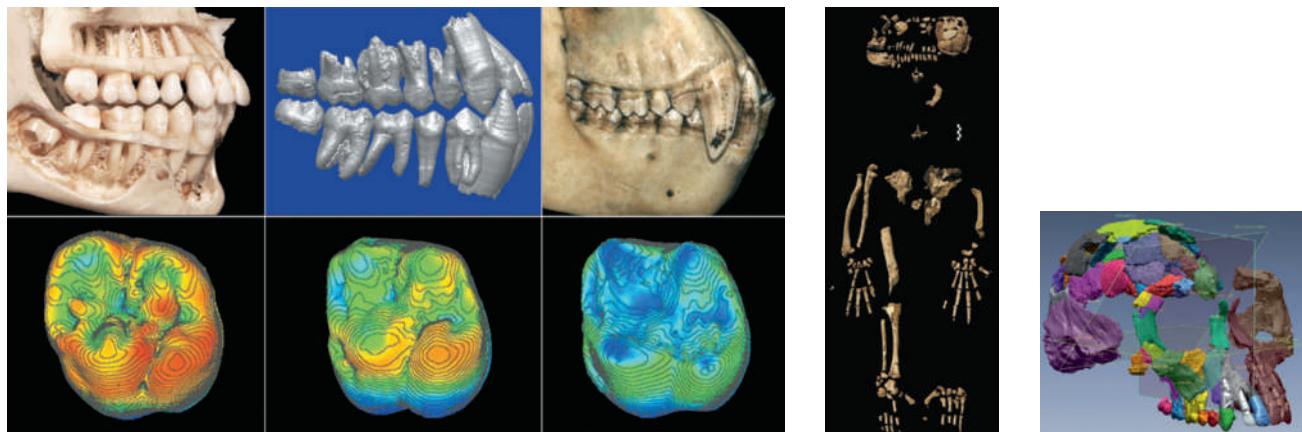
Ardipithecus ramidus (4.4 MYA) and *Ardipithecus kadabba* (5.8–5.2 MYA)

In 2009 an entire issue of the journal *Science* was devoted to fossils of *Ardipithecus*, a genus first discovered in 1994, from northeastern Ethiopia near the Red Sea. Not since the Apollo space missions had an entire issue of *Science* been devoted to such a singular research focus, indicating the importance of the fossilized remains of this very primitive hominin (Figure 10.13). The international Middle Awash team, led by Tim White, Berhane Asfaw, and Gen Suwa, made the discoveries over many years at a late Miocene site of Aramis in the Middle Awash region of an ancient river delta called the Afar Triangle (see Insights and Advances: Treasures of the Afar Triangle on page 304). In the past, Aramis was a dense forest inhabited by ancestors of modern colobine monkeys and forest antelopes as well as *Ardipithecus*. This is very interesting because we expected to find the earliest hominins living in open savanna habitat, not closed forests like those in which apes live today (see Chapter 10). Although there has been some debate as to just how forested Aramis was, it seems clear that it was not the uninterrupted grassland we had expected (see Chapter 8; Cerling et al., 2010; White et al., 2010).

Ardipithecus ramidus ("ground-living root hominin") is argued to be a primitive hominin, but the presence of more primitive traits than *Australopithecus*, including thinner enamel and less postcanine enlargement or **megadontia**, led the Middle Awash team to assign the fossils to a new genus, *Ardipithecus*. They argue that *Ardipithecus* was a hominin on the basis of its somewhat smaller canine with wear on its tip rather than its back side and the anterior position of its foramen magnum, which may indicate it was bipedal. The researchers note that *Ardipithecus* has relatively long arms and an abducted (grasping) big toe but a pelvis that indicates bipedal locomotion, at least some of the time. They have reconstructed its locomotor behavior to be heavily reliant on arboreal activity but with some bipedality as indicated by the heavily reconstructed pelvis. In addition, the brain size is very small at 300–350 cc, and the molars are ape-like (not megadont) in size with enamel thickness intermediate between apes and humans. There is almost no dimorphism in the canine.

The Middle Awash group argues that the evidence from *Ardipithecus* suggests that some of the traits that we have taken for granted as primitive conditions for the African

Figure 10.13 *Ardipithecus* has large canine teeth that are only slightly smaller than those of living apes. The oldest of the Ethiopian hominins at 5.7 million years old, *Ar. kadabba* was ancestral to the 4.4 million-year-old *Ar. ramidus* and perhaps the rest of the hominin lineage. The upper figures compare from left to right, human, *Ardipithecus* and ape dentitions and below these detailed topography of their molars. The *Ardipithecus ramidus* skeleton is quite complete but very fragmentary. The skull is a reconstruction with individual fragments color coded.



apes and our ancestors (such as knuckle-walking and great sexual dimorphism) evolved several different times in several different ape lineages including independently in chimpanzees, bonobos, gorillas, and hominins—but others disagree. Several researchers argue that *Ardipithecus* could as easily be just one of many of the apes that radiated in the Miocene (Wood & Harrison, 2011). These workers point out that Miocene apes experimented with a number of different adaptive regimes in diet and locomotion, and that convergence of characters including even those that are often thought to indicate bipedalism occur in many taxa—for example, the Miocene ape *Oreopithecus* shows characters of the foot and pelvis similar to early hominins. Some Miocene apes also show wear on the tip of the canine, rather than a full CP₃ honing complex. Thus, the possibility remains that *Ar. ramidus* may not be directly ancestral to later hominins. A newly discovered foot skeleton from Burtele, Ethiopia dated to 3.4 million years ago is similar to *Ardipithecus* but a contemporary of *Australopithecus afarensis* (Haile-Selassie et al., 2012). The Burtele foot seems to suggest that hominins evolved more than one way of being bipedal; the lineage represented by *Ardipithecus* and Burtele retained extensive grasping capabilities of the foot, whereas *Australopithecus* was a more committed terrestrial biped.

In 2004, fossils thought to be minor (subspecific) variants of *Ar. ramidus* that had lived much earlier, around 5.7 to 5.8 million years ago, were announced. On the basis of the more ape-like dentition, the discoverers have proposed elevating the former variant of *Ar. ramidus* called *Ar. r. kadabba* to its own species, *Ardipithecus kadabba*. These finds by Yohannes Haile-Selassie and colleagues have expanded our understanding of the range of variation in *Ar. ramidus*, and their anatomy and age suggest to some that the genera *Orrorin* and *Sahelanthropus* should be lumped into the genus *Ardipithecus* (Haile-Selassie et al., 2004a). If these are all hominins, then early hominins would be defined by absence of a functional CP₃ honing complex and a complicated mosaic of facultative bipedalism and arboreality.

Selective Pressures and the Origin of Hominins

By now you are probably wondering what it was about bipedalism that helped our distant ancestors to survive? Were they more energy efficient? Could they get more food? Were they more attractive to mates? Many scenarios have been proposed for what selective pressures favored the origin of bipedalism (Figure 10.14 on page 305).

ENERGETIC EFFICIENCY Environmental changes between 5 and 8 million years ago may have favored the ability to walk upright. In the late Miocene of Africa, grasslands

Insights and Advances

Treasures of the Afar Triangle

The Afar Triangle of northeastern Ethiopia (Figure A) is among the most famous of hominin fossil-bearing regions. It is not unique in the sheer quantity of fossils it has produced; the Gobi Desert of Mongolia has far more dinosaurs and early mammals, for example. But the Afar has produced the most extensive record of human evolution, including examples from the earliest days of the hominini until the dawn of modern people.

Today the Afar is a dry, dusty badlands that features baking hot days, chilly nights, and a stark, otherworldly landscape. But between 6 and 2 million years ago, the Afar was a fertile valley, the delta of a great river called the Awash, which flowed through the region en-route to the sea. It is in and around the Awash that the most exciting finds have been made.

In 1972, Maurice Taieb led Donald Johanson to an unexplored site in the Afar called Hadar (from *Ahda’ar*, or “treaty stream” in the local Afar language). This 20-km² region holds an exquisitely preserved record of hominin evolution. In late 1973 Johanson’s team made the first major discovery, the fossil knee of an unknown primitive hominin that was later dated to 3 million years ago. In late 1974, during a follow-up expedition his team discovered more fossils, including the now-famous Lucy. Then in 1975, Johanson’s team unearthed the “First Family,” a group of at least 13 individuals of Lucy’s species, *Australopithecus afarensis*. In the three decades since, *Au. afarensis* has become the best known of the early hominins and in 2006 the spectacular partial skeleton of an *Au. afarensis* child was discovered from the nearby Dikika region (Innovations: Dikika and Development on pages 312–313). The region also recently yielded the oldest member of the genus *Homo* as well (Villmoare et al., 2015).

Not far from Hadar, the international Middle Awash team including Tim White, Berhane Asfaw, Giday WoldeGabriel, and Gen Suwa discovered new hominins in the early 1990s and 2000s. *Ardipithecus ramidus* and *Ar. kadabba* lived in the then-forested Afar some 1.5 to 3 million years before *Australopithecus afarensis* roamed there.

More recent hominins and their artifacts have also been found in the Afar. In the late 1990s, the Middle Awash team found the earliest evidence of hominin meat-eating and butchery at Bouri, only 40 miles from Hadar. The fossilized remains of a 2.5-million-year-old hominin, named *Australopithecus garhi*, were found just a short distance from butchered antelope remains. And at Woranso-Mille a new 3.3–3.5-million-year-old species, *Australopithecus deyiremeda*, was announced in 2015.



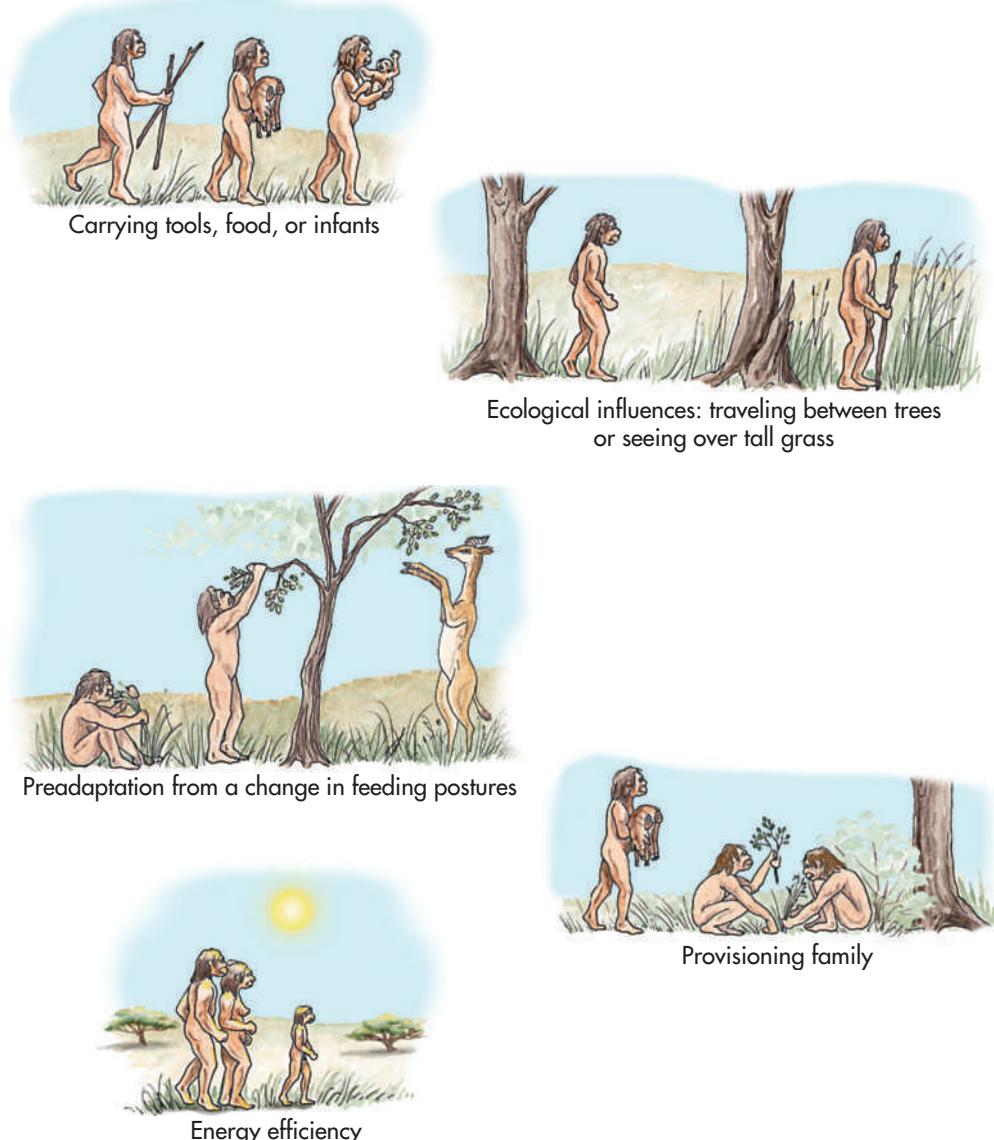
Figure A Location of the Afar triangle.

In 2000–2001, Ethiopian paleoanthropologist Sileshi Semaw’s team found what were then the oldest known stone tools at Gona, dated to about 2.6 million years ago (see Chapter 11). The team also found a nearly complete cranium of a 1.5 to 2-million-year-old hominin of the genus *Homo*, and numerous other hominin remains. More recently, a nearby site, Dana Auole, has yielded stone tools that may be even older than those from Gona. From younger levels of the geological strata have come hand axes and remains of *Homo erectus* from 1.5 to 1 million years ago, as well as the famous Bodo specimen of a hominin that appears transitional between *Homo erectus* and more modern *Homo sapiens* (see Chapters 11 and 12).

The Afar was also home to some of the very earliest members of our species, *Homo sapiens*. In 1997, the Middle Awash team discovered 160,000-year-old specimens of early modern humans, from Herto (see Chapter 13). The skulls from Herto form the recent end of an amazing spectrum of human use of the Afar region extending from the dawn of humankind to the present.

expanded and forests decreased in size. This trend culminated in the widespread savannas we find in East Africa today. Increased grassland resulted in a wider scattering of the food trees that protohominins needed for their meals, so they had to forage over longer distances across more open country. With increased travel across open country, natural selection may have driven the evolution of a more energy-efficient mode of transport, namely bipedalism.

Figure 10.14 Several scenarios for what led to the origin of habitual bipedalism.



Bipedal walking is a more efficient way of traveling than walking on all fours, at least if we compare human and chimpanzee locomotion. Peter Rodman and Henry McHenry (1980) pointed out that although humans do not necessarily walk more efficiently than all quadrupeds, they certainly walk more efficiently than knuckle-walking apes. In other words, if hominins evolved from a knuckle-walking ancestor, then the shift to upright posture would have made perfect energetic sense (but see the Insights and Advances box on page 298 regarding this controversy). Although there is still some argument about the relative efficiency of early hominin walking, most studies suggest that bipedal walking (but not running) is a more efficient means of locomotion than knuckle-walking (Leonard & Robertson, 1997). Recent experiments suggest that oxygen consumption is greater in chimpanzees than in humans when walking bipedally, and models for early *Australopithecus* suggest even they would be substantially more efficient than are chimpanzees (Pontzer et al., 2009). This greater efficiency in getting between food patches may have had other advantages as well, such as allowing hominins to maintain group size even as the Miocene forests dried (Isbell & Young, 1996).

Another way in which the body plan of a biped may have been more efficient than its ape ancestor is in its ability to dissipate heat. Because overheating poses a greater risk to the brain than to other parts of the body, Dean Falk and Glenn Conroy (1983, 1990)

suggest that successful hominins in open (unforested) areas had a means of draining blood (the vertebral plexus) that also cooled the brain. The idea is provocative: the circulatory system as a radiator designed to keep a growing brain cool, enabling more and more brain expansion in one lineage but not in another. However, the correlation between this drainage system and environments in which there is little shade isn't perfect, and modern humans don't all have this adaptation. In addition, Pete Wheeler (1991) has shown that bipeds dissipate heat faster than quadrupeds in a different way because they stand slightly taller above the ground, and when exposed to midday sun they present less surface area to be heated. Although hominins may have been better at dissipating heat from their bodies and brains than their last common ancestor, this doesn't necessarily mean that this was the advantage that led to bipedalism. It could be that better heat dissipation was a side benefit enjoyed by hominins once bipedalism arose for other reasons or that it was one of many advantages that led to the origin of bipedalism.

ECOLOGICAL AND DIETARY INFLUENCES ON BIPEDALISM As we have seen, environmental changes in the late Miocene led to shrinking forests and expanded grassland environments with new survival challenges. Many researchers have observed that standing upright would have offered greater ability to see over tall grass or to scan for potential predators across the savanna. Gaining a better view of one's surroundings by walking upright has long been advocated as the selective advantage necessary to drive the evolution of bipedalism. But other researchers ask why the enormous changes to the anatomy that allow habitual bipedalism would have taken place, when an occasional look over tall grass might have been just as effective without requiring these fundamental anatomical changes.

And there may have been dietary advantages to bipedalism as well. Perhaps a lineage of fossil apes became bipedal because of the value of standing upright for feeding in fruit trees. Researchers from the 1970s to the present all envision a protohominin that became increasingly bipedal for the feeding advantages that this posture offered, whether it be to pluck ripe fruits more efficiently (Hunt, 1990; Stanford, 2002), to shuffle between food patches (Jolly, 1970), or to walk atop tree limbs (Tuttle, 1981). Whether such feeding benefits would have favored the conversion to full-time bipedalism remains to be answered.

SEXUAL SELECTION, MATING STRATEGIES, AND BIPEDALISM Perhaps bipedalism arose because it conferred mating benefits on protohominins that walked upright. Nina Jablonski and George Chaplin (1993) argued that bipedalism would have been beneficial to males engaging in social displays. Male chimpanzees often stand upright briefly when they assert their dominance over other males during charging displays. Walking upright would allow males to look impressive and presumably mate more. It is unclear why this benefit would lead to habitual bipedalism and all the accompanying anatomical alterations rather than just a temporary behavioral bipedality.

In the 1980s, C. Owen Lovejoy proposed a model that tied together information about ancient climate, anatomy, and reproductive physiology to explain the evolution of bipedalism. He argued that the slow reproductive rate of the hominin lineage, like that of many of the fossil ape lineages, would have led to our extinction if we had not found some means of increasing reproduction. He also argued that the evolution of the monogamous mating system offered a way to increase the likelihood of infant survival, and he saw male provisioning of females and their young as critical to this system. However, males needed to ensure their paternity and females needed to ensure continual male support. As forests contracted, males had to walk farther to find food to carry back to the females they were guarding from the attentions of other males. Bipedality raised the energy efficiency of walking and enabled the male to carry food in his arms. If female protohominins did not "announce" through swellings on their rears that they were ovulating, they would have had an advantage because the provisioning male would need to remain in the near vicinity or return constantly to increase his chances of mating when the female was fertile. The female's physiology, fortified by the extra nutrition she received from her now-attentive mate, could

produce more offspring. The interval between births shortened, and the emerging hominins not only staved off extinction but also invaded a new grassland niche.

A number of faults might be found with Lovejoy's model; for example, bipedality arose millions of years before hominins moved into the grassland niche and the earliest hominins may not have had monogamous mating systems as they were likely to have been highly sexually dimorphic (see Chapter 7). It is important to emphasize, however, that a complex evolutionary change like bipedality is more likely to be brought about by a web of factors, such as those proposed by Lovejoy, than by a single cause.

Australopithecus and Kin

10.4 Detail the various species of the genus *Australopithecus* and kin, including their anatomical characteristics and temporal and geographic range.

Recognizing the very earliest members of a group in the fossil record is difficult both because the fossil record is fragmentary and because the more ancient the ancestor, the less likely it will be to look like its living descendants. The earliest potential hominins just discussed fall into this nebulous category in which it is very hard to differentiate an early hominin from an ape.

However, most of the early members of the hominini do not suffer from this ambiguity and are assigned to the genus *Australopithecus*. The name *Australopithecus*, roughly meaning "southern ape," was coined by Raymond Dart in the 1920s for the very first specimen of the genus which was discovered in South Africa. Since that time, fossil discoveries have revealed an adaptive radiation of species that filled a variety of habitat types in eastern, southern, and central Africa and are now known to have lived from 4.2 to about 1.0 million years ago. The genus *Australopithecus* includes species of bipedal apes that are small bodied (64–100 lbs.) and small brained (340–500 cc), had moderately prognathic faces, and a mosaic of primitive and derived cranio-dental anatomy (Figure 10.15). As we discover new specimens and new taxa, we will no doubt expand both the geographic distribution and the time span for this group and raise additional questions about their origins and descendants (Figure 10.16 on pages 308–309).

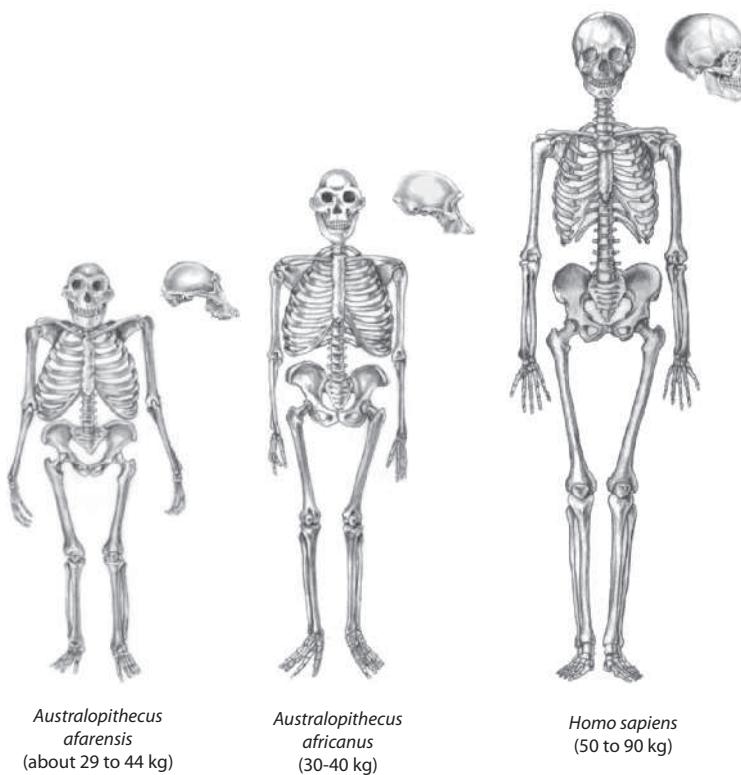
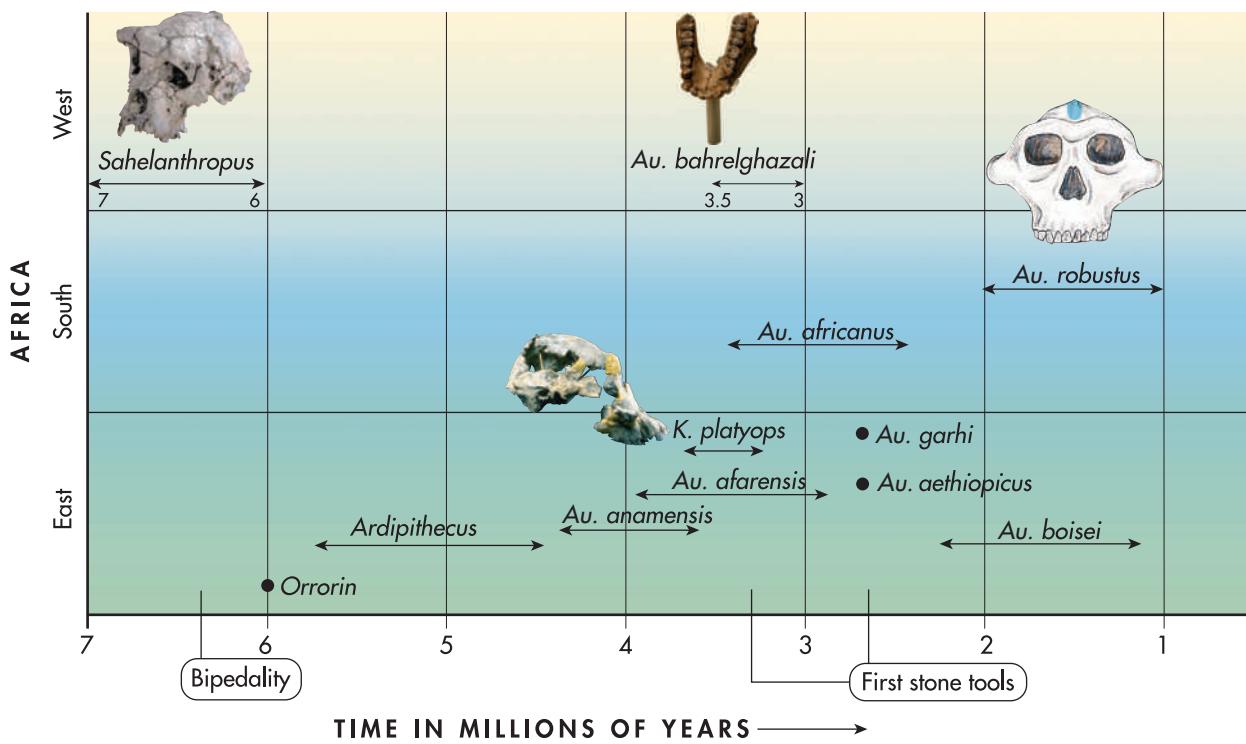


Figure 10.15 Comparison of hominin skeletons. The australopithecines (left) were short bipedal primates, most with relatively long arms and short legs. Compared to modern humans (right) the australopithecine torso was broad and funnel shaped.

Early Hominin Evolution

FIGURE 10.16 The earliest hominins appeared around 6 million years ago in western and eastern Africa. About 4 million years ago *Australopithecus*, a bipedal genus characterized by small brains, large jaws, and small body size arose. *Australopithecus* is probably the first stone tool maker, and one species is likely to have given rise to *Homo*. Several species of the genus overlapped in time and space, probably avoiding competition by relying on slightly different diets.

In one lineage, the robust australopithecines (*Au. aethiopicus*, *Au. robustus*, and *Au. boisei*), several species evolved massive jaws, molar teeth, and cranial skeletons optimized for producing large chewing forces. These hominins probably relied on hard-to-open food items during times of nutritional stress.



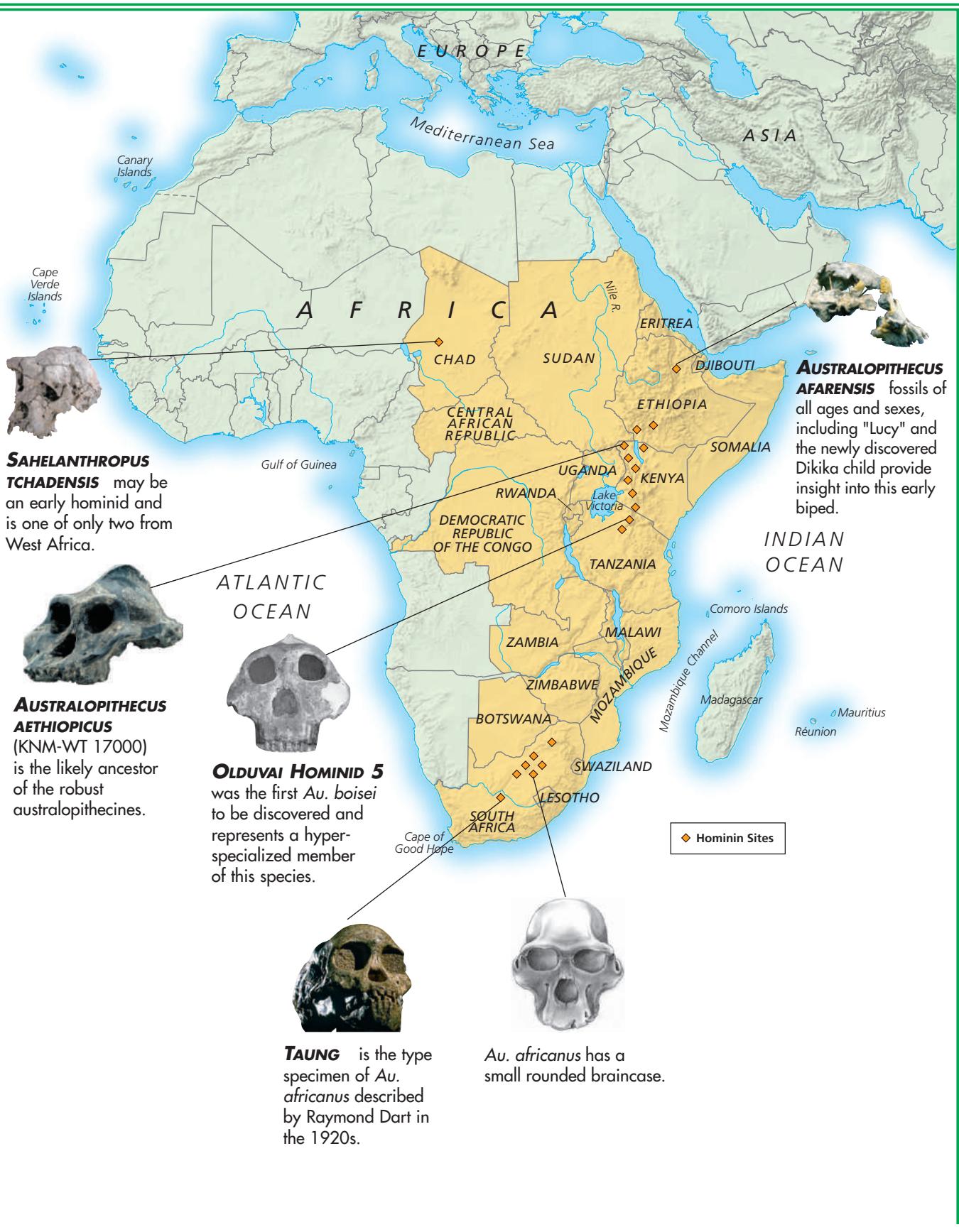


Figure 10.17 The remains of *Australopithecus anamensis* from Kenya date to about 3.9 to 4.2 million years old.



type specimen

According to the laws of zoological nomenclature, the anatomical reference specimen for the species definition.

Australopithecus anamensis (4.2–3.9 MYA)

Around 4 million years ago members of *Australopithecus* first appear. The oldest and most primitive of these is *Australopithecus anamensis* (Figure 10.17). Announced in 1995, *Au. anamensis* (“southern ape of the lake”) was discovered by a team led by Meave Leakey. At separate sites near Lake Turkana, Kanapoi, and Allia Bay, Leakey’s team uncovered dozens of cranial and postcranial bone fragments, dating to 4.2 to 3.9 million years ago. The oldest of these is just 200,000 years younger than *Ardipithecus ramidus*, leaving precious little time for some major anatomical changes to occur if *Ardipithecus* is ancestral to *Australopithecus*. Other remains, discovered in 1965 by a Harvard University excavation, have also been assigned to this species. Associated fossils of fish and aquatic animals indicate that both Allia Bay and Kanapoi were streamside forests in the early Pliocene, when *Au. anamensis* roamed the area.

Australopithecus anamensis provides early incontrovertible evidence of bipedality. In particular, its tibia has thickened bone at its proximal and distal ends, where bipeds place stress on their lower legs. And the tibial plateau, where the tibia meets the femur, is enlarged as the result of the greater weight bearing experienced by the bipedal lower limb.

The *Au. anamensis* teeth and jaws are more primitive than those of later hominins but more derived than those of early hominins such as *Ardipithecus*. The dental arcade is U-shaped, with parallel sides and large anterior teeth, and the palate is shallow, all features that are more ape-like than human. Although the canine is smaller than in *Ardipithecus*, the root of the canine is longer and more robust in *Au. anamensis* than in *Australopithecus afarensis*, and there is a distinct CP₃ complex. But the molars of *Au. anamensis* are shorter and broader. As in later *Australopithecus*, the molar enamel of *Au. anamensis* is distinctly thicker than in the more primitive *Ardipithecus ramidus*, all characters that make *Au. anamensis* a hominin.

In many respects, the fossils of *Au. anamensis* strongly resemble those of *Au. afarensis*, and some researchers think the two species should be considered one and the same. However, *Au. anamensis* is more primitive than *Au. afarensis*, especially in aspects of the mandible and dentition, and this led Leakey’s team to assign the fossils to a new hominin species. These two species seem to be good examples of an ancestral-descendant lineage (Kimbrel et al., 2006).

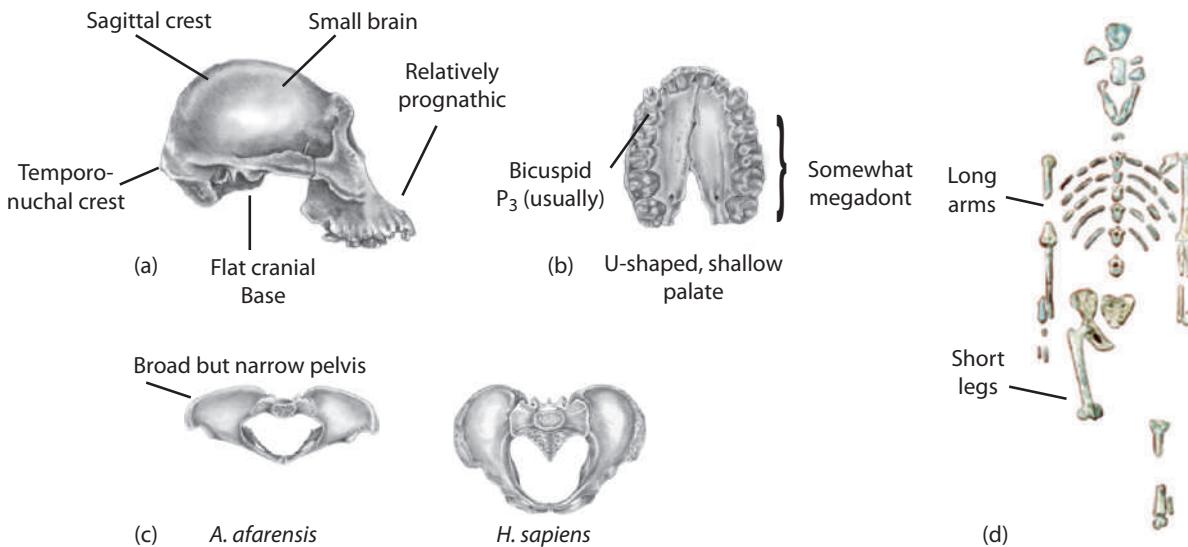
Australopithecus afarensis (3.9–2.9 MYA)

In 1974 Donald Johanson and his team discovered Lucy, the famed skeleton of *Australopithecus afarensis*, at Hadar in the Awash Valley of the Afar Triangle of Ethiopia (see Insights and Advances: Treasures of the Afar Triangle on page 304). The discovery of the diminutive A.L. 288-1 (Lucy’s museum catalog number) was extraordinary for two reasons. First, her anatomy is more primitive than that of any hominin discovered up to that time, and it includes a clear mosaic of human-like and ape-like features. She was tiny, standing just a little over a meter tall and possessing a brain about the size of an adult chimpanzee’s.

Second, her skeleton is more complete than that of nearly any other fossil human. Although more primitive hominins have been discovered since, none is nearly so well studied, and *Au. afarensis* has remained the benchmark by which the anatomy of all other early hominins is interpreted. In addition to Lucy, thousands of finds of *Au. afarensis* have been made in the Afar and other East African localities in the past 30 years, including the 2006 discovery of a child’s partial skeleton near Dikika in the Afar (see Innovations: Dikika and Development on pages 312–313). In fact, the **type specimen** of the species, the specimen that according to the laws of zoological nomenclature serves as the original anatomical reference for the species, is the LH 4 mandible from Laetoli, Tanzania.

There are several key anatomical features of *Au. afarensis* (Figure 10.18), some of which are shared with *Au. anamensis* suggesting the two species form a lineage. The cranium and teeth of *Au. afarensis* are intermediate in appearance between those of

Figure 10.18 Key features of *Australopithecus afarensis* include (a) a small cranial capacity and cranial crests, (b) a shallow, U-shaped palate with reduced canines, and (c, d) features of the postcranial skeleton that indicate habitual bipedality.



a living ape and a modern human. Brain size is small but slightly larger than that of earlier hominins and living apes (range 350–500 cc).

A complete skull recovered by Bill Kimbel and Don Johanson shows that the *Au. afarensis* face was prognathic, but not as much as that of the living apes, and the cranial base was relatively flat, similar to that of living apes (Kimbel et al., 2004) (Figure 10.19). Cranial crests, flanges of bone on the braincase for muscle attachment, are present, including both a **sagittal crest** (for the temporalis muscle) and a **compound temporonuchal crest** (formed where the neck muscles approach the temporalis muscles). These crests tell us that *Au. afarensis* still placed a premium on chewing, needing more space on its small head to attach large chewing muscles. The dental arcade is U-shaped, with large anterior teeth, parallel rows of cheek teeth, and a shallow palate, all primitive, ape-like traits. But as expected of a hominin, the canine teeth are much smaller than those of a chimpanzee or of the earlier hominins *Ardipithecus* and *Au. anamensis* but larger than those of more recent hominins or other *Australopithecus* species. With smaller canine teeth, no CP₃ honing complex is present in *Au. afarensis*, and many specimens have premolars with two cusps. The molar and premolar teeth are modest compared with those of later *Australopithecus* but much larger than those of the earliest hominins and *Au. anamensis*.

In its postcranial skeleton, *Au. afarensis* is clearly an accomplished biped. *Au. afarensis* possesses a pelvis with short, broad iliac blades that curve around the side of the animal, forming the attachment area for the gluteal muscles. The femur is angled in toward the knee, which keeps the foot under the animal's center of gravity; the condyles on the lower end of the femur are enlarged; and the groove for the patella is deepened. The tibia is modified to bear more weight, and the big toe is in line with the other toes. Indirect evidence of bipedal walking in *Au. afarensis* comes from the Laetoli footprint track pictured at the start of this chapter that, on the basis of its age and location, is thought to have been made by *Au. afarensis*. All these characters tell us that *Au. afarensis* was a striding biped and clearly, therefore, a hominin.

The postcranial skeleton also differs from that of modern humans, however (see Figure 10.15 on page 307). The thorax is more funnel shaped, similar to an ape's, perhaps indicating that *Au. afarensis* had a large gut and a largely vegetal diet. *Au. afarensis* arms

sagittal crest

Bony crest running lengthwise down the center of the cranium on the parietal bones; for the attachment of the temporalis muscles.

compound temporonuchal crest

Bony crest at the back of the skull formed when an enlarged temporalis muscle approaches enlarged neck (nuchal) muscles, present in apes and *A. afarensis*.

Figure 10.19 A complete cranium of *Au. afarensis* from Hadar, Ethiopia, shows a prognathic face and small braincase.



Innovations

Dikika and Development

Evolution often proceeds by modifying the pattern of development. Slight modifications during growth can lead to large anatomical differences between adults. Such

modifications might alter the rate and timing of growth, or they might alter processes; for example, depositing bone at a certain spot in one species while resorbing bone in that same spot in another species. New technologies

such as X-rays, scanning electron microscopy, computed tomography (CT), and microCT are being used to understand growth in fossil hominids. First, however, fossil children must be discovered.

In 2006, Zeresenay Alemseged and his team announced a spectacular discovery of an infant skeleton of *Australopithecus afarensis* from Dikika in Ethiopia dated to about 3.3 million years old. This child's bones were retrieved over several field seasons in three different years. The work included the careful survey of an entire slope and the screening of excavated sediments. Most of the skull and part of the postcranial skeleton, especially the arm, was recovered, but many of the bones were cemented together by sediment. The analyses would include CT scanning to determine which bones and teeth were present and how old the child was. Although you would suppose that children's remains are rarely preserved in the fossil



record, almost every fossil hominin species has at least one fairly well-preserved subadult specimen. Indeed, the first

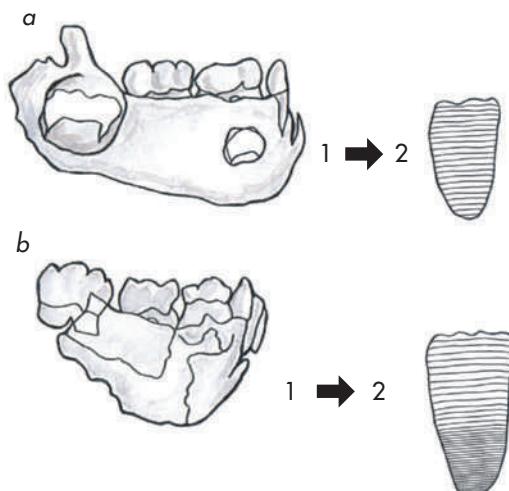
australopithecine ever discovered was the Taung child from South Africa.



The first step in understanding development of any fossil specimen is to evaluate its developmental age. If the fossil has teeth, dental development is the best means for assessing age (see also Chapter 17). Radiographs, X-rays like the ones your dentist takes, and CT scans can be used to visualize the relative development of the tooth crown and its roots (Dean, 2007). Using comparative standards for apes and humans a developmental age can be assigned. In the case of Dikika, only baby teeth were visible externally, but adult teeth could be seen developing in the jaw. An ape developmental standard suggests the child was about 3 years old when she died. The same techniques can be applied to other species. For example, the three-dimensional CT scan of King Tut reveals his third molars (wisdom teeth) were unerupted, which is consistent with his reported age of 19 years at the time he died.



More detailed information about growth rate and timing is revealed by examination of the microstructure of tooth crowns and roots. Tooth enamel is laid down in daily increments, with darker bands accumulating about once a week. By counting these bands and the space between them, relative rate of growth can be assessed. Beynon and Dean (1986) used crown development to show that robust australopithecines developed their incisors more quickly than did non-robust species like



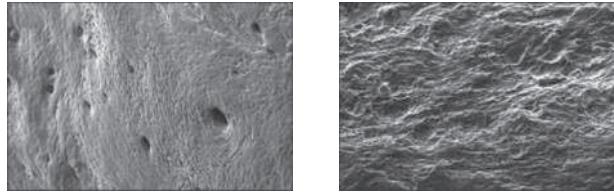
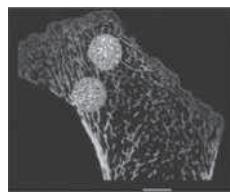
Dikika. And both groups erupt their teeth at earlier ages than do living humans.



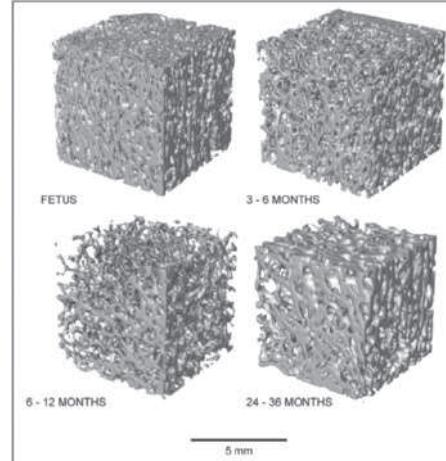
Robust and non-robust species of similar dental ages also show different patterns of facial growth. Using scanning electron microscopy (SEM), scientists can see whether bone in

a particular region of the skeleton was being deposited or resorbed (Bromage, 1987). Melanie McCollum (2007) has analyzed growth in the face of an extensive sample of recent chimpanzees and human children, and compared this with patterns in fossil children, including non-robust

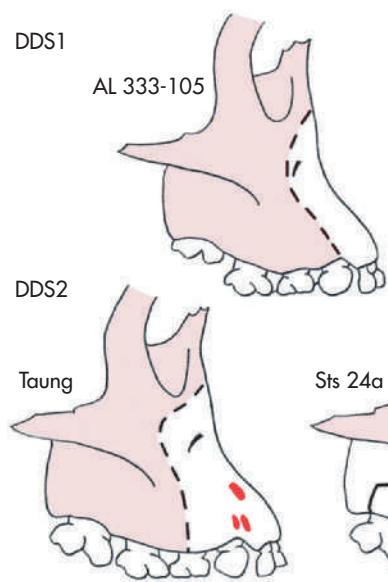
The most recent technology to be applied to understanding growth is microCT—or computed tomography able to visualize structures of very, very small scale. Using this technology Tim Ryan and Gail Krovitz (2006) have established how the spongy bone in the top of the femur changes in density and organization during growth. They looked at the changes in humans from fetal to about 9 years old to understand how becoming bipedal might influence bone structure. Around 2 or 3 years of age, the three-dimensional structure of the top of the femur reorganized in ways that were consistent with changes in loading caused by unassisted walking as opposed to crawling. Their work establishes a baseline for understanding how changes in behavior influence structure—an understanding that one day may help us understand fossil specimens such as the Dikika 3-year-old.



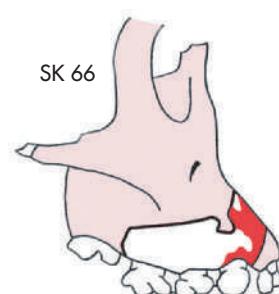
species such as the Taung Child (*Au. africanus*) and the Hadar Baby (A.L. 333-105, *Au. afarensis*), the same species as the Dikika 3-year-old, and *Au. robustus* (SK-66). Robust species show bone resorption on their anterior maxilla, while non-robusts of the same age do not. This response is in some small way responsible for the facial differences in adults of these species.



Non-robust *Australopithecus*



Robust *Australopithecus*



are somewhat longer relative to leg length than in modern humans but their anatomy is unlike that of modern apes who use their arms for walking. *Au. afarensis* also has more curved phalanges of both the toes and fingers; smaller, perhaps more flexible tarsal bones; and aspects of the shoulder and hip joints that may indicate some level of arboreality. However, work by Carol Ward and colleagues shows that important aspects of the foot's arch system were already in place in *Au. afarensis* (Ward et al., 2011).

This mosaic pattern of postcranial anatomy indicating a successful biped that probably also spent time in the trees has stirred debate about the type of bipedalism practiced by *Au. afarensis*. Perhaps the pelvic and lower limb anatomy of *Au. afarensis* indicate that the species walked nearly as efficiently and gracefully as we do today (Johanson et al., 1982; Lovejoy, 1978, 1988). But anatomical aspects of the feet, toes, and lower limbs all seem to suggest some degree of adaptation to arboreality (Stern & Susman, 1983; Susman et al., 1984). Although it seems clear that on the ground *Au. afarensis* moved about on two legs, they may have retreated to the trees to escape from predators, to forage for fruits and leaves during the day, and to sleep at night. Habitat reconstructions based on antelope remains found at *Au. afarensis* sites suggest the hominins were living in woodlands rather than on open savannas (see Chapter 8; Reed, 1997), which supports the idea that trees could have served as a refuge from predators or as sleeping areas for these hominins.

It is likely that *Au. afarensis* lived in groups, and because they were very sexually dimorphic, they probably were not monogamous. The largest adults from Hadar are, in some measures, nearly twice the size of the smallest *Au. afarensis* (Lucy is one of the very smallest). This extensive range of variation has led some experts to suggest that *Au. afarensis* is actually two species, not two sexes. However, the prevailing opinion is that *Au. afarensis* shows a high level of sexual dimorphism similar to that of modern orangutans (McHenry, 1991; Gordon et al., 2008) (Table 10.2). From this we infer that *Au. afarensis* had a polygynous mating strategy because in living primates great sexual dimorphism usually is associated with multiple mates (see Chapter 6).

Australopithecus bahrelghazali (3.5–3.0 MYA)

As we have seen, most early fossil hominins have come from eastern Africa, with two exceptions: the early possible hominin *Sahelanthropus tchadensis* and the later-living *Australopithecus bahrelghazali*. In 1995, Michel Brunet announced the discovery of the first hominin from West Africa, *Au. bahrelghazali* ("the hominin from Antelope Creek"). The species is known from a single fossil: the front of a mandible with seven teeth (Figure 10.20). Most researchers think that *Au. bahrelghazali* is in fact a member of *Au. afarensis* or at least that it is too fragmentary to form the basis of a new species. Analysis of the mandibular symphyses (the part near where a chin would be) of the original

Table 10.2 Comparisons of *Au. afarensis*, Great Apes, and Modern Humans (data from McHenry & Coffing, 2000 and Smith & Jungers, 1997)

| | Average Cranial Capacity (cc) | Sexual Dimorphism (Male Weight/Female Weight) |
|--------------------------|-------------------------------|---|
| <i>Au. afarensis</i> | 450 | 1.6 |
| <i>Au. africanus</i> | 450 | 1.4 |
| <i>Au. (P.) robustus</i> | 500 | 1.2 |
| <i>Au. (P.) boisei</i> | 500 | 1.4 |
| Bonobo | 350 | 1.3 |
| Chimpanzee | 400 | 1.1–1.3 |
| Gorilla | 500 | 1.7–2.4 |
| Orangutan | 400 | 2.0–2.2 |
| Modern human | 1,350 | 1.2 |

fossil and an additional fossil suggest they are somewhat differently shaped than those of *Au. afarensis*, however (Guy et al., 2008). The significance of these finds will remain uncertain until additional fossils are found, but they are important confirmation that hominins lived over much of the African continent, not only in East Africa.

Australopithecus deyiremeda (3.5–3.3 MYA)

Recently, the name *Australopithecus deyiremeda* was given to craniodental fossils between 3.3 and 3.5 million years of age discovered in the Woranso-Mille localities in Ethiopia (Haile-Selassie et al., 2015). The fossils are argued to differ from *Ardipithecus* in having thicker enamel (among other things) and from the *Au. anamensis/afarensis* lineage in having differently shaped mandibles but smaller postcanine teeth. *Australopithecus deyiremeda* was found in the same region as the Burtele foot that shows a locomotor adaptation unlike that of *Au. afarensis* and one perhaps related to *Ardipithecus*. There is no certain association between *Au. deyiremeda* and the Burtele foot, but the new species suggests that at least two species of *Australopithecus* co-existed, and possibly three if the foot does not belong to *Au. deyiremeda*.

Kenyanthropus platyops (3.5 MYA)

Working on the arid western shore of Lake Turkana in northern Kenya, a place made famous by many other fossil finds, Meave Leakey and her team discovered an early hominin dated to 3.5 million years ago (Leakey et al., 2001). Leakey and Fred Spoor thought the specimens, particularly a nearly complete but crushed cranium, were sufficiently different from members of the genus *Australopithecus* that they should be given a new genus name (Figure 10.21).

The researchers based their argument on the specimen's surprisingly flat face, a derived trait of later hominins rather than of *Au. afarensis* and its kin, and its small molar teeth, a condition more primitive than the other *Australopithecus*. They proposed the name *Kenyanthropus platyops* ("the flat-faced hominin from Kenya"). Some researchers think *Kenyanthropus* should be considered just another species of *Australopithecus* or even a member of *Au. afarensis*, although it differs from *Au. afarensis* not only in facial morphology but also in having other, more primitive cranial characters. Tim White (2003) suggests that the specimen was so deformed during fossilization that interpretation of *Kenyanthropus'* relationships to other hominins may be in error. But detailed examination of the deformation seems to show that the fundamental anatomy of the maxilla was not changed by the deformation and that the face is substantially flatter than *Au. afarensis* (Spoor et al., 2010).

Whether a distinct genus or a separate species, at 3.5 million years ago *Kenyanthropus* lived at the same time as *Au. afarensis*. The presence of multiple taxa, or an adaptive radiation based on dietary differences, as Leakey's group suggests, means that one of these taxa is not a direct ancestor of modern people. It is not possible at this time to determine which is more closely linked to later hominins. But we now know that the early days of the bipedal hominin radiation were more complex, and perhaps less linear, than we had realized.

Australopithecus garhi (2.5 MYA)

The Middle Awash team discovered fossil fragments of a previously unknown hominin at Bouri, Ethiopia that may yield information about how these creatures lived. Located near other hominin discoveries in

Figure 10.20 The mandible of *Au. bahrelghazali*. The first hominin found in western Africa, *Au. bahrelghazali* dates to about 3.5 million years ago.

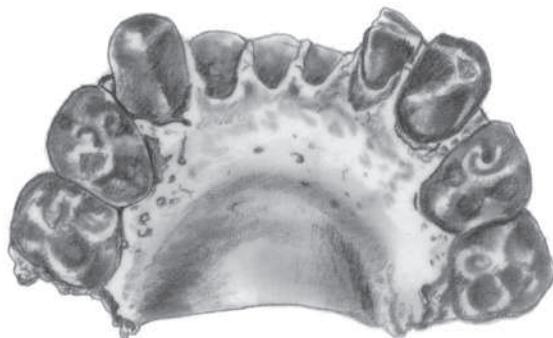


Figure 10.21 The cranium of *Kenyanthropus platyops* dates to about 3.5 million years ago in Kenya. The species takes its name from the very flat face.

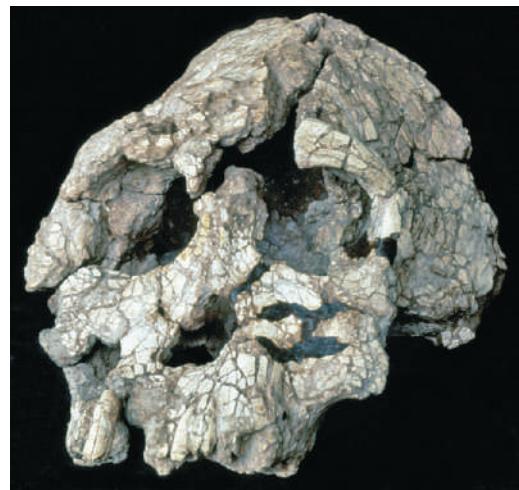


Figure 10.22 *Australopithecus garhi* dates to about 2.5 million years ago in Ethiopia and was found in the same beds as early stone tools. It is slightly younger than *Au. afarensis* and its cheek teeth are more robust.



the Middle Awash Valley of the Afar region of Ethiopia, the fossils are about 2.5 million years old (Asfaw et al., 1999). *Australopithecus garhi* ("the unexpected southern ape from the Afar") had a small brain (450 cc), a prominent prognathic face, large canines, and a sagittal crest (Figure 10.22). In most respects *Au. garhi* is quite primitive anatomically. Some workers argue that *Au. garhi* may be better interpreted as a late surviving member of *Au. afarensis*; remember that species existed until about 2.9 million years ago in the same geographic area. Besides its age, *Au. garhi* differs from *Au. afarensis* in just a few anatomical characters, including having larger cheek teeth (molars and premolars) that diverge from one another near the back of the palate and a slightly larger canine.

Regardless of its taxonomic attribution, the proximity of *Au. garhi* fossils to what were then the earliest known use of stone tools may be significant. At Bouri, and also at nearby Gona, archeologists found stone tools in association with the fossilized remains of antelope and other likely prey species. These animal bones show cut marks and percussion marks, unmistakable evidence that early hominins had been using stone tools to butcher carcasses.

We cannot say whether *Au. garhi* was the butcher, but no other early hominin fossils have been found in the same strata. At the time, this was the earliest evidence of tool use by *Australopithecus*. However, recently a set of cutmarks from 3.4 million years ago at Dikika, Ethiopia were argued to be evidence of even earlier tool use (McPherron et al., 2010), and 3.3-million-year-old stone tools themselves were more recently found in West Turkana, Kenya and announced in 2015 (Harmand et al., 2015; see Chapter 11).

Australopithecus africanus (3.5–<2.0 MYA)

We have thus far examined only hominins that occurred in West and East Africa. But southern Africa also saw a major radiation of hominin species during the Pliocene. In fact, the first *Australopithecus* ever discovered, the Taung Child, was discovered in southern Africa, and as we've seen gives the genus its name, roughly translated as "southern ape" or "southern ape-man."

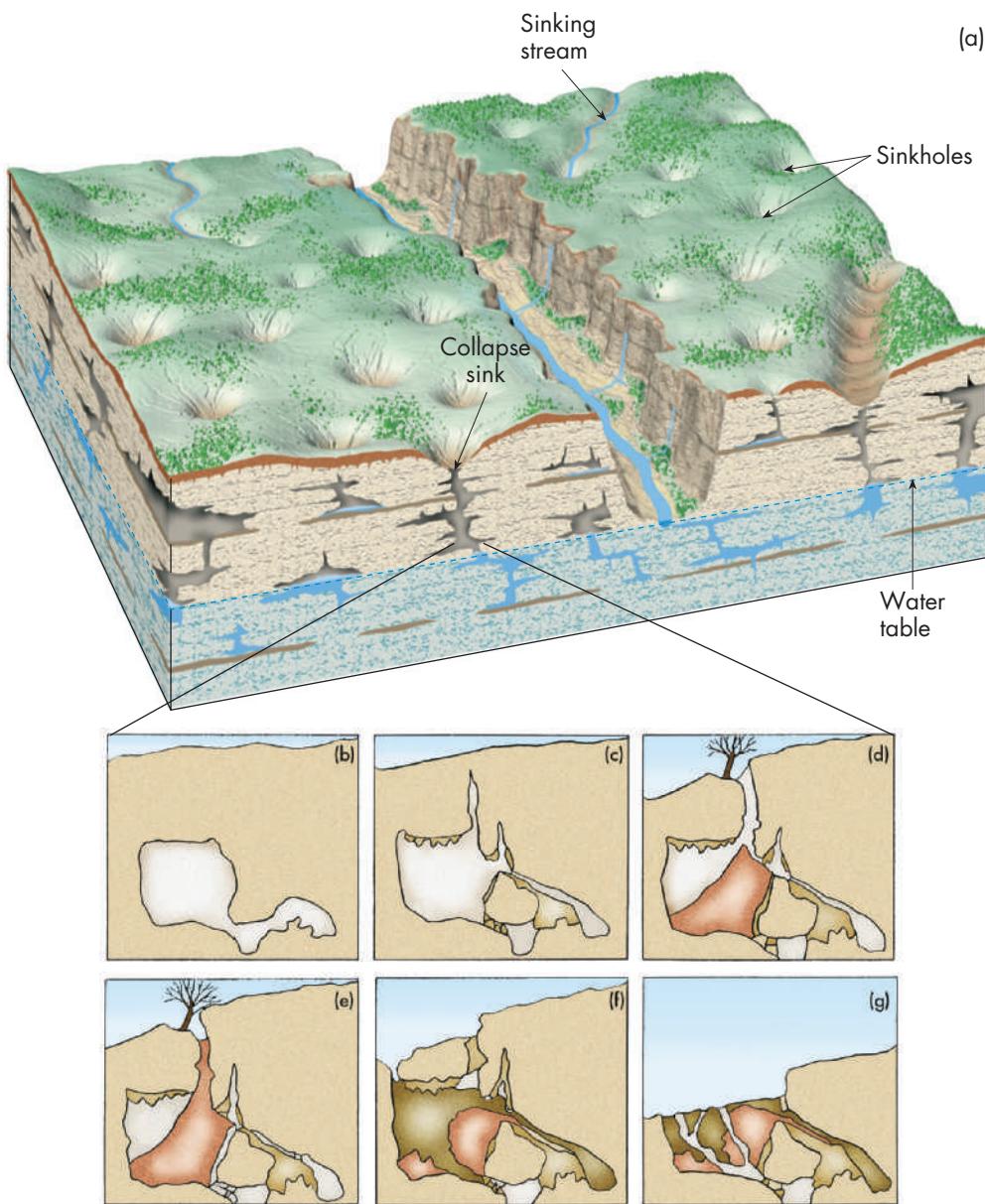
There are a few key differences between the study of fossils in southern and eastern Africa. Unlike the open-air sites of East Africa, most South African fossil sites are in cave and cliff deposits. Hominins and other animal remains are found in a mixture of ancient marine limestone and bone cemented into a **breccia**. The hominins did not live in the caves in which they were found, although the caves could easily be misinterpreted this way because natural processes can produce fossil deposits that look very much like they were created by humans. Careful taphonomic study of the caves and their included fossils reveals instead that the skeletal remains probably fell into the South African caves, which themselves are the result of dissolution of the bedrock by groundwater (see Chapter 8). South African caves, which form when the original limestone is dissolved by groundwater and then filled by air when the water table drops, often appear as sinkholes in the ground usually with trees growing along their rims, similar to those seen in parts of Florida (Figure 10.23). Animals are thought to have fallen into these caves by accident or in some cases to have been introduced after having been killed by carnivores, such as leopards, which cache their kills in the branches of trees overhanging the sinks to protect them from larger carnivores (Brain, 1981).

There is another key difference between the East and South African fossil record. Volcanic ash that forms the matrix in which many East African fossils are embedded can be dated quite precisely using the $^{40}\text{Ar}/^{39}\text{Ar}$ techniques you read about in Chapter 8. However, South African deposits cannot be dated using these

breccia

Cement-like matrix of fossilized rock and bone. Many important South African early humans have been found in breccias.

Figure 10.23 South African cave sites were formed by the dissolution and collapse of (a) bedrock that later trapped sediments and animals, including hominins. (b) Initially, bedrock is dissolved by groundwater. (c) When the water table lowers, there may be roof collapse into the chamber and stalagmite/stalactite formation. (d) With time, the chamber may erode further, eventually connecting to the surface. (e) Vegetation and trees often grow near these wet openings and sediments and animals may fall into the chambers. (f) Over time other openings to the surface may form introducing new sediments and bones. (g) Erosion of the surface exposes the stratigraphy of these sediments, the relative ages of which are difficult to interpret because of their complex history.



techniques. Some uranium series dates and some cosmogenic radionuclide dates have been attempted, but mostly paleontologists must rely on geomagnetic polarity data and relative dating methods. They compare the fauna (biostratigraphy) and geology (lithostratigraphy) of rock strata containing human fossils with strata in other regions such as East Africa that contain similar fossil sequences but can be more precisely dated. This provides an estimate of the age of the deposits. However, the stratigraphy of the South African caves is complex, so establishing the sequence of which fossil species lived contemporaneously with others sometimes is not possible.

Figure 10.24 The Taung child, the first of the australopithecines to be discovered, is the type specimen for *Australopithecus africanus*. It has been suggested that large birds of prey may have been responsible for some of the predation on this early species.



endocast

A replica (or cast) of the internal surface of the braincase that reflects the impressions made by the brain on the skull walls. Natural endocasts are formed by the filling of the braincase by sediments.

In 1924, Raymond Dart, a young professor of anatomy in Johannesburg, South Africa, received a shipment of crates loaded with fossils collected from the Taung limestone quarry. One of the crates held a tiny partial skull of a primitive hominin baby (Figure 10.24). The face and teeth were attached to a fossilized impression of the interior of the braincase as well, a so-called natural **endocast**. After carefully extracting the specimen from the limestone matrix, Dart realized that this endocast preserved the size and shape of the baby's brain.

"The Taung Child" appeared to be a very young, ape-like hominin who retained some baby teeth, which suggested an age of 5 or 6 years, based on modern human growth rates. This estimate of Taung's age at death has long been in debate because we can't be sure whether early hominins grew up along the same trajectory as modern people or as the great apes. Recent research suggests *Australopithecus* followed a developmental rate similar to an ape and that the Taung Child was actually just 2 or 3 years old at the time it died.

In an article for the British science journal *Nature*, Dart (1925) argued that Taung was a hominin, based on the position of the foramen magnum, which was on the bottom of the cranium, as it would be in a biped. An authority on the brain, Dart devoted much space in the article to describing the features of the brain's surface that could be detected from the endocast, features that supported his contention that Taung was a direct link between the small-brained apes and larger-brained humans. Dart derided the place accorded to Piltdown man (see Chapter 8: Insights and Advances: The Piltdown Hoax on page 238), which he thought had too ape-like a jaw to be human, and also the *Homo erectus* skull dubbed Java Man (see Chapter 11). He concluded his paper by acknowledging Darwin's long-ago assertion that Africa, not Europe or Asia, was the birthplace of humanity.

In a series of letters to *Nature*, nearly all of the great minds of early twentieth-century paleoanthropology rejected the significance of the Taung discovery. They still accepted Piltdown as evidence both of the big-brained nature of early humans and of Britain as the cradle of humankind. The majority thought that Taung was merely a new variety of ape and implied that Dart (who had a reputation as a grandstander) had sought attention for himself in his bold assertions about the fossil.

Because of the controversy surrounding Taung and the entrenched view about Piltdown, it was not until nearly 1950 that *Australopithecus* was given its rightful place as a southern African forerunner of modern humans. Meanwhile, many other discoveries of fossils of the same species as Taung were being made. Most of these fossils have been dated to between 3.5 and 2.4 million years ago, with the possibility that some of the material may be much younger, possibly little more than 1 million years old.

The oldest *Australopithecus africanus* fossils come from Sterkfontein, Taung, Gladysvale, and Makapansgat (Figure 10.25). In the 1930s, Dart's colleague Robert Broom, a Scottish-born doctor and amateur paleontologist, followed up on Dart's early claims for hominins in South Africa. In 1947, Broom discovered a partial skull of a presumed female *Au. africanus* from Sterkfontein, a limestone quarry near Johannesburg. Broom called the fossil "Mrs. Ples," short for the genus name *Plesianthropus* that he assigned to it (Figure 10.26).

Figure 10.25 The site of Gladysvale in South Africa is excavated for *Australopithecus* remains.



This discovery, estimated to date to 2.6 million years ago, made it impossible for skeptics of Taung to insist that *Au. africanus* might have only been an ape because the adult Mrs. Ples was clearly bipedal (Broom, 1947). Later, Phillip Tobias made important contributions in this area as well, and hundreds of *Au. africanus* specimens of various ages and probably both sexes have been found since Broom's initial work. A nearly complete skeleton of *Au. africanus* nicknamed "little foot" was extracted from the deposits at Sterkfontein by Ron Clarke. Recently, $^{26}\text{Al}/^{10}\text{Be}$ dates suggest little foot might be as old as 3.67 million years old—older than the Lucy skeleton (Granger et al., 2015). The same study showed that tools from a different part of the site were dated to 2.18 million years, indicating this cave system was accumulating animal bone for more than 1.5 million years!

Australopithecus africanus is more derived than *Au. afarensis* in several aspects of its cranial skeleton (Figure 10.27). *Australopithecus africanus* has a larger braincase (about 450–550 cc, still quite small by modern standards), a rounded vault that lacks cranial crests and has fewer air cells in it, a less prognathic face, and a more flexed cranial base than *Au. afarensis*. The teeth of *Au. africanus* are generalized and the molars more modestly proportioned than in later, more specialized australopithecines such as *Au. robustus* and *Au. boisei*. This has led to an informal classification into gracile australopithecines, including *Au. africanus*, and robust australopithecines for *Au. robustus*, *Au. boisei*, and *Au. aethiopicus*. *Australopithecus africanus* has small anterior teeth, especially canines, compared with earlier hominins such as *Au. afarensis* but larger anterior teeth than most of the later robust australopithecines. However, the molars of *Au. africanus*, although clearly larger than in earlier forms, are smaller than the enormous molars of the robust australopithecines.

Australopithecus africanus was a small-bodied biped that possessed the broad and short iliac blade of the pelvis and structural adaptations in the spine, leg, and foot that characterize habitual bipeds. Based on an extensive collection of postcranial remains, body size has been estimated at about 65–90 pounds for *Au. africanus* (which is slightly smaller than the later robusts). *Australopithecus africanus* has the same general body plan as *Au. afarensis*, with a more funnel-shaped thorax than in humans, although *Au. africanus'* arms may be shorter (Figure 10.15 on page 307).

Figure 10.26 Francis Thackeray holding Sterkfontein 5 (STS 5), a presumed female *Australopithecus africanus*, that shows the rounded vault and moderate facial prognathism of that species.



Figure 10.27 Key features of *Australopithecus africanus* include a rounded vault without cranial crests, a slightly flexed cranial base, and moderate facial prognathism.

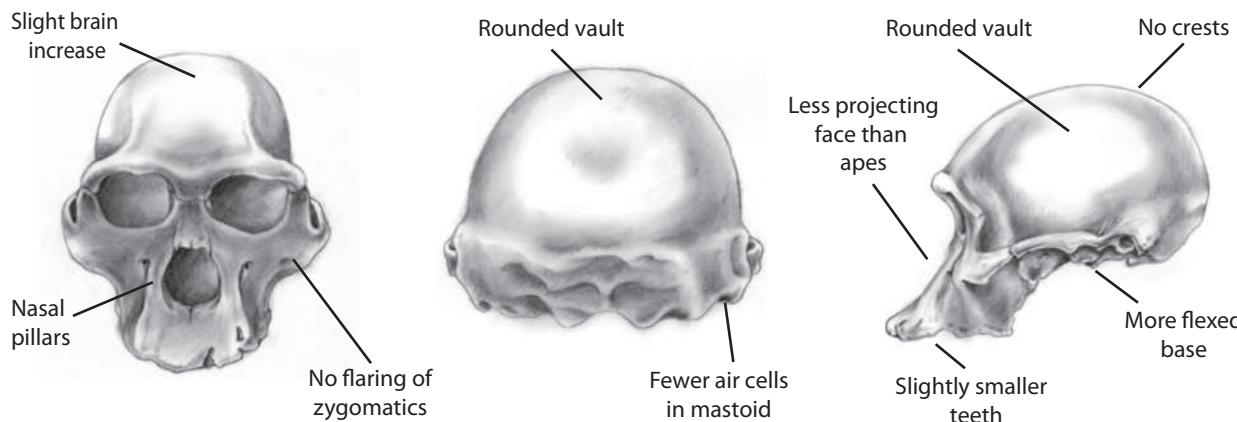


Figure 10.28 *Australopithecus sediba* shares small brain size with other members of *Australopithecus* but also has a relatively broad braincase that some think links it to genus *Homo*.



The other animals found with *Au. africanus* suggest that these hominins, like those in eastern Africa, were living in woodland and open woodland environments (Reed, 1997). These wooded areas may have provided some protection from predators. There are currently no earlier hominins in South Africa than *Au. africanus*, but it is generally assumed that *Au. africanus* evolved from an early population of East African hominins, probably *Au. afarensis* or *Au. anamensis*, that migrated to the south.

Australopithecus sediba (1.97–1.78 MYA)

A newly discovered South African hominin named *Australopithecus sediba* was announced in 2010 by a team led by Lee Berger of the University of the Witwatersrand (Figure 10.28). The geological age of the site, based on uranium-lead dating, is between 1.977 and 1.78 million years. Importantly, the remains include both cranial and postcranial bones, of both an adult and juvenile. Like other *Australopithecus* fossils, the brain size is small, around 420–435 cc, and the body size is small with long arms. But unlike other fossils, these also show some characteristics similar to genus *Homo* and sometimes even *H. erectus* (a more advanced form than the earliest members of the genus). In particular, *Au. sediba* is said to share derived characters with *Homo* that include dental size and shape, particularly of the molars and canines, a broad frontal, a derived face, and derived features of the pelvis. Berger and colleagues have argued that these shared characters imply that *Au. sediba* is uniquely related to *Homo* and perhaps even *Homo erectus* (Berger et al., 2010). But the features could be independently acquired in *Au. sediba* and *Homo* (that is, they could be homoplasies) and thus not tell us about close relatedness at all. The newness of the finds means that much more work is needed to differentiate among these hypotheses.

The Robust Australopithecines (or Paranthropines)

hard-object feeding

Chewing tough, hard-to-break food items such as nuts or fibrous vegetation.

The robust australopithecines are a group of early hominins that appear to have been an evolutionary dead end because of their extreme anatomical specializations. The first robust species was found in 1938 in South Africa by Robert Broom, and the East African species was found at Olduvai Gorge, Tanzania, in 1959 by Mary Leakey (Figure 10.29).

The robust australopithecines are united by a suite of cranial features related to their feeding adaptation that made them extremely efficient at producing a great deal of force at their molars (Figure 10.30). These cranial features often are thought of as an adaptation to **hard-object feeding**, chewing tough food items such as hard-shelled nuts or fibrous vegetation or possibly lots of low quality grasses or sedges. In fact, early fossils were nicknamed “nutcracker man” for this reason.

Scientists think that these adaptations allowed robust australopithecines to survive during times when not much food existed because they were specialized for eating a kind of food that other hominins could not eat. Most of the time robuts probably ate a lot of different things, but when food was scarce they relied on their “fallback food.” What that fallback food is remains debated. Isotopic research on South African robuts shows that they were omnivores, probably eating some kind of animal protein (perhaps termites) at some times of the year. But isotopic work from East Africa suggests *Au. boisei* could have fed on low quality foods like grasses and sedges (Cerling et al., 2011) and recent comparative work argues that they, much like recent yellow baboons, might have focussed on the high quality tuber of these grasses, such as tiger-nut (Macho, 2014). There is also

Figure 10.29 Olduvai Hominin 5 (OH 5) is a hyper-robust member of *Australopithecus boisei* discovered in Tanzania by Mary Leakey.



evidence in South Africa that they may have used bone tools to access this food, and they have been found with stone tools, as well, suggesting that they were fairly intelligent creatures. However, their reliance on tough foods whether hard objects or sedges during times of resource scarcity seems to become more specialized through time. Eventually, this overspecialization would lead to their demise when food resources changed too dramatically and their fallback foods disappeared.

Whatever the food items and however often they were eaten, they seem to have favored an anatomy to produce large bite forces. The **muscles of mastication** that produce chewing force are maximized in size and placement for mechanical efficiency (Figure 10.30). The robust australopithecine skull reflects these changes. One of these muscles, the temporalis, which sits on the side of the braincase, lifts the mandible. (You can feel your own temporalis doing the work of chewing if you touch your temples while closing your jaw.) In the robust species, the temporalis is enlarged and moved forward, which is reflected in the presence of an anterior sagittal crest for its attachment, the presence of extreme **postorbital constriction** to accommodate its large size, and the flaring of the **zygomatic arches** laterally to accommodate the bigger muscle (Figure 10.31). Another muscle, the masseter, sits on the outside of the jaw and also raises the mandible. (You can feel your masseter work if you put your fingers on the

Figure 10.30 Key features of robust australopithecines include adaptations to heavy chewing such as a large sagittal crest and flaring zygomatics, a dished face, and strongly flexed cranial base.

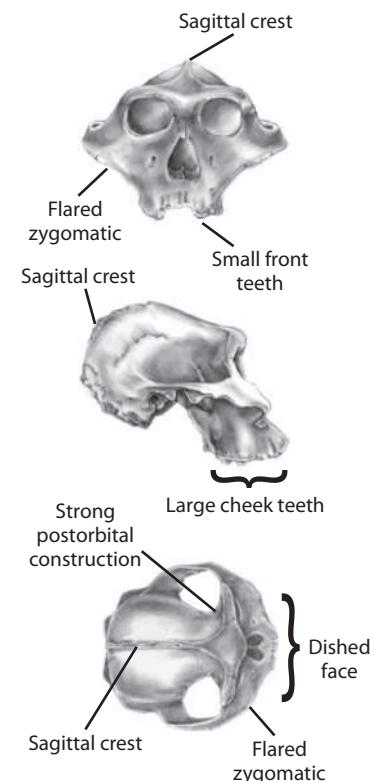
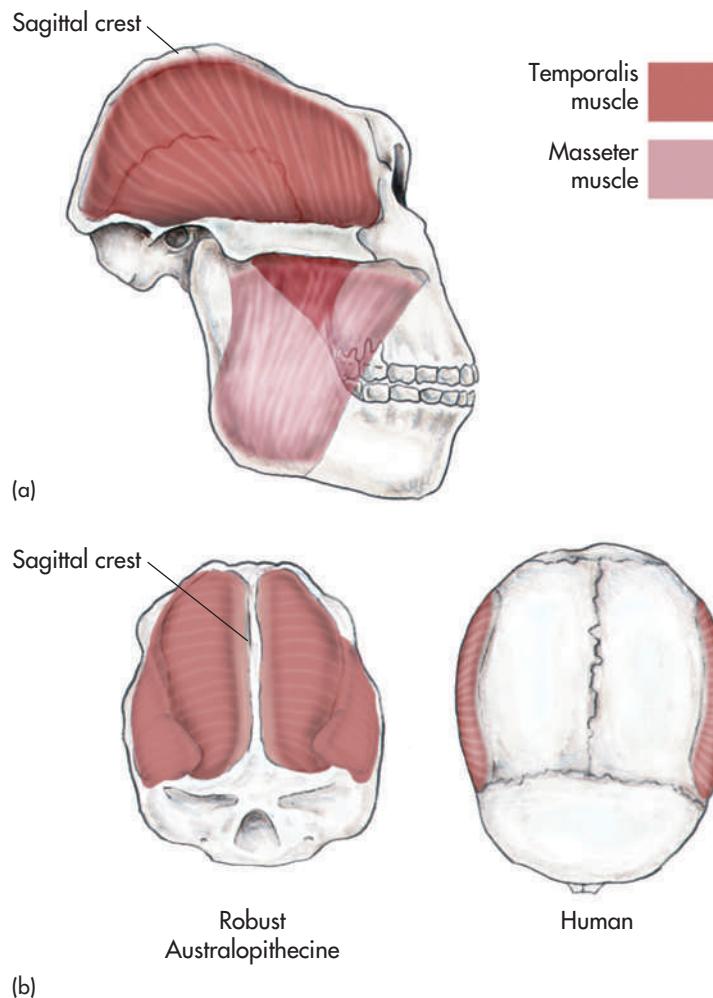


Figure 10.31 Muscles of mastication in robust australopithecines. (a) The temporalis muscle (red) attaches to the sagittal crest and the mandible, and the masseter muscle (pink) attaches to the zygomatic bone, which is moved directly over the molar teeth. (b) From above we can see that robust australopithecines had much greater muscle attachment area on their skulls than do modern humans (right).



muscles of mastication

The chewing muscles: masseter, temporalis, medial and lateral pterygoids.

postorbital constriction

The pinching-in of the cranium just behind the orbits where the temporalis muscle sits. Little constriction indicates a large brain and small muscle; great constriction indicates a large muscle, as in the robust australopithecines.

zygomatic arch

The bony arch formed by the zygomatic (cheek) bone and the temporal bone of the skull.

outside and rear of your lower jaw and clench your teeth.) The masseter is moved forward over the teeth in robusts by the placement of the zygomatic (cheek) bones to which the muscle attaches in a more forward position. This results in a dished face in which the cheeks extend further forward than does the nose. Flexing the cranial base brings the face (and the teeth) up under the vault and chewing muscles, including the masseter. The mandible is large and deep, and the face is tall to counter these muscle forces. The molars and premolars are enormous, further indicating that at least at some times of the year these hominins relied on a diet that included tough objects. The premolars are like small molars and are referred to as molarized. In contrast, the anterior teeth are tiny, indicating what little importance they had in the dietary habits of the robusts.

Habitat reconstructions based on the other animals found at robust australopithecine sites suggest that these hominins, like *Au. africanus* and those in eastern Africa, were living in woodland and open woodland environments (Reed, 1997). However, some robusts seem also to have lived in slightly more open habitats but always to be associated with streams or waterways.

Some scientists think that the robust australopithecines are so different from other *Australopithecus* that they should be placed in their own genus, *Paranthropus*. The decision to define a new genus for a set of closely related species requires evidence that these species, in this case the robusts, share an adaptive plateau that separates them from other related species. Proponents of the use of *Paranthropus* argue that the specialized chewing apparatus of the robusts is evidence of such an adaptive plateau. By using this separate genus name these scientists also are accepting that all the robust species are more closely related to one another than they are to species outside of *Paranthropus* and thus that they descend from a recent common ancestor who also shared some part of this adaptation. As we shall see, other scientists disagree as to how closely related the robust species are to one another, so in this book we take a conservative approach and include them in *Australopithecus*.

AUSTRALOPITHECUS (P.) AETHIOPICUS (2.7–2.5 MYA) There is no evidence that the robust lineage left any descendants, but there is some tantalizing evidence about its origin. In 1985, Alan Walker and Richard Leakey found the skull of a very primitive robust australopithecine that is a good candidate for the ancestor of both later robust species, *Au. (P.) boisei* and *Au. (P.) robustus*, and also shows some links to other early hominins (Walker et al., 1986). The fossil was discovered on the western shore of Lake Turkana, an area famous for many other fossil hominin finds. The fossil had been stained black by minerals in the sediment in which it was buried and therefore was dubbed “the Black Skull” (Figure 10.32). Walker and Leakey assigned the fossil, also known by its museum number as KNM-WT 17000, to *Au. boisei* because it retains key traits derived in *Au. (P.) boisei*. But it also retains more primitive characters and because of this mosaic anatomy, most scientists now call it *Au. (P.) aethiopicus*.

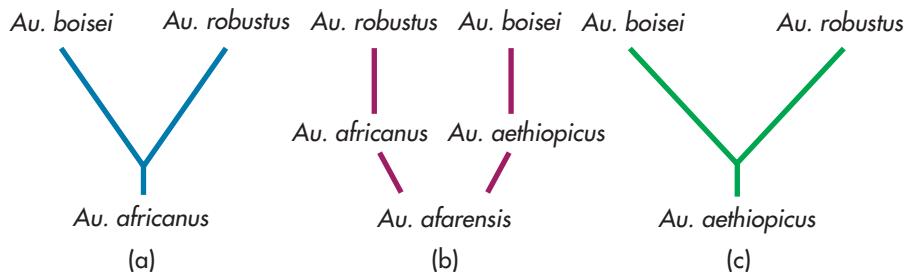
Figure 10.32 *Australopithecus aethiopicus*, called the “Black Skull” because of its manganese staining, is an early robust form dating to about 2.5 million years ago in Kenya.



Australopithecus (P.) aethiopicus shares the suite of masticatory (chewing) characters described for the robust australopithecines but with some modifications and some more primitive characters as well. *Au. (P.) aethiopicus* has a sagittal crest, dished face, flared zygomatics, and huge molars that both *Au. (P.) boisei* and *Au. (P.) robustus* possess, although the sagittal crest is positioned more posteriorly in *Au. (P.) aethiopicus* (Figure 10.32). But *Au. (P.) aethiopicus* also retains primitive traits from an earlier hominin, probably *Au. afarensis*. *Australopithecus (P.) aethiopicus* differs from other robusts and is more similar to *Au. afarensis* by being small brained (about 400 cc), with a prognathic face, flat cranial base, and large anterior teeth. There are no known postcranial remains of *Au.(P.)*

Figure 10.33 Some possible phylogenies for the robust australopithecines.

(a) *Au. africanus* may give rise to both *Au. robustus* and *Au. boisei*. (b) *Au. afarensis* may give rise to two separate lineages, one of East African robusts and the other of South African robusts. (c) Or *Au. aethiopicus* may give rise to both *Au. robustus* and *Au. boisei*.



aethiopicus. At 2.5 million years old, *Au. (P.) aethiopicus* is also slightly older than *Au. (P.) boisei* but younger than *Au. afarensis*.

Many paleoanthropologists think that *Au. (P.) aethiopicus* is primitive enough to be the evolutionary link between the early trunk of the hominin family tree and the specialized branch that led to the robust australopithecines (Figure 10.33). However, because *Au. (P.) aethiopicus* and *Au. (P.) boisei* uniquely share features (such as a heart-shaped foramen magnum) that differentiate them from *Au. africanus* and *Au. (P.) robustus*, some scholars still consider it possible that the East and South African robusts could represent two more distantly related lineages that have converged on a shared anatomy based on a similar dietary adaptation to hard-object feeding, at least during fallback periods.

AUSTRALOPITHECUS (P.) BOISEI (2.3–1.2 MYA) The culmination of the lineage that started with *Au. (P.) aethiopicus* is *Au. (P.) boisei* (Figure 10.29). In 1959, the skull that Mary Leakey found while working alone one day at Olduvai became the type specimen for a new genus and species, *Zinjanthropus boisei* ("hominin from Zinj; after a benefactor named Boise"). It was later renamed *Australopithecus boisei* (Leakey, 1959).

Since 1959, East African sites in Kenya, Tanzania, and Ethiopia have yielded a plethora of *Au. (P.) boisei* remains, both cranial and postcranial. Although the Leakeys did not know it at the time, Zinj represented the most specialized end of this East African species of robusts. The species spans the time period from about 2.3 to about 1.2 million years ago, based mostly on radiometric ages. The brain size is about the same as that of the robusts from South Africa, and the postcranial skeleton is large, with an estimated body size between 75 and 110 pounds (McHenry, 1992, 1994).

The cranial skeleton of *Au. (P.) boisei* reflects the suite of masticatory adaptations discussed previously and some features shared with *Au. (P.) aethiopicus* but not shared with the South African forms; these include the shape of the nasal bones and browridge, and the absence of nasal pillars. However, an important fossil find from Konso, Ethiopia, shares the South African condition of some of these features, muddying the distinctions.

AUSTRALOPITHECUS (P.) ROBUSTUS (2.0–1.5 MYA) When Robert Broom discovered the first robust australopithecine in 1938 at Kromdraai in South Africa, most of the scientific community still doubted the presence of early hominins in Africa. However, Broom recognized that the forward location of the foramen magnum indicated a biped and thus a hominin rather than a robust ape skull (Figure 10.34). This was also a species quite different from the more gracile australopithecine fossil from Taung. The characters that led Broom to his conclusion are the suite of masticatory characters discussed previously. These characters led Broom to name the genus *Paranthropus* ("next to man") and the species *robustus*. Later the Swartkrans remains were reassigned to genus *Australopithecus*. However, if the robust species for a separate genus, then by the

Figure 10.34 *Australopithecus robustus* is a South African robust australopithecine first discovered in 1938.



laws of zoological nomenclature the genus name for all three species reverts to *Paranthropus* because this was the first generic name proposed for any other species.

Australopithecus (P.) robustus is known principally from Kromdraai, Swartkrans, and Drimolen; and based on biostratigraphy it dates to about 2.0–1.5 million years ago. Its cranial capacity is between 500 and 550 cc, and the postcranial skeleton indicates a body size of about 70–90 pounds (McHenry, 1993, 1994). *Australopithecus (P.) robustus* differ from their East African counterparts in several minor characters, including the shape of the nasals and browridge and the presence of bony pillars next to the nose.

In addition to hard-shelled, tough foods, isotopic studies suggest that *A. (P.) robustus* also ate substantial quantities of animal protein (see Chapter 8 to read about the method). Andrew Sillen (1988) found that the ratio of isotopes of strontium and calcium in *Au. (P.) robustus* fossils was consistent with what we would expect in a grassland inhabitant whose diet was composed at least partly of animal protein; *Australopithecus africanus* does not have such values. Julia Lee-Thorp and her colleagues (1994) suggested on the basis of carbon isotopic values that *A. (P.) robustus* probably the protein source came from eating grass-eating insects such as termites. Supporting this idea are the wear patterns found on the ends of animal bones probably used by *Au. (P.) robustus* as digging sticks (d'Errico et al., 2001). The researchers think that, unlike chimpanzees who improvise termite-collecting tools from blades of grass and twigs (see Chapters 7), the robust australopithecines used a more powerful bone tool to open up the massive mounds of hardened soil in which termites live.

Implications of the Australopithecine Radiation

10.5 Show your understanding of the implications of the Australopithecine radiation by discussing the evolutionary relationships among the species in the genus *Australopithecus* and begin to explain their evolutionary radiation in Africa.

Just as the Miocene period was a time of great diversification of the apes, the Pliocene was a time of adaptive radiation and diversification of the early hominins. We still do not know how large this radiation was, but frequent new discoveries suggest that many more species of australopithecines and other hominins remain to be found. Some of the increase in diversity in the Pliocene results from the “naming game,” the splitting of previously named species or genera into two or more new taxa. But most of the recently named species are based on new fossil discoveries.

Cohabitation

It is difficult for us to imagine today that at various times in the past, two or even three hominin species lived in the same regions of the African continent (Table 10.3). In some of these cases, two species occurred at the same time and in the same habitat. When two or more species with similar diets and behaviors coexist in the same place, scientists predict that some key aspects of their biology will diverge as a result of competition. If this does not occur, then one species or the other probably should become rare or extinct in the face of direct competition with the other. The australopithecine species that appear to have shared the same habitat at the same time show striking morphological differences. This suggests that natural selection molded them to avoid feeding competition.

One good way to understand the likely ecological relationship between sympatric early hominins is to look at how living great apes share a habitat. In Africa, there are many forests in which chimpanzees and gorillas coexist. Both apes travel on the ground to find food, but chimpanzees spend far more time feeding in trees than gorillas do.

Table 10.3 Examples of Potentially Contemporaneous Hominins by Region

| Age (MYA)* | West Africa | East Africa | South Africa |
|------------|----------------------------------|---|--|
| ~6 | <i>Sahelanthropus tchadensis</i> | <i>Orrorin tugenensis</i> <i>Ardipithecus kadabba</i> | |
| 3.9 | | <i>Australopithecus afarensis</i> , <i>Au. anamensis</i> | |
| 3.5 | <i>Au. bahrelghazali</i> | <i>Au. afarensis</i> , <i>Au. deyiremeda</i> , <i>Kenyanthropus platyops</i> | <i>Au. africanus</i> |
| 2.5 | | <i>Au. garhi</i> , <i>Au. aethiopicus</i> | <i>Au. africanus</i> |
| 2.5–2 | | <i>Au. boisei</i> , <i>Au. garhi</i> | <i>Au. africanus</i> , <i>Au. robustus</i> |
| 2–1.5 | | <i>Au. boisei</i> , <i>Homo sp.</i> | <i>Homo sp.</i> , <i>Au. sediba</i> , <i>Au. robustus</i> |

*MYA = millions of years ago

Both build nests each night, but gorilla nests usually are on the ground, and chimpanzee nests normally are high in trees. And although both species prefer fruit to all other forest foods, gorillas fall back on high-fiber leafy foods in lean seasons, whereas chimpanzees forage far and wide to continue eating fruits. In other words, although these two large-bodied apes are similar in many respects, there are key differences that probably are the result of their ancestors evolving together in African forests and that today allow them to coexist (Tutin, 1996; Stanford & Nkurunungi, 2003).

In addition to *Au.(P.) africanus* and *Au. (P.) robustus* in southern Africa, potential cases of sympatry in the hominin fossil record include *Au. (P.) boisei* (robust) and early genus *Homo* (gracile) in eastern Africa, *Au. garhi* and *Au. (P.) aethiopicus* in eastern Africa, and *Au. afarensis* and *K. platyops* in eastern Africa. In all these cases it has been argued that anatomical differences between taxa reflect differences in dietary adaptations that suggest the hominins were partitioning the available resources, which allowed them to coexist.

Tools and Intelligence

We used to think that only members of our own genus *Homo* were clever enough to make tools. Australopithecines were considered dim-witted in comparison and without tools. However, until the 1960s tool making was also unknown in the living great apes. Although no nonhuman primates make stone tools, making tools from other materials is common in the great apes and even in some monkeys. Chimpanzees make and use probes to extract insects and other food items, make sponges to soak up liquids, use hammers to crack open nuts, and wield branches as weapons against prey and other chimpanzees (see Chapter 6). Other apes and even capuchin monkeys use organic tools, although they may not make them (see Chapter 7, Innovations: Culture in Nonhuman Primates on pages 212–213). We might expect, then, that early hominins such as australopithecines fashioned tools, perhaps out of organic materials, but did not necessarily make durable tools.

In the 1950s, Dart interpreted the animal remains from early hominin sites as evidence of what he called the **osteodontokeratic culture** in which he envisioned australopithecines using the bones, teeth, and horns of animals as tools (hence the name he gave the culture). Dart also considered the australopithecines to be blood-thirsty hominins. Recent research suggests that the accumulated remains found in South African cave sites probably represent natural accumulations of bone rather than australopithecine tool kits. Although his evidence has not held up under more recent scrutiny, Dart may have been right in thinking that *Australopithecus* made and used tools.

osteodontokeratic culture

A bone, tooth, and horn tool kit envisioned by Raymond Dart to be made by *Australopithecus*.

There is tantalizing evidence that australopithecines were smarter than we might think. The earliest evidence of tool use in the genus used to be the possible association between *Au. garhi* and the butchered remains of animals about 2.5 million years ago in Ethiopia. But in 2015, 3.3-million-year-old stone tools from East Africa were announced (Harmand et al., 2015). Given their age, the maker had to be an australopithecine, probably *Au. afarensis*. At later sites in eastern and southern Africa, stone tools are found in the same beds and even at the same localities as the remains of robust australopithecines. No other hominin genera are known from these particular contexts, so this may indicate the production and use of stone tools by australopithecines. And as we saw earlier, *Au. robustus* may have used animal bones as digging sticks.

Hand anatomy also gives us a small clue that the robust australopithecines may have been capable of tool production. The robusts share thumb anatomy that is similar to that of tool-making hominins such as ourselves and other members of the genus *Homo*, but earlier species of *Australopithecus* such as *Au. afarensis* lack this anatomy. This may indicate that the robusts could make stone tools, although it does not tell us whether they did.

If tool production requires sophisticated cognitive skills, then the australopithecines were at least as sophisticated as living great apes and if the ages for the West Turkana tools hold up, these tools imply that some groups of *Australopithecus* sometimes made and used stone tools. However, it is not until around 2 million years ago, well into the australopithecine radiation, that we see the ubiquitous use of stone tools. Thus the additional access to resources that these tools provide seems unlikely to have been among the primary reasons that the genus arose. The increasing reliance on stone tools after 2 million years ago might, however, signal a behavioral difference between *Australopithecus* and the later evolving *Homo*.

Ancestors and Descendants

There are several ways to envision the relationships among the early hominin species we have introduced in this chapter (Figure 10.35). Based on anatomy, many scientists derive *Au. afarensis* from the more primitive *Au. anamensis* and then see *Au. afarensis* as the base of the radiation of *Au. africanus*, *Au. garhi*, and *Au. aethiopicus*, and possibly the *Homo* lineage. Each of these lineages takes the *Au. afarensis* anatomy in a slightly different direction depending on the environmental conditions in which it lived and by which individuals were selected for or against. Discovery of the Burtele foot and *Au. deyiremeda* potentially complicate the picture of a single mid-Pliocene species for all later hominins. Given the recency of these finds, more work is needed to understand how these groups relate to one another and later hominins. Many see *Au. (P.) aethiopicus* giving rise to the robust radiation of *Au. (P.) boisei* and *Au. (P.) robustus*, whereas others derive the East African robusts from *Au. (P.) aethiopicus* but the South African robusts from *Au. africanus*. This splitting into South and East African lineages means that these scientists don't think the robusts shared a last common ancestor exclusive of other australopithecines and therefore are not part of a separate genus, *Paranthropus*. *Australopithecus africanus*, *Au. afarensis*, and *Au. garhi* have all been implicated as possible ancestors for the genus *Homo*, and *Au. sediba* is even considered a possible ancestor to *H. erectus*, although this will require substantially more evidence. However, one thing that almost all scientists agree on is the idea that the robust australopithecines are too specialized to be ancestral to genus *Homo*. The key to a good potential ancestor is that it exists early enough to give rise to the later groups, is not more derived than those groups, and has characters that look as if they could give rise to later groups.

Because the fossil record is sparse, each new fossil discovery throws the tree into brief disarray, after which paleoanthropologists try to sort out the most likely phylogeny suggested by the sum of the evidence. This may seem as though scientists

cannot agree, but disagreement is a healthy feature of evolutionary science. Each new find tests previous hypotheses and produces new interpretations, new research, and new results that push the state of our understanding of human ancestry forward.

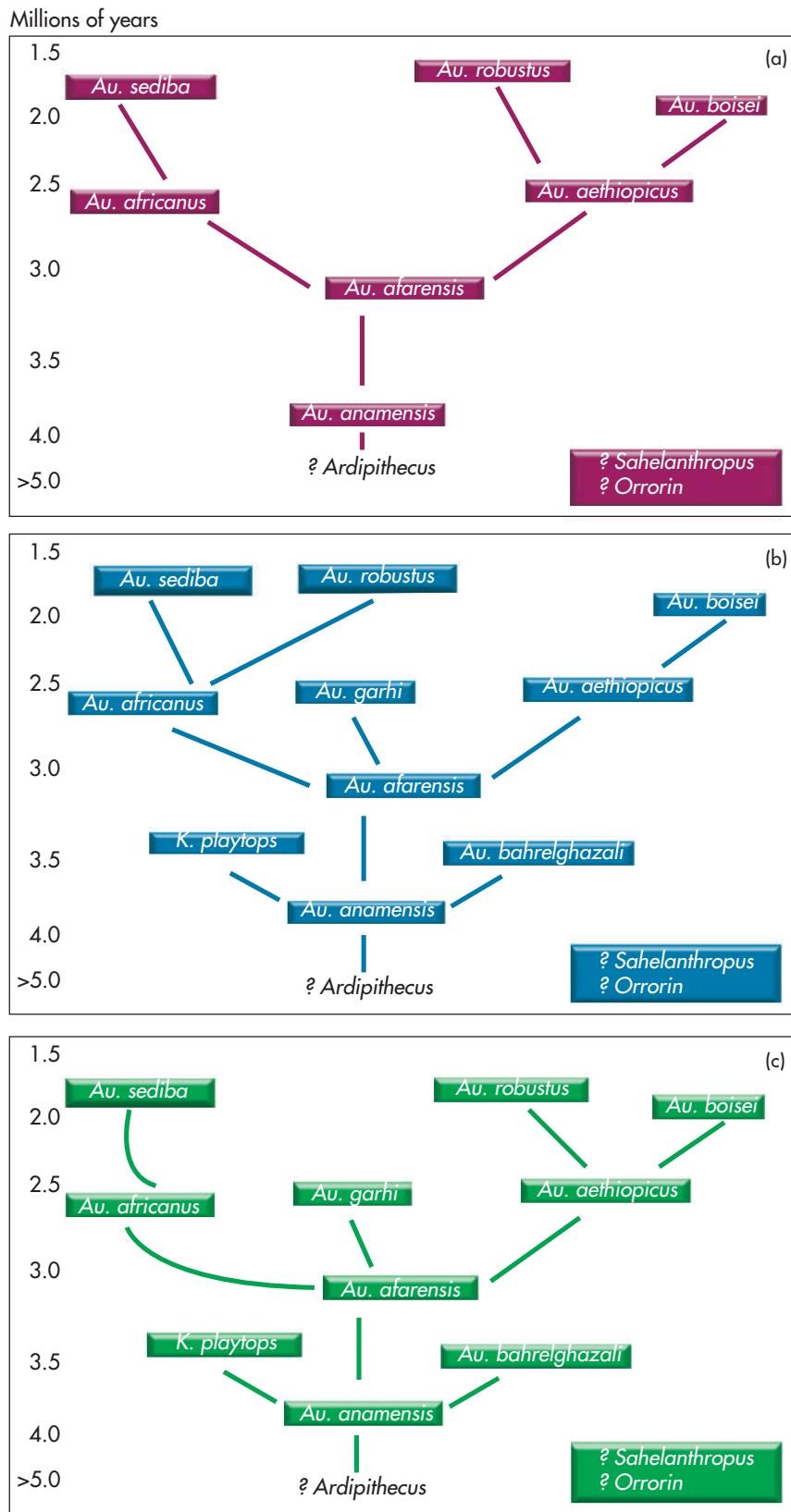


Figure 10.35 Three possible phylogenies for the australopithecines with *Au. Anamensis* as the stem ancestor and recognizing a small number of species and close relationships between (a) *Au. robustus* and *Au. boisei*, (b) a larger number of species and only distant relationship between *Au. robustus* and *Au. boisei*, or (c) a large number of species and a close relationship between *Au. robustus* and *Au. boisei*.

Summary

BECOMING A BIPED

10.1 Outline the anatomical changes necessary for becoming a biped.

- The foramen magnum is placed on the inferior of the cranium.
- Vertebral bodies bear progressively more weight lower in the column and so are largest in the lumbar region.
- The spinal column has two secondary curvatures (in the cervical and lumbosacral regions) that keep the center of gravity directly above, rather than in front of, the feet of the biped.
- The arm is not weight-bearing and is relatively gracile and foreshortened with short straight fingers.
- The femur is angled from hip to knee to bring the foot directly below the center of gravity.
- The femoral condyles are enlarged to bear greater weight, and the groove for the patella is deep to prevent dislocation.
- The foot has arches for shock absorbing and short, straight phalanges.
- The pelvis is bowl-shaped, with the ilium shortened and rotated around the side of the biped, which reorients the gluteal muscles into a position in which they can provide support while standing on only one foot.

WILL YOU KNOW A HOMININ WHEN YOU SEE ONE?

10.2 Answer the question will you know a hominin when you see one? by being able to describe the anatomical features that define the hominins.

- The canine is reduced in size and often lacks a CP₃ honing complex.
- Eventually the dental arcade is relatively parabolic in shape.
- Brain size increases, but is small in the earliest hominins.

ARDIPITHECUS AND THE FIRST HOMININS

10.3 Discuss the anatomical characteristics of *Ardipithecus* and the first hominins and the selective pressures that might have favored the origin of bipedalism.

- The earliest hominins appear in Africa between 5 and 7 million years ago.
- They include *Sahelanthropus*, *Orrorin*, and *Ardipithecus*.
- They all lack a functional CP₃ honing complex and may not be fully bipedal.
- Several kinds of scenarios have been proposed for the origin of hominids.
 - Bipedality is more energy efficient than knuckle-walking, and bipeds dissipate heat faster so they might be favored, especially in a savanna environment.
 - Postural adaptations to particular food resources (from trees, or specialized grasses) might favor bipedalism.
 - Bipeds have freed hands that can be used to carry infants, weapons, or food; the latter may be important to provisioning by males.

AUSTRALOPITHECUS AND KIN

10.4 Detail the various species of the genus *Australopithecus* and kin, including their anatomical characteristics and temporal and geographic range.

- Members of the genus *Australopithecus* are small-bodied, small-brained, bipedal African apes with both primitive and derived characters.
- Less well-known species between 2.5 and 3.5 MYA are *Au. bahrelghazali*, *Au. garhi*, and *K. platyops*.

- *Au. anamensis* is likely ancestral to *Au. afarensis*.
- Primitive characters of *Au. anamensis* include a shallow, U-shaped palate and large anterior teeth.
- Derived characters of *Au. anamensis* include somewhat smaller canine crown, thick enamel, and adaptations to bipedalism.
- *Au. afarensis* is more derived than *A. anamensis* and may be ancestral to later *Australopithecus*.
- Primitive cranial characters of *Au. afarensis* include cranial cresting (compound temporo-nuchal and sagittal); a prognathic face; a shallow, U-shaped palate; and large anterior teeth.
- Derived characters of *Au. afarensis* include somewhat smaller canine crown and root, somewhat smaller anterior dentition, and slight enlargement of the posterior dentition.
- *Au. africanus* is more derived than *Au. afarensis* and may have a unique relationship to *Au. robustus* or *Homo*.
- Derived characters of *Au. africanus* include a rounded vault (absence of cranial cresting), a somewhat flexed cranial base, and a more parabolic dental arcade.
- Small bodied and brained (around 420 cc), *Au. sediba* had long arms and a broad braincase and derived face, and some changes to the pelvis are like *Homo*.
- The robust australopithecines appear to have been an evolutionary dead end.
- Species of robusts include the East African *Au.(P) aethiopicus*, *Au. (P) boisei*, and South African *Au. (P) robustus*.
- The robust species show a suite of craniodontal adaptations for producing high bite forces including postcanine megadontia.

IMPLICATIONS OF THE AUSTRALOPITHECINE RADIATION

10.5 Show your understanding of the implications of the Australopithecine radiation by discussing the evolutionary relationships among the species in the genus *Australopithecus* and begin to explain their evolutionary radiation in Africa.

- East and South African sites differ in their geology with radiometric dates being more feasible in East Africa.
- Most scholars agree that robust australopithecines did not give rise to genus *Homo* because the robusts are so specialized.
- *Au. anamensis* and *Au. afarensis* form an ancestor descendant lineage, and later australopithecines may have arisen from this.

Review Questions

- 10.1 In what specific ways does the skeleton of a biped reflect its form of locomotion?
- 10.2 What is the CP₃ honing complex and how does it change during hominin evolution?
- 10.3 What species might be the earliest hominins and what does their anatomy and environment tell us about the selective pressures that might have facilitated their evolution?
- 10.4 How does the genus *Australopithecus* differ from the earliest hominins and how does anatomical variation across its species tell us about their adaptations?
- 10.5 In the australopithecine radiation, who is likely to be ancestral to whom and why?

Key Terms

acetabulum, p. 295
australopithecines, p. 299
breccia, p. 316
cervical vertebrae, p. 294
coccyx, p. 294
compound temporonuchal crest, p. 311
CP₃ honing complex, p. 297
cranial crests, p. 299
endocast, p. 318
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vertebral column, p. 294
zygomatic arch, p. 321

Chapter 11

Origin and Evolution of the Genus *Homo*



Learning Objectives

- 11.1** Detail the climate and the evolution of *Homo* in the Pliocene and Pleistocene.
- 11.2** Discuss the anatomical characteristics used in defining the genus *Homo*.
- 11.3** Discuss the arguments surrounding the earliest genus *Homo*, including those for recognizing one species of early *Homo* versus those for recognizing two.
- 11.4** Understand and explain the relationship among early tool use, hunting, and scavenging, including how Oldowan stone tools are made and used.

11.5 Explain who *Homo erectus* was, including the anatomical differences between *H. erectus* and *H. habilis*.

11.6 Discuss the distribution and characteristics of *Homo erectus* around the world.

11.7 Discuss the lifeways of *Homo erectus*.

For the following few weeks, the excavating brought nearly nonstop excitement, but there was some meticulous scientific work behind the celebrations . . . The bones kept coming, right up to the last moment, so we knew we would have to come back. Nearly everything we found was part of our skeleton . . . When we closed down the site for the season, on September 21, 1984, we had found more of *Homo erectus*—the classic missing link—than anyone had ever seen. The next four field seasons laboring in the pit, as we came to call the enormous excavation, would see 1,500 cubic yards of rock and earth moved by hand. Our schoolboys, who worked with us faithfully year after year, grew from adolescents to young men while the Nariokotome boy, as we took to calling the specimen, grew from a fragment of skull to the most complete early hominin skeleton ever found.

—from *The Wisdom of the Bones*, by A. Walker and P. Shipman

The discovery of the skeleton of the Nariokotome boy, the remains of a *Homo erectus* youth, dramatically changed our understanding of early *Homo*. What we know about the transition from *Australopithecus* to earliest *Homo* rests ultimately on the fossil record. And what we know of the fossil record, including the discovery of the Nariokotome boy, rests in equal parts on skill, perseverance, planning, and sheer luck. In fact, the early fossil record of genus *Homo* is remarkably sketchy in comparison to the australopithecine record, making the task of understanding the origin of the genus that much more difficult.

In this chapter we examine the early radiation of the genus *Homo*, from its beginnings in apelike hominins to the first migrations out of Africa and into other parts of the Old World. We discuss the definition of the genus and the appearance of *Homo erectus*, whose larger brain and body size may signal a shift in diet, who makes increasingly sophisticated tools, and who may use fire. And we examine early tool technologies and subsistence. Finally we consider the debate over later stages of *H. erectus*.

Climate and the Evolution of *Homo* in the Pliocene and Pleistocene

11.1 Detail the climate and the evolution of *Homo* in the Pliocene and Pleistocene.

The origin and evolution of our genus seems to be related to fluctuations in climate. During the early Pliocene, ice sheets became permanent features at both the north and the south poles. Cyclic glaciation began about 3 million years ago and became increasingly intense throughout the Pleistocene. The first appearance of fossils of the genus *Homo* around 2.7–2.9 million years ago coincides with a period of great variability in the fossil record (that is, when we see the most changes in the occurrence of different species of mammals).

Many workers have argued that these climatic fluctuations were critical to the origins of our lineage, the hominins, in Africa. For example, Elisabeth Vrba has proposed that quick changes, or pulses, in climate resulted in “turnovers,” or

extinctions in animal communities. Her turnover-pulse hypothesis suggests that during some of these pulses we also see the origin and extinction of some hominin groups. René Bobe and Anna Behrensmeyer also see changes in abundance of mammalian species in response to climate, especially between 4 and 2 million years ago. They suggest that the origin of our genus, *Homo*, coincided with the periods of greatest climatic variability.

It may be that humans are adapted to such periods of climatic instability and that our intelligence and adaptability may have been honed as a result of it (Potts, 1996; Antón et al., 2014). Around 2.5 million years ago, glacial cycles began to become more severe. Oxygen-isotope curves suggest the glaciation was so severe that it lowered sea levels enough to connect island Southeast Asia to mainland Asia for the first time. This was important as hominins started to move out of Africa. Starting about 1.8 million years ago, a series of glacial events intermittently lowered sea levels enough to connect mainland and Southeast Asia, allowing animals and hominins like *H. erectus* to cross back and forth between the two at times and to be isolated from one another at other times. Before hominins left Africa, however, the selective pressures of changing climate and diet resulted in changes to their skeleton that we can see in the fossil record.

Defining the Genus *Homo*

11.2 Discuss the anatomical characteristics used in defining the genus *Homo*.

Recall that a genus name implies a certain adaptive strategy, so the switch from *Australopithecus* to *Homo* should tell you to expect to see a suite of adaptive differences between species in the two genera. In general, genus *Homo* differs from australopithecines by having a larger braincase; a smaller, less projecting face; smaller teeth; and eventually a larger body and more efficient striding bipedalism. These features may be related to an adaptation that includes a shift to a more animal-based diet, greater ranging, and greater food processing through tool use. However, early members of the genus *Homo* differ less strongly from australopithecines than do later members and therefore are harder to distinguish from them. In fact, the first species of *Homo* are not all that different from some australopithecines in some ways.

There is much taxonomic debate over the application of species names to fossil *Homo*. Depending on the scientist, earliest *Homo* is conceived of either as a single, variable species (*H. habilis*) or as multiple, less variable species (usually *H. habilis*, and *H. rudolfensis*). Similarly, *H. erectus* is seen as either one species or two species, *H. ergaster* and *H. erectus*, and the presence of any of these taxa in Europe and the transition to modern humans is hotly debated. All this disagreement results in part from the paucity of the fossil record, differences in species concepts (lumpers versus splitters), and the inherent difficulty of applying a static classification system to the dynamic process of evolution.

Earliest Genus *Homo*

11.3 Discuss the arguments surrounding the earliest genus *Homo*, including those for recognizing one species of early *Homo* versus those for recognizing two.

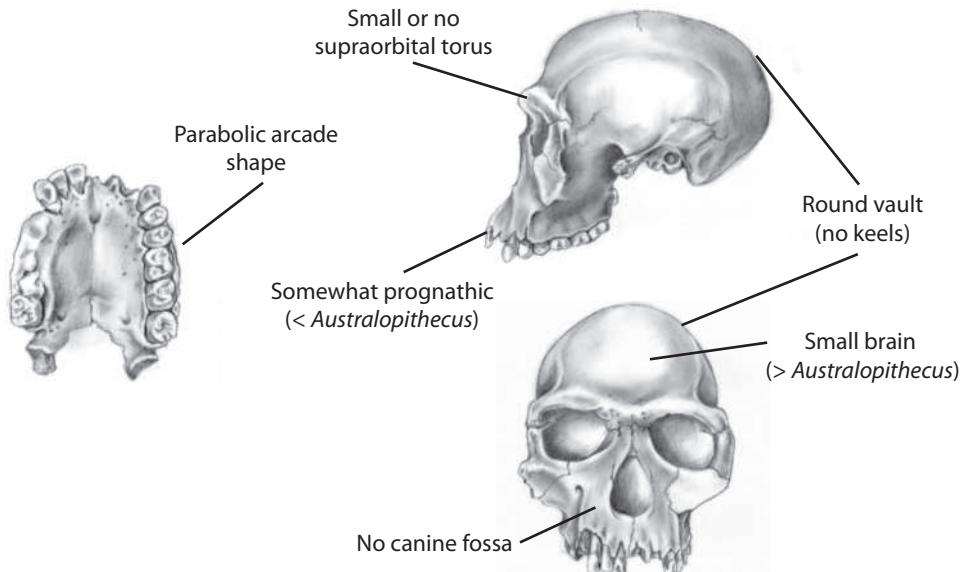
The genus *Homo* appears to have originated sometime between 2.5 and 3 million years ago, but its origins are obscure in part because the fossil record for this time is not well known. Until recently, the earliest fossil *Homo* were fragmentary remains

dating to 2.3–2.4 million years old from Hadar and Omo in Ethiopia, Uraha in Malawi, and possibly the Chemeron Formation in Kenya. Hints from isolated teeth in Ethiopia suggested the emergence of more derived species about 400,000 years earlier, or in the 2.7–2.9 million year range, but the specimens were too incomplete to be certain. This age range was confirmed recently when early *Homo* fossils dated to 2.75–2.8 million years old were announced from Ledi-Geraru, Ethiopia (Villmoare et al., 2015). As we've seen with other early ancestors, the Ledi-Geraru remains show a mix of primitive and derived characters. The dentition, especially the P_3 (which is more symmetrical) and molars align the fossils with *Homo* as do some features of the mandible including its height and where the ramus ascends. But some features, especially of the mandibular symphysis, are more primitive and similar to the condition in *A. afarensis*. This anatomy establishes that the earliest changes in the *Homo* lineage include those to the teeth and jaws, but because there are no intact crania it remains unclear what brain size might have been. These early remains give rise to more complete specimens known from after 2 million years ago that allow the recognition of multiple species. While most of the discussion of early *Homo* centers around the relatively complete crania from East Africa, hints of early *Homo* are also to be found in South Africa (see Insights and Advances: *Homo naledi* and The Cradle of Humankind on pages 336–337).

Homo habilis (1.9–1.4 MYA)

In the 1960s, Louis and Mary Leakey discovered a nearly 2-million-year-old juvenile partial skull at Olduvai Gorge, Tanzania. Olduvai Hominid 7 (OH 7) possessed a brain larger (at about 690 cc) than any known *Australopithecus* and differed markedly from the "robust" *Australopithecus*, *Zinjanthropus boisei*, also from Olduvai (see Chapter 10). Louis Leakey, Philip Tobias, and John Napier included OH 7 in the new species *Homo habilis*, or "the skilled human or handy man," referring to the use and manufacture of stone tools (Figure 11.1). This behavior, the authors argued, was the adaptive plateau of the genus and differed from *Australopithecus*. Since that time the unique association between *Homo* and stone tools has come into question, and most anatomists would argue that the species designation should be made on morphological not behavioral

Figure 11.1 Key anatomical features of *Homo habilis* include reduced facial size, a parabolic palate, and some brain enlargement.



grounds in any event, but the evidence for an early, relatively small-brained species of *Homo* has been supported.

In the early 1970s at Koobi Fora on the eastern shore of Lake Turkana Richard Leakey's team found abundant additional fossils of *H. habilis* at Koobi Fora, Kenya and these along with other fossils from Olduvai Gorge form the main sample for this species. The earliest date to about 1.9 million years old, and a recently discovered palate from Ileret Kenya extends the time range of *H. habilis* to 1.4 million years ago (Spoor et al., 2007) indicating some temporal overlap with *H. erectus* (Figure 11.2). The best known *H. habilis* specimens are two relatively complete crania from Koobi Fora: a small-brained cranium with a fairly complete face known by its museum catalog number, KNM-ER 1813, and another braincase and associated mandible, KNM-ER 1805. Both have small brains at 510 and 580 cc, respectively, much smaller than OH 7's. But careful work by Fred Spoor's team on the OH 7 mandible confirms its association with the Koobi Fora fossils (Spoor et al., 2015)—so it would seem that *H. habilis* included a range of smaller and larger brain sizes.

Compared to *Australopithecus*, *H. habilis* has a somewhat expanded average brain size, smaller jaws, molar and premolar crown sizes, more rounded cranial vaults (although some do show a bit of cresting) and less prognathic faces. But it also is a bit more primitive retaining more parallel sided tooth rows and relatively large anterior teeth compared to other early *Homo*. For many years after its discovery *H. habilis* was the only early *Homo* species accepted, but since the 1970s there have been a few clues that there might be other species.

Although some of these specimens are bigger-brained than others, none show the extensive cranial and absolute postcranial enlargement seen in *H. erectus*. Bernard Wood and Marc Collard (1999) suggested that the smallest-brained early *Homo* resembles larger-brained australopithecines and should be relegated to *Australopithecus* because of similarities that suggest they shared similar patterns of behavior and ecology. Wood and Collard particularly focus on differences in the postcranial skeleton between *H. erectus* and *H. habilis*. In this book we use *H. habilis* rather than *Australopithecus habilis*, because the postcranial fossil record is so sparse and hard to assign even to species that we are reluctant to use it as evidence for including or excluding species from the genus. Nonetheless, Wood and Collard have given important food for thought to researchers studying the emergence of the genus *Homo*.

Homo rudolfensis (2.1–1.78 MYA)

In the early 1970s, Richard Leakey's team also discovered a nearly intact cranium that they referred to *H. habilis*, but which others have used as the type specimen of a separate *Homo* species—*H. rudolfensis*. This cranium, known by its National Museums of Kenya catalog number KNM-ER 1470, is approximately 2.1 million years old and has a relatively large cranial capacity of 775 cc (Figure 11.2). Although assigned initially

Figure 11.2 The crania and especially the faces of KNM-ER 1813 and 1470 differ enough that some scientists include them in two different species. See Table 11.1.



Table 11.1 Cranial Differences between Key Early *Homo* Fossils

| | KNM-ER 1813 | KNM-ER 1470 |
|--------------------|-------------------|----------------------------|
| Cranial capacity | 510 cc | 775 cc |
| Browridges | Moderate to small | None |
| Arcade and Face | Parabolic | Flat anterior palate |
| Dental proportions | Larger premolars | Narrow premolars to molars |

Insights and Advances

Homo naledi and The Cradle of Humankind

Fifty kilometers northwest of the teeming urban sprawl of Johannesburg a series of limestone caverns have yielded an impressive array of human ancestors. In 1999, UNESCO recognized the importance of the region by designating the area a World Heritage Site. Formally known as *The Cradle of Humankind*, the site comprises many important *Australopithecus* sites such as Sterkfontein, Swartkrans, Kromdraai, and Malapa (Figure A and see Chapter 10). In the early 1900s, before hominin fossils were known from East Africa, the cradle produced important specimens of *A. africanus* at Sterkfontein and *A. (P.) robustus* from Kromdraai and Swartkrans, which were studied and analyzed by Robert Broom, Raymond Dart, Philip Tobias, John Robinson, and others. Originally, fossil discoveries were accidentally made during limestone quarrying, but scientists soon started the deliberate investigation of similar areas, and Sterkfontein in particular became the extended focus of excavation by Tobias, Ron Clarke, and others. More recently Sterkfontein has seen the successful application of $^{26}\text{Al}/^{10}\text{Be}$ dating methods to estimate the age of the little foot skeleton to 3.67 million years ago (see Chapter 10). And a spectacular new set of finds from the Rising Star cave system has been given the new species name *Homo naledi*.

Among the many thousands of specimens of *Australopithecus* from the area there are also specimens of early *Homo*. Many of the early *Homo* remains, like many fossils elsewhere, are isolated teeth. Fred Grine has compared these to *Australopithecus* from East and South Africa and to early *Homo* from East Africa and argued for the existence of a species of early *Homo* that may not be either *H. habilis* or *H. rudolfensis*. In addition, fragmentary cranial remains from Swartkrans show some similarities to the *H. erectus* fossils from Dmanisi, Georgia.



Figure A Geographic distribution of early hominins. Hominins are limited to the continent of Africa until about 1.7 million years ago. Some of the important sites for australopithecine and other early hominin fossils are located on the map. Although most known sites are in eastern and southern Africa, *Australopithecus* likely inhabited most of the African continent.

In the last decade two important new sites have been found in the cradle, both of which have been argued to relate to early *Homo*. We learned in Chapter 10 about *Australopithecus sediba* discovered from the site of Malapa and argued by Lee Berger's team to have an ancestral relationship to *Homo*. In 2013 a cave system called Rising Star yielded a plethora of fossil remains of a large number of individuals. Berger's team found the Rising Star fossils deep in a cavern system accessible only after an arduous climb and a squeeze through some very tight spots (Figure B). Indeed, the chamber was so hard to reach that the excavators were a specially selected crew of petite caver/archaeologists who were remotely observed by larger members of the crew. Although it is initially a gentle walk into the cave, to reach the chamber with the fossils requires a squeeze through an opening just 7 inches wide! Using social media, the expedition finds were blogged about and tweeted in real time. From this we know that during the three week excavation more than 1,000 fragments from all parts of the skeleton were recovered even though only a small part of this Dinaledi chamber was excavated (Figure C). And in the waning days of the expedition a second chamber was discovered.

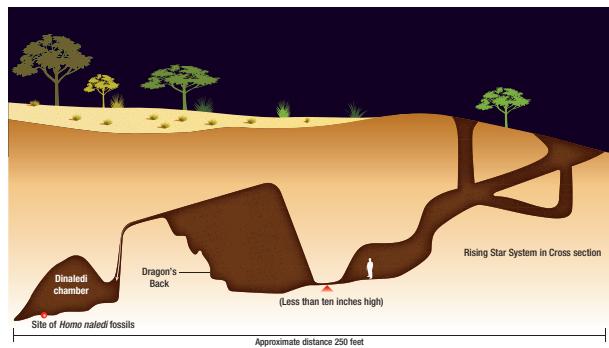


Figure B Cross-section through the approach to the Dinaledi Chamber. To access the chamber an easy walk is followed by a tight squeeze, steep climb, and narrow chute.



Figure C Scientists examine recently retrieved remains from Dinaledi.

The cave system is just a few meters from Swartkrans where both *Homo* and *A. (P.) robustus* fossils have been found suggesting that the Dinaledi remains might represent either genus (or both). While the paleoanthropological community waited, the team ran an intensive workshop to study what ended up being over 1500 pieces. In September of 2015 the answer was in, the Rising Star team announced the new species *Homo naledi* (naledi means star in the local dialect). In two papers in the digital journal eLife they reported on the fossils and on the cave geology. The fossils represent the remains of at least 15 individuals, include parts of nearly all the bones of the body, and encompass a range of ages, but are mostly those of the young and the old (Figure D). And the crania have some telltale signs that they belong to the genus *Homo*. However, the fossils are a funny mix of primitive and derived characters – the brain size is measurable in two specimens and is just 465 and 560 cc's, respectively (Figure E). That's about the size of most australopithecines, even though a well-preserved tibia from Dinaledi suggests at least one tall individual. And some aspects of the teeth (Figure F) and the postcranial skeleton, are also primitive but others are more derived. This mix of primitive and derived features, the team argues, doesn't seem to match any presently known species, hence the new name. And they would argue, the mix of features in the species may tell us something about the origin of the genus itself.

But the age of the fossils and how they got into the remote chamber remains unknown. Since the finds are in cave deposits, uranium series methods or $^{26}\text{Al}/^{10}\text{Be}$ methods may prove useful for dating (see Chapter 8). Indeed, the Dinaledi chamber has a series of flowstones associated with the fossils that should be datable using uranium-series techniques, but so far the team has not been able to yield an age. So we don't know for sure that these fossils speak to the origin of *Homo*, they

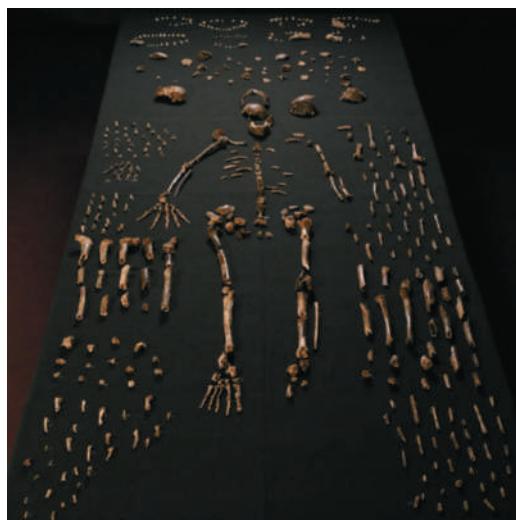


Figure D The fragments from Dinaledi exhibited in anatomical position. Note these represent at least 15 individuals and overlapping body parts.

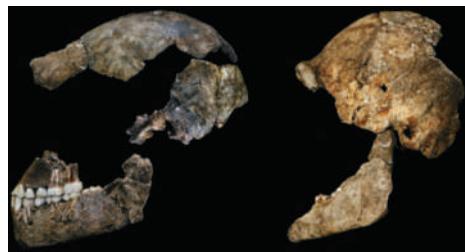


Figure E Two more complete crania of *H. naledi* have cranial capacities of 465 and 560 cc's.



Figure F A view of the lower jaw of *H. naledi* reveals primitive and derived traits.

could be of an entirely different time period altogether. The Cradle of Humankind preserves archaeological and fossil sites of later *Homo* as well as earlier *Australopithecus* so there is no fundamental reason why *H. naledi* couldn't be of one of these ages. What the geologists do know is that this is not a set of hominins that died in one single catastrophic event. Instead, the chamber provides evidence that the sediments and bones accumulated over time and through multiple depositional events. And so far they don't look like they accumulated like so many other South African cave assemblages have—through the action of carnivores or porcupines (see Chapter 10); for one thing, none of the remains show signs of having been gnawed or punctured, signs that are frequent in other assemblages. But why there were so many hominins in such a hard to reach spot is a mystery – Could there be an unknown cave entrance? Could this signal purposeful disposal of the dead?

The *Homo naledi* fossils are so abundant that it will take the scientific community a long while to study and understand them. Immediately some scientists have argued they represent two species and others have argued that the remains represent a single well known species like *H. erectus*. Some agree that this could be a sign of purposeful disposal of the remains, others suggest that there are other perhaps more likely explanations. Whatever your position, *H. naledi* suggests that indeed, we are just beginning to sample the richness of the Cradle of Humankind.

to *H. habilis*, many scholars thought that the differences between the largest (1470) and smallest Koobi Fora early *Homo* crania were too great to fall within the variation of a single species. The smallest (KNM-ER 1813) has a brain almost one-third smaller (only 510 cc) than the largest specimen and a differently proportioned face. For many years, there were too few fossils to be certain. Was the single specimen KNM-ER 1470 just an odd *H. habilis*? Or, was its morphology evidence of another species of early *Homo*.

In the 2000s, the mother daughter team of Meave and Louis Leakey returned to Koobi Fora to take up the search, and they found that missing evidence in the form of a small face and a large jaw that match the anatomy of KNM-ER 1470 (Leakey et al., 2012). Importantly, the face (KNM-ER 62000), although diminutive, shares the same anatomy as 1470. The front of the maxilla is foreshortened and flattened across the anterior teeth, and the premolar is reduced as well. The large mandible (KNM-ER 60000) is the most complete early *Homo* mandible known and matches the proportions of the upper jaws. Apparently, *H. rudolfensis* included both large and small individuals.

The two species of early *Homo* seem to be very different in terms of facial anatomy, but not size, and it is unclear which of the two species of early *Homo*—*H. habilis* or *H. rudolfensis*—gave rise to later species of *Homo*. *H. rudolfensis* is the more derived species, but its facial anatomy doesn't seem to anticipate that of *H. erectus*. On the other hand, *H. habilis* is more primitive and probably makes a better more generalized ancestor for *H. erectus*. Whoever gave rise to later *Homo*, the anatomical differences between the two early species suggest there were at least two species of genus *Homo* living sympatrically in East Africa between 1.5 and 2.0 million years ago along with sympatric *Australopithecus*. Their anatomy suggests they may have partitioned the environment based on resources (much as we saw with the australopithecines).

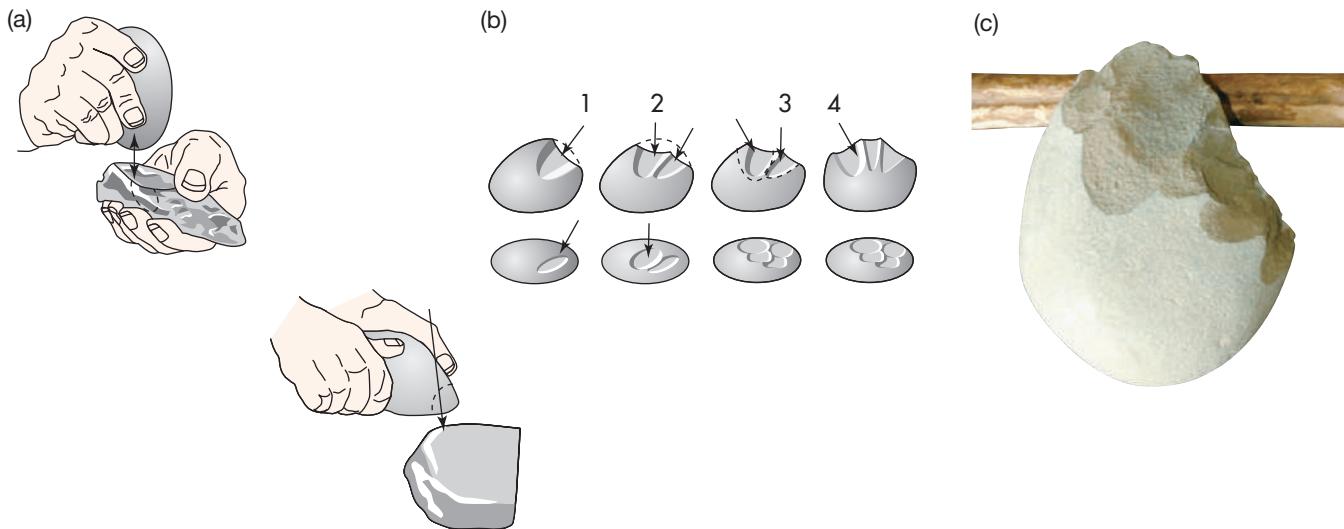
However, some researchers continue to argue that the largest and smallest early *Homo* fossils are a male and a female of the same species. This single species would be known as *H. habilis* (because of the priority of the name historically) and may ultimately have given rise to *H. erectus*. Whatever you call these fossils, there is clear evidence that they made and used stone tools. Whether they were the first or the only hominins to make stone tools is debated, but we know that this practice began in earnest around 2.5 million years ago—although earlier tools are known.

Early Tool Use, Hunting, and Scavenging

11.4 Understand and explain the relationship among early tool use, hunting, and scavenging, including how Oldowan stone tools are made and used.

As we saw in Chapter 10, there is some evidence of stone tool use around 3.3–3.4 million years ago, but it is rare. A set of 3.4 million year old cutmarks from Dikika, Ethiopia are argued to be evidence of even earlier tool use (McPherron et al., 2010), and 3.3 million year old stone tools themselves were more recently announced from West Turkana, Kenya (Harmand et al., 2015). We don't know for certain which early hominin made which tools because we don't find hominin fossils actually holding the tools. We can only infer tool use by the association between tools and hominin remains in the same excavations. Even this is dangerous, because antelope are the most abundant fossils found in association with stone tools, and we are quite sure the antelope are not the toolmakers! If the age for the West Turkana tools is correct, the only option for a hominin maker had to be an australopithecine. The next known stone tools are about 2.6 million years ago, also from Ethiopia. And then around two million years ago, well into the australopithecine radiation, we start to see the ubiquitous use of stone tools. And the level of usage from then on seems to signal a shift

Figure 11.3 Oldowan tools are simple flake tools struck from a core using (a) a hammerstone or an anvil technique. The flakes are often removed from only one side of the core (b), and are useful for cutting through hides, muscle, and plant material. (c) An experimentally made Oldowan type core.



in the importance of stone technologies for how hominins survived. Because of the timing, we think that the foraging shift these tools represents is likely to be telling us about adaptive strategies in *Homo* not *Australopithecus*.

The earliest tools are known as the **Oldowan** industry, so named for their first discovery at Olduvai Gorge in Tanzania (Figure 11.3). We refer to stone tools made in a particular way or tradition as a **tool industry**. Oldowan tools consist mainly of **cores**, lumps of stone, often river cobbles modified from the original rock by the removal of pieces from it, and **flakes**, the small fragments taken from the core. Archaeologists used to think the core itself was the tool, but experimental evidence suggests the flakes were used as cutting and scraping tools. The cores probably were used to produce flakes until they became too small and were discarded (Schick & Toth, 1993). Flakes can be extremely sharp and are effective at cutting through tough animal hides and removing meat from bones. Other Oldowan tools called **hammerstones** were used to crack open the bones of large animals to extract marrow and to remove flakes from cores. Oldowan tools are deceptively simple in appearance; if you held one you might not be able to distinguish it from a naturally broken piece of rock. However, archaeologists, some of whom are proficient stone toolmakers themselves, use various clues to distinguish stone tools from naturally broken stone.

Tool making was first and foremost an adaptation to the environment of the late Pliocene. Through the use of stone tools hominins could cut open animal carcasses and break into the fat stored in their bones. These animal foods became an increasingly important adaptive strategy for early humans. Early *Homo* seems to have carried tools with them rather than constantly discarding or continually making them anew. Initially, stone wasn't moved far from its source, but used relatively locally, say within a kilometer or so. But by around 2 million years ago, stone was being moved over 10 km (about 6.25 miles) from its source location, signalling a very strong energetic commitment to transporting and using it (remember, rocks are heavy, and the toolmakers are walking). If early humans carried their tools around, it must be because those tools were an important part of their daily routine. Just think about the things you choose to put in your backpack each day—like your cell phone, books, laptop and wallet—and what that means about their importance in your daily life.

Oldowan

The tool industry characterized by simple, usually unifacial core and flake tools.

tool industry

A particular style or tradition of making stone tools.

core

The raw material source (a river cobble or a large flake) from which flakes are removed.

flake

The stone fragment struck from a core, thought to have been the primary tools of the Oldowan.

hammerstone

A stone used for striking cores to produce flakes or bones to expose marrow.

butchering site

A place where there is archaeological evidence of the butchering of carcasses by hominins. The evidence usually consists of tool cut marks on fossilized animal bones or the presence of the stone tools themselves.

quarrying site

An archaeological site at which there is evidence that early hominins were obtaining the raw material to make stone tools.

home base

Archaeological term for an area to which early hominins may have brought tools and carcasses and around which their activities were centered.

Archaeologists specializing in the study of stone tools have categorized the patterns of tool use at various Oldowan sites in East Africa. Some of these are thought to have been **butchering sites**: A variety of mammal bones, some bearing cut and percussion marks made by stone tools, have been found with such tools. A site at Olduvai Gorge contains the remains of a hippo with cut marks on its bones along with scores of flakes, suggesting the hippo had been butchered by early hominins. Stone implements are found in great abundance at **quarrying sites**, where hominins went to obtain the raw material for the tools. A third type of site is what the archaeologist Glynn Isaac (1978) called a **home base**. Isaac hypothesized that hominins repeatedly brought butchered carcasses back to a more comfortable central place, perhaps near a shade tree or a water hole, where they slept and ate in greater safety than at the site where the animal was killed. At such a site, the hominins would have been manufacturing or refining tools as well. Other archaeologists are skeptical of this idea, arguing that natural processes such as movement of remains by water, wind, and animals may account for what look like human-created bases of activity. Still others think that the accumulations may represent caches of material made by hominins for their later use rather than campsites. However they formed, after 2 million years ago, sites with stone tools are a ubiquitous part of the human fossil record.

Despite the enormous amount of evidence of meat eating, in the form of butchered bones, the debate about the role of meat in the early human diet has a long and tumultuous history. We don't know how often a group of early *Homo* might have actually eaten meat or how important meat (or marrow) was in their diet. Did a group of *H. habilis* butcher and consume one large mammal per week? Per month? Per year? Did all members of the group participate in this butchering activity and in the feast? How much did the incorporation of stone tool manufacture and annual consumption affect other aspects of early hominin behavior, ecology, physiology, and biology? It seems that after 2.5 million years ago, meat eating took on increasing importance, but whether that also included hunting is a point of some contention.

Hunting and Scavenging

We would like to know whether our own lineage arose with the help of hunting or scavenging because each of these activities entails a different set of behavioral adaptations. There are currently three main models for how early hominins acquired carcasses. Perhaps bands of early humans courageously attacked and slaughtered large and dangerous game (hunting). Or maybe they fought off large predators such as saber-toothed cats to gain access to significant amounts of meat (confrontational scavenging). Or they might have crept nervously up to decomposing, nearly stripped carcasses to glean a few scraps of meat and fat (passive scavenging). Mostly, however, discussion focuses on general differences between hunting and scavenging.

In 1966 a perspective on human evolution known as "Man the Hunter" was presented in which men played the important role of obtaining the highest-quality nutrients and the calories that their households would use. The original proposal, put forward by Sherwood Washburn and Chet Lancaster, set out to explain the 3.5-fold increase in human brain size and complexity as "evolutionary products of the success of the hunting adaptation." According to Washburn and Lancaster, "men hunt while women gather." This scenario also implied that men had a natural right to occupy the glamour role of clever-minded forager, meat provider, and conqueror in human societies because hunting selected for intelligence. Ever since, many scenarios of human evolution have focused on male activities rather than female ones as the core human adaptations.

Many anthropologists took issue with the "Man the Hunter" perspective, because in some of the traditional societies that are most vaunted for the man's role in hunting, up to 85% of the protein obtained by a household came not from men but from women

gathering foods such as nuts, tubers, and small animals (Tanner & Zihlman, 1976). The reaction to “Man the Hunter” had the effect of swinging scientific research toward examining the possibility that *H. habilis* and kin were scavengers, not hunters, and that they were not necessarily the sole accumulators of fossil bone (Brain, 1981). Some fossilized carcasses even seem to have been chewed on by carnivores first and butchered later. When anthropologists Rick Potts and Pat Shipman studied the bones of animals from Oldowan sites, they found cut marks made by ancient, sharp-edged tools as well as tooth marks made by the gnawing of contemporaneous lions, hyenas, leopards, and other carnivores (Figure 11.4). When they examined these more closely, they saw that on some of the bones, the human-made cut marks were on top of the carnivore tooth marks, evidence that humans were cutting flesh from the bones *after* they had already been chewed by a predator. The implication was clear: On at least some occasions, hominins were scavengers, not hunters.

To be a scavenger rather than a hunter affects every aspect of daily life. Instead of depending on an ability to chase down and kill elusive prey, a scavenger relies on finding the kills made by other animals and then somehow taking some of the meat. Many scavengers, such as vultures and jackals, are tolerated by larger carnivores at a kill; would early hominins have been? Through the 1980s, archaeologists adopted new experimental approaches to understanding the role that the hominins may have played in those ecosystems (see Insights and Advances: Understanding the Meat-Eating Past through the Present on page 342). These studies suggested that ample scavenging opportunities existed for hominins 2 million years ago. By the 1990s, field studies of meat eating by wild chimpanzees showed that even without tools, apes can capture and consume large quantities of small mammals (Boesch & Boesch, 1989; Stanford, 1998). And John Yellen (1991) showed that modern hunter-gatherers consume large amounts of meat in the form of small mammals, none of which would leave any archaeological evidence had early hominins done the same. Archaeologists began to reinterpret the models for hominin scavenging behavior, arguing that aggressive, active carcass piracy was far more likely than passively locating dead animals that were already mostly consumed by primary predators (Bunn & Ezzo, 1993).

Early views of the hunting and scavenging debate tended to emphasize a black or white approach, which is rarely the way that living creatures behave. Instead perhaps early *Homo* acquired animal resources in any form they could, through both hunting for small animals and scavenging carcasses. Modern foragers do the same. Cultural diversity in modern chimpanzee populations suggests that some populations of early genus *Homo* could have hunted, whereas others may have preferred scavenging, and both strategies probably were included in a flexible behavioral repertoire. Regardless of whether meat was obtained by hunting or scavenging, the archaeological record shows that hominins increasingly used stone tools to assist in the consumption of large animals. The two innovations of stone tool manufacture and animal resource exploitation undoubtedly shaped much of subsequent human evolutionary history.

Figure 11.4 Carnivores such as these wild dogs have skeletal adaptations for eating meat. In contrast, early *Homo* used stone tools to obtain meat and marrow.



Who Was *Homo erectus*?

11.5 Explain who *Homo erectus* was, including the anatomical differences between *H. erectus* and *H. habilis*.

Sometime around the Plio-Pleistocene boundary, about 1.8 million years ago, hominins underwent a major adaptive shift. This is reflected in the fossil record by body

Insights and Advances

Understanding the Meat-Eating Past through the Present

In the 1970s and 1980s Glynn Isaac, an innovative experimental archaeologist who thought the past could be better understood through direct analogies with the present, mentored a series of students who turned to the behavior and ecology of living carnivores to understand how early hominins might have used animal resources. In many modern ecosystems, even after a predator is done eating, the carcass provides rich sources of fat and protein in the form of bone marrow and brain that support a community of scavengers, a community that might have once included early hominins.

Field studies of lions, hyenas, and other African carnivores on the Serengeti showed that early hominins would have had an ample supply of resources from carcasses left over after kills by lions and leopards, especially in woodlands located near streams where scavengers like hyenas are often delayed in finding the kills (Blumenschine, 1987; Figure A). And when eating predators and scavengers follow a customary sequence in which they rapidly devour the hindquarters, then the ribs and forelegs, followed by the bone marrow, and finally the contents of the head (Blumenschine, 1986).

This sequence can be used to identify hunting and scavenging in the fossil record. Because scavengers eat the remains of what hunters leave behind, they should eat a disproportionate quantity of the last body parts with edible meat. Blumenschine and his students have expanded these actualistic studies for understanding hominin access to kills and interpreting what kinds of predators were involved based on the tooth marks left on bones. Tanzanian archaeologist Jackson Njau has identified crocodiles as important predators (Njau & Blumenschine, 2006), and Briana Pobiner uses tooth marks on fossil bone to distinguish between different-sized carnivores (Figure B).

Another of Isaac's students, archaeologist Curtis Marean (1989) thinks that early *Homo* could have occupied a scavenging niche simply by cleaning up after saber-toothed



Figure A Hyenas and other scavengers may have competed with early hominins for access to carcasses.

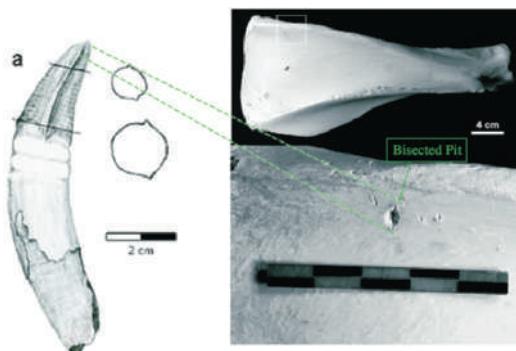


Figure B Crocodiles leave distinctive bite marks that reflect the shape of their teeth, as shown by this work by Njau and Blumenschine (2006).

cats. Saber-tooths were among the top predators in many East African habitats 2 million years ago. Some were powerful, solitary hunters that could kill animals with much more meat than they themselves could hope to eat or store, leaving a potential niche for a scavenging hominin to fill.

And Isaac's students Nicholas Toth and Kathy Schick used actualistic studies to understand how sites formed at archaeological localities such as Koobi Fora, Kenya (Schick & Toth, 1993). Toth learned to make stone tools and using these replicas a group of archeologists butchered the carcass of an elephant (which had died of natural causes in a zoo and was donated as a research subject). They showed that using only the simple core and flake tools of the Oldowan industry, early humans could have sliced through the thick hide of large animals.

Collectively, their work supports the possibility that early humans, such as *H. habilis*, could have made a good living simply by scavenging already dead animals with the help of tools (Figure C). However, it doesn't rule out the possibility of hunting, especially of smaller prey. And perhaps most important to remember is that any kind of butchery of large prey and movement of parts of a carcass to another place for consumption, alone or in a group, may have had important implications for hominin sociality.

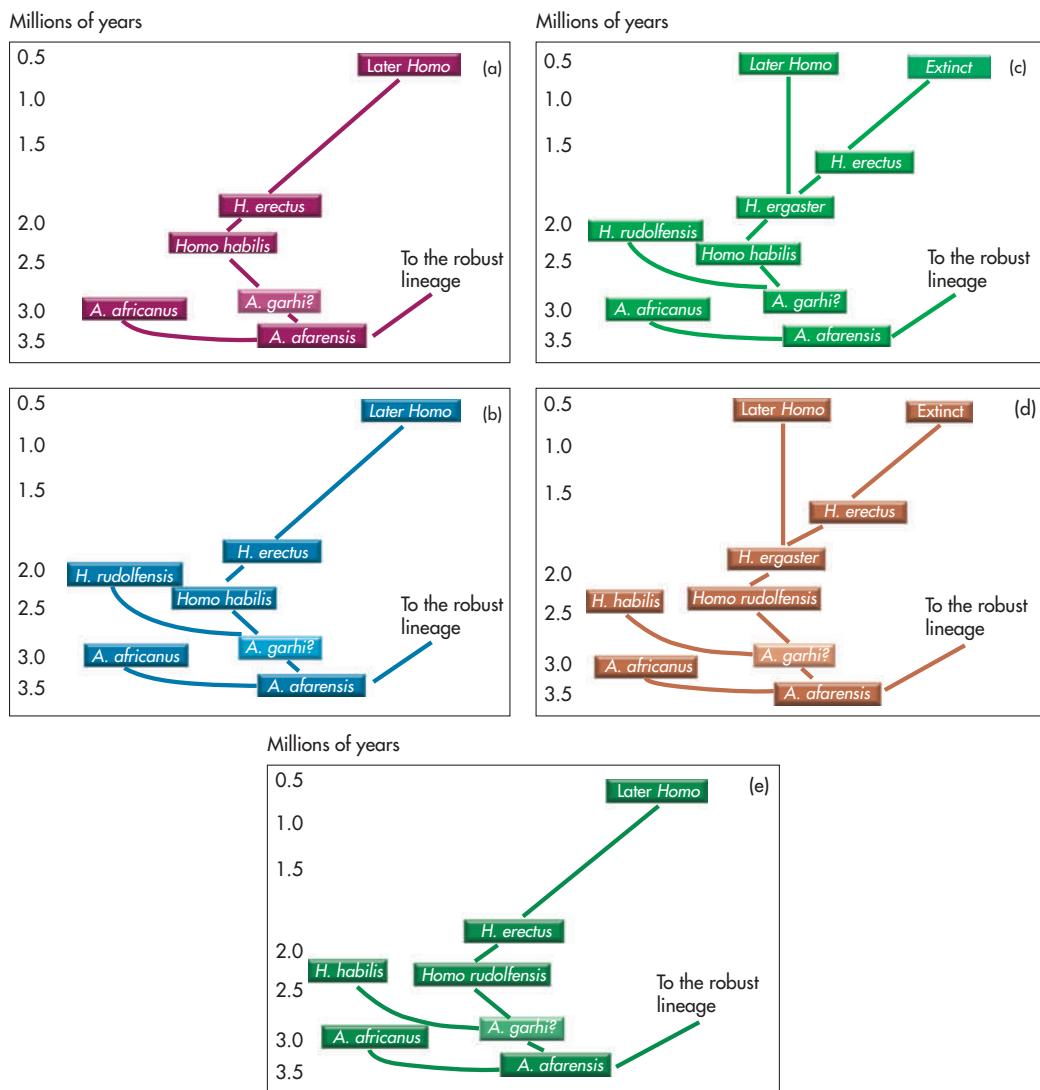


Figure C Animal carcasses like this South African wildebeest provide important nutrition for both hunters and scavengers.

and brain size increases and tooth size decreases that may signal an increase in diet quality and a larger home range, perhaps similar to that of modern humans. These changes may have been this group's response to environmental and climatic changes during that time period. Remember, however, that while the early *Homo* lineage was responding to these climate changes by adaptive shifts, another—the robust australopithecines—responded not by changing but by intensifying its previous adaptation to tough object feeding. A bit more than a million years ago, these robust australopithecines went extinct, probably having become too specialized to accommodate climate fluctuations and changes in their favored food items.

H. erectus appeared in Africa about 1.8–1.9 million years ago and seems to have been the first hominin to leave the continent, probably around 1.7 or 1.8 million years ago (Figure 11.5). Some paleoanthropologists call these earliest *H. erectus* by another name, *Homo ergaster* (Figure 11.5) (Wood & Collard, 1999). Whatever you call them, these hominins quickly left Africa. But just why they left is a source of debate. What is certain is that dispersal probably was the result of multiple movements of small groups of hominins into new territories.

Figure 11.5 Possible phylogenies for early *Homo*.



supraorbital torus

Thickened ridge of bone above the eye orbits of the skull; a browridge.

angular torus

A thickened ridge of bone at the posterior inferior angle of the parietal bone.

occipital torus

A thickened horizontal ridge of bone on the occipital bone at the rear of the cranium.

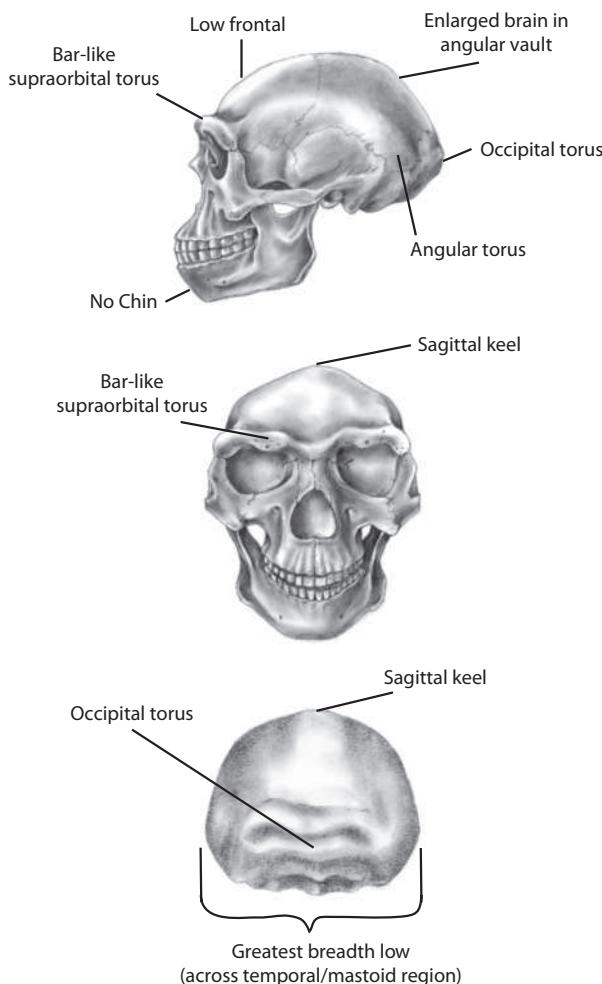
sagittal keel

Longitudinal ridge or thickening of bone on the sagittal suture not associated with any muscle attachment.

metopic keel

Longitudinal ridge or thickening of bone along the midline of the frontal bone.

Figure 11.6 Major features of *Homo erectus* include increased brain size, an angular vault, and cranial superstructures (such as tori and keels).



The last members of the species go extinct a million to 1.5 million years later, being found in the middle Pleistocene of Indonesia and China. Thus, *H. erectus* was an extremely successful species that overlapped for some time with hominins from other parts of the world, such as Europe and Africa, which seem to be transitional between *H. erectus* and either Neandertals or modern humans (see Chapter 12).

Anatomical Features

H. erectus is characterized by a somewhat larger body and brain, small teeth, and a uniquely shaped skull compared with earlier *Homo*. In its postcranial skeleton *H. erectus* shows the beginnings of a modern human body plan, larger body size, and with perhaps a less funnel-shaped thorax than earlier hominins and living apes.

THE SKULL AND TEETH *H. erectus* crania are easily identified by their shape (Figures 11.6 and 11.7). The brain case is thick-boned and robust, much longer than it is wide, relatively low and angular from the side, and pentagonal in rear view. The angularity of the skull is enhanced by a series of cranial superstructures, regional thickenings of bone along certain sutures and across certain bones. These include thickenings such as the prominent bar-like **supraorbital torus** or browridge on the frontal, a thickened **angular torus** on the back of the parietal, and the **occipital torus**, a ridge of bone that runs horizontally across the occipital. In addition, the forehead has a low, sloping, or receding appearance and is often separated from the supr-

orbital torus by a gully or furrow. The pentagonal rear view is formed by other thickenings including those along sutures such as the **sagittal keel** along the sagittal suture that joins the two parietals and the **metopic keel** along the midline frontal at the site once occupied by the metopic suture of the infant. The pentagon is widest at its base; the sides slant inward from there to the lateral part of the parietal and then turn in to meet at the tip of the pentagon, which is formed by the sagittal keel. Although it is easy to see these anatomical features, it is not so clear why they exist. Unlike the cranial crests of earlier hominins and apes, these thickenings are not related to muscle attachments. And their function, if any, is unclear. Possibly they were a way to strengthen the braincase as brain size increases.

Homo erectus brain size ranges from about 550 cc to over 1,200 cc, averaging around 900 cc (Table 11.2). Partly as a result of this expansion, the degree of *postorbital constriction* is less than in australopithecines but still marked compared with later *Homo*. Of course, key factors in determining the cognitive ability of a species lie not only in sheer brain volume but also with the organization of the brain. Certainly in absolute brain size, *H. erectus* was less cognitively endowed than modern humans. However, the brain size of *H. erectus* also shows regional and evolutionary variation, indicating progressive but slow increase in the lineage through time (Antón & Swisher, 2001; Leigh, 1992). Brain size increases by about 160 cc per million years in *H. erectus* but by about 800 cc per million years from archaic *H. sapiens* to modern humans (Figure 11.8).

Early brain size increases in *H. erectus* may occur simply in proportion to body size increases in the species and real (that is, disproportionately large) brain size evolution seems not to occur until archaic *H. sapiens*, just a few hundred thousand years ago. Because there are so few associated skeletons, it is difficult to know

Figure 11.7 Compared with modern humans, *Homo erectus* has a larger face, lacks a chin and canine fossa, and has a more angular vault and smaller brain.

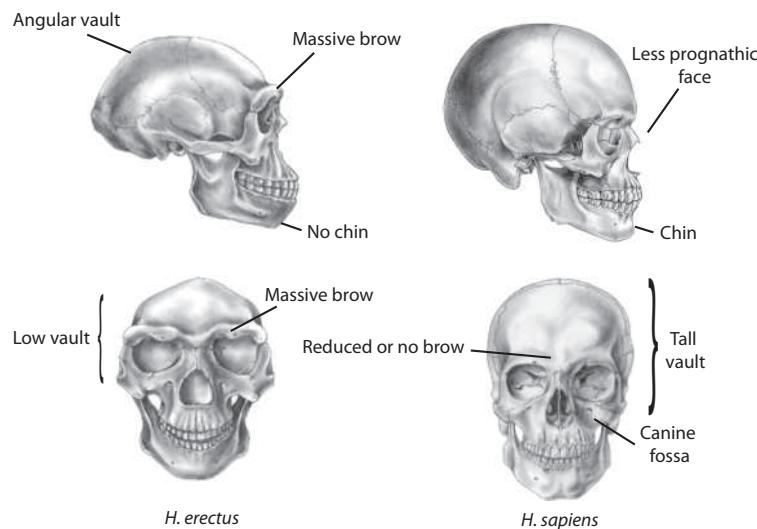


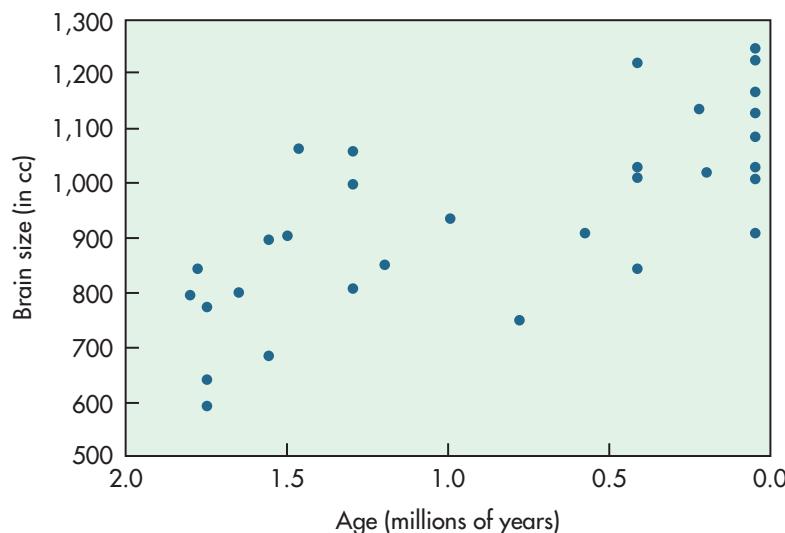
Table 11.2 Cranial Capacities for *Homo erectus*

| Region | Range (cc) |
|-----------|------------|
| Africa | 690–1,067 |
| Georgia | 546–750 |
| China | 855–1,225 |
| Indonesia | 800–1,250 |

whether the increased brain size of *H. erectus* was a unique adaptation or simply a result of their larger body size.

The jaw of *H. erectus* was as robust and powerfully built as the rest of the cranial complex, but compared to earlier hominins, including other early *Homo*, it was

Figure 11.8 Although average brain size increases gradually through time in *H. erectus*, individuals with small brains are present even late in time. Dots represent individual fossils.



shovel-shaped incisors

Anterior teeth which on their lingual (tongue) surface are concave with two raised edges that make them look like tiny shovels.

platymeric

A bone that is flattened from front to back.

platycnemic

A bone that is flattened from side to side.

Figure 11.9 The Nariokotome *H. erectus* skeleton is that of a boy between 7 and 8 years of age.



reduced in robusticity. The proportions of the mandible contrast with the small teeth in some of the earlier *H. erectus* specimens especially in Africa (Wolpoff, 1999). And the teeth are differently proportioned to one another. For example, the molars of *H. habilis* get progressively larger toward the back of the mouth, but in *H. erectus* the last molar is differentially smaller, and the cusps are positioned differently as well. The lingual (tongue) sides of the incisors are concave, often with ridges along their edges forming the shape of a tiny shovel; referred to as **shovel-shaped incisors**. This shape likely prevents damage when the front teeth are exposed to heavy wear from food or other uses. Some researchers have attempted to link ancient Asian *H. erectus* populations with modern Asian people, based on this apparent continuity of incisor shape (see Chapter 13). However, because most *H. erectus* specimens from all regions possess this trait, as do Neandertals, it seems more likely that it is a primitive trait for the genus that may or may not suggest a link between modern and ancient Asian populations.

BODY SIZE AND SHAPE Despite the large numbers of *H. erectus* skulls and teeth that have been found over the past century, what we know of the postcranial skeleton comes from just three partial skeletons and some isolated bones, mostly from East Africa and the Republic of Georgia. The most important of these is the remarkably complete KNM-WT 15000 skeleton—the Nariokotome boy whose discovery is described at the beginning of this chapter (Figure 11.9). These specimens suggest not only that *H. erectus* was robustly proportioned but also that some individuals were fairly tall as adults, between five and a half and six feet (Walker, 1993; McHenry & Coffing, 2000; Graves et al., 2010). The long bones of the arms and legs are thick; the femur is **platymeric**, which means it is flattened from front to back, and the tibia is **platycnemic**, flattened from side to side. These features are distinctive to *H. erectus* but not *H. sapiens* and do not differentiate *H. erectus* from later Neandertals or archaic *H. sapiens*.

In addition to being taller on average, *H. erectus* in Africa may also have been narrow hipped, at least based on reconstructions of pelvis shape in KNM-WT 15000 by Chris Ruff (Figure 11.10). These body proportions—long and linear—seem to follow the latitudinal cline seen in modern humans adapted to tropical environments (see Chapter 5). If the reconstructions are correct, and there is some argument about this, then they suggest that *H. erectus* was dissipating heat in much the same way that we do, that is, by sweating. This ability to dissipate heat may have allowed *H. erectus* to be more active during midday. However, a 1.5 million year old pelvis from Gona, Ethiopia, may challenge this opinion (Simpson et al., 2008). The pelvis has been argued to be a small *H. erectus* female, and it is much smaller and wider than previous ideas about the *H. erectus* pelvis. If it is *H. erectus*, and there is some argument about this since there are no cranial remains with it, the Gona pelvis would suggest both greater sexual dimorphism and a more primitive, wider body build for *H. erectus* than we previously thought (see Innovations: What's Size Got to Do with It?, on pages 364–365).

Homo erectus versus *Homo ergaster*

As was the case with *H. habilis*, opinions differ about whether *H. erectus* constitutes one widely dispersed, variable species or two (or more) distinct species, *H. erectus* and *H. ergaster*. The argument focuses mainly on the early African and Georgian forms of *H. erectus* that some researchers recognize as *H. ergaster*, using the mandible KNM-ER 992 as the type specimen.

The main differences between *H. ergaster* and *H. erectus* are summarized in Table 11.3 and include more gracile crania with less pronounced browridges in African forms and more robust and thicker-browed Asian forms, with larger teeth and more

Figure 11.10 (a) Body weight estimates from fossil remains show that *H. erectus* had a larger body than earlier hominins did. (b) But the gona pelvis, pictured here, suggests that some *H. erectus* may have been very small indeed.

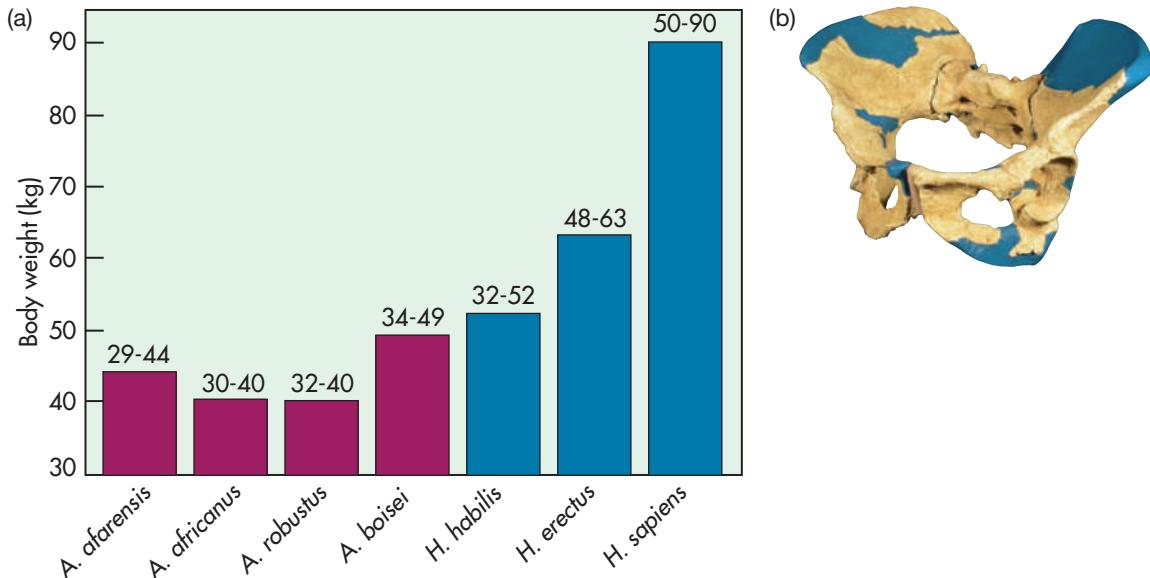


Table 11.3 Comparison of *Homo ergaster* and Classic *Homo erectus*

| Region | Skeleton | Date (MYA) |
|--------------------|---------------------------|---|
| <i>H. ergaster</i> | E. Africa Rep. Georgia | Thinner cranial bones Less pronounced browridges |
| <i>H. erectus</i> | Asia | Thicker cranial bones More pronounced browridges |

*MYA = millions of years ago

pronounced cranial superstructures (keels and tori, discussed previously). There are also archaeological differences, with some of the African forms found in association with somewhat more advanced tools, whereas even later forms of Asian *H. erectus* continue to make Oldowan-like tools, (see “The Lifeways of *H. erectus*” on page 358). In practice, *H. ergaster* is used to refer to early African *H. erectus* specimens and is considered by many to be only a slight regional variant of the pan–Old World species *H. erectus* (Rightmire, 1993; Antón, 2003). Here we will consider *H. ergaster* a regional variant or subspecies of *H. erectus*.

Homo erectus around the World

11.6 Discuss the distribution and characteristics of *Homo erectus* around the world.

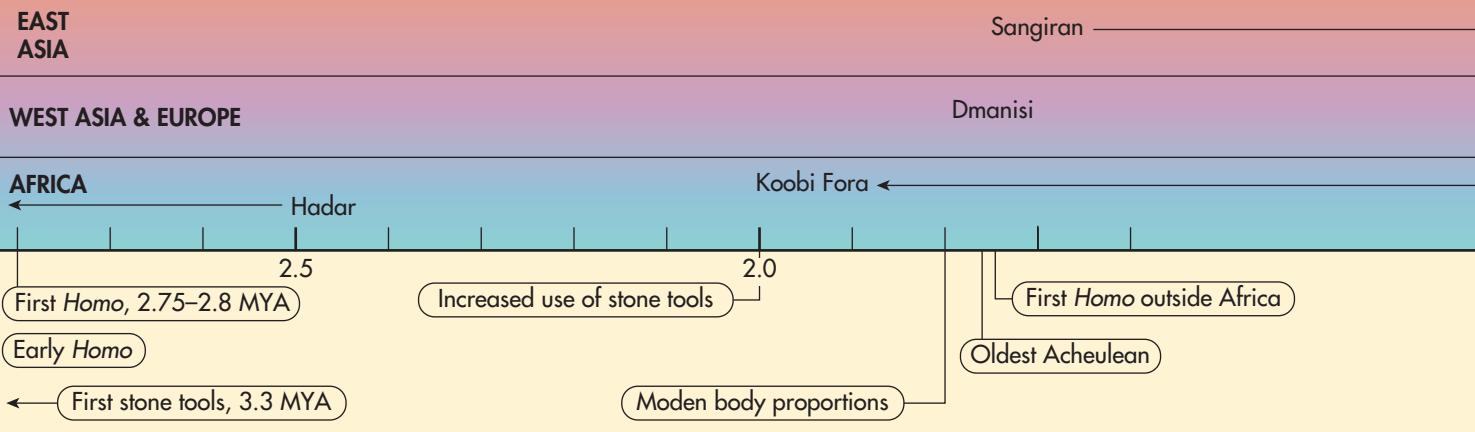
If we accept *H. erectus* as a single, widely dispersed species, then it represents more than 1.5 million years of time and a broad geographic range (Figure 11.11 on pages 348–349). *H. erectus* sites range in age from about 1.8–1.6 million years to 100,000 years (and perhaps much younger in Indonesia). *H. erectus* is found first in Africa (where it

The Genus *Homo* Through Time

FIGURE 11.11 The genus *Homo*, characterized by changes in the dentition, first appeared in the fossil record about 2.8 million years ago. The genus eventually developed larger brain and body sizes and spread out of Africa around 1.8 million years ago.



Fragmentary remains of *H. antecessor* are the earliest accepted remains in Europe.



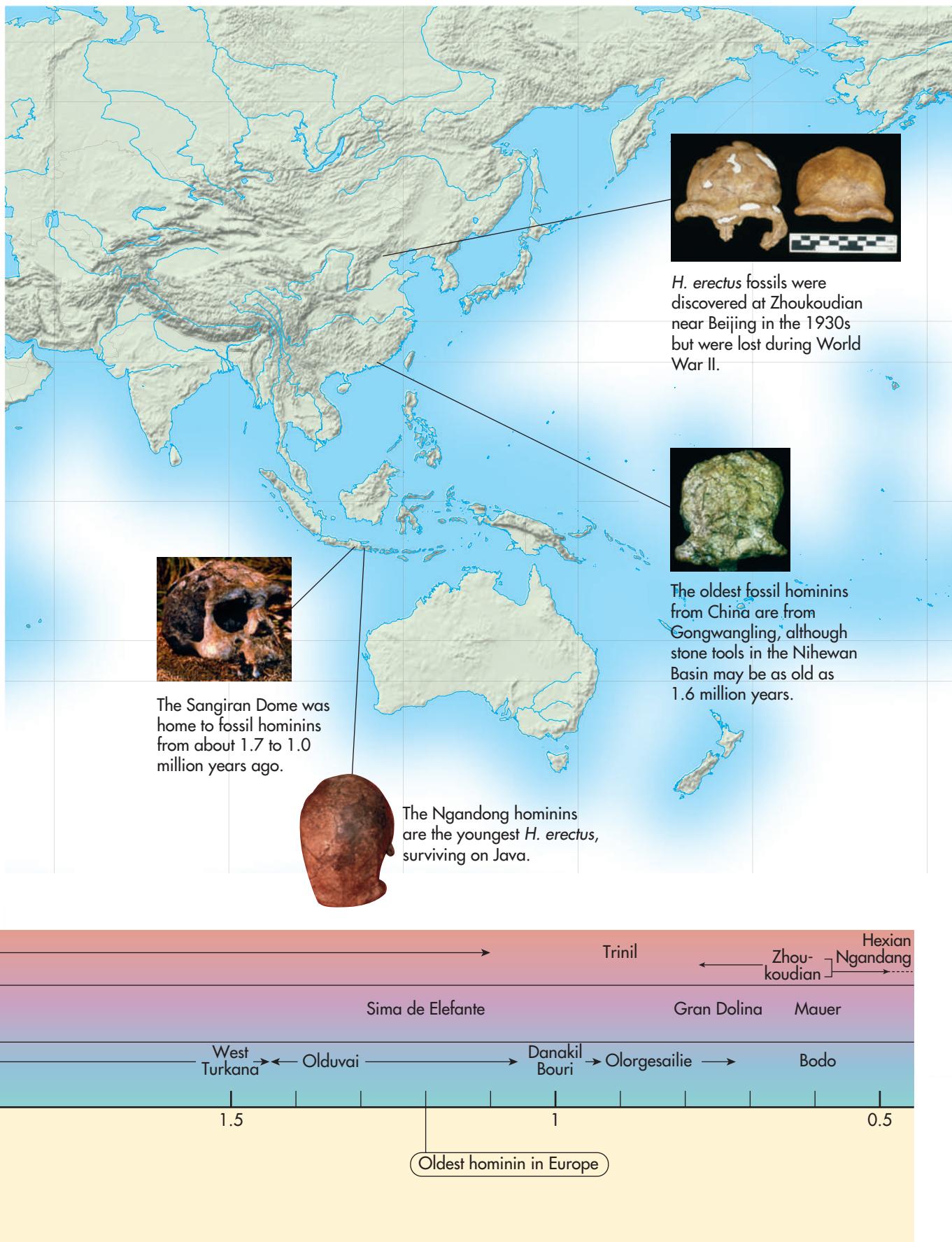


Figure 11.12 The cranium of early African *H. erectus* KNM-ER 3733 is about 1.63 million years old.



persisted until about 1 million years ago), in the Republic of Georgia at > 1.7 million years ago, in island Southeast Asia by about 1.8 million years ago (persisting until at least 500,000 years ago), and only later in continental Asia from about 800,000 to about 200,000 years ago. There are also archaeological sites without bones in China that are as old as 1.6 million years and probably were made by *H. erectus*, although we can't prove this. There is controversy as to whether *H. erectus* is found in western Europe, with many researchers arguing that the fossils that appear there from about 800,000 until 200,000 years ago belong to a different lineage than *H. erectus* (see later in this chapter and Chapter 12).

African Origins

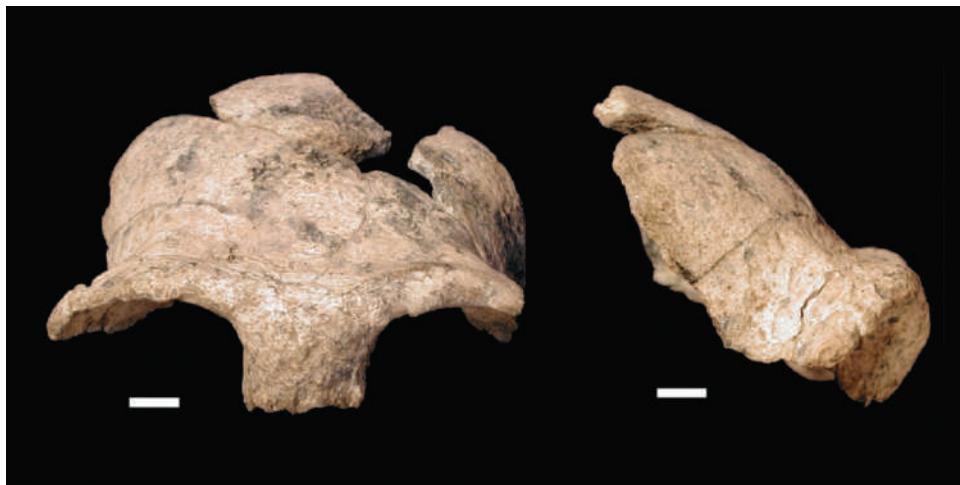
The earliest fossil evidence for *H. erectus* comes from Koobi Fora in Kenya 1.8–1.9 million years ago. The oldest complete remains are a largely complete cranium, KNM-ER 3733, dated at 1.63 million years old and with a cranial capacity of only about 850 cc (Figure 11.12). Slightly older remains from Koobi Fora of 1.89 and 1.95 million years ago may also be *H. erectus* but are fragmentary or are parts of the postcranial skeleton that cannot be identified to species with certainty. Many other fossils from East Turkana exhibit similar anatomy and range in age from about 1.5 to 1.78 million years (or older). An exciting recent find is the partial cranium from Ileret, Kenya (part of the Koobi Fora Formation), dated to 1.55 million years ago, was discovered that has a very small cranial capacity (~690 cc) and some characteristics more typically found in Asian *H. erectus* (Figure 11.13) (Spoor et al., 2007). The discovery of this fossil argues for including African and Asian *H. erectus* in a single species and tells us important things about size variation in *H. erectus* (see Innovations: What's Size Got to Do with It?, on pages 364–365).

Important African *H. erectus* fossils also come from the western side of Lake Turkana and Olduvai Gorge. The Nariokotome skeleton from West Turkana described in the vignette is important for understanding growth and body proportions (see “*Homo erectus* Life History” on page 362). The largest-brained African *H. erectus*, OH 9, is from Olduvai Gorge. With a cranial capacity of a little more than 1,000 cc, OH 9 dates to about 1.47 million years ago. However, some of the latest *H. erectus* in Africa are also the smallest, including OH 12, from Olduvai, dated to perhaps as little as 780,000 years ago, with a capacity of only 727 cc, and the

Figure 11.13 The recently discovered Ileret calvaria from Kenya is the smallest *H. erectus* and shares many traits with Asian *H. erectus*. Ileret is shown next to the largest of the African *H. erectus*, OH 9.



Figure 11.14 A small adult *Homo erectus* from Olorgesailie, Kenya, is also one of the youngest in Africa at about 900,000 years old.



recently discovered Olorgesailie hominin at about 900,000 years old (Figure 11.14) (Potts et al., 2004). These fossils highlight the differences in size among *H. erectus* individuals.

H. erectus from the Bouri Formation of the Middle Awash, Ethiopia, (Asfaw et al., 2002) and the Danakil Depression in Eritrea are around 1 million years old (Figure 11.15) (Abbate et al., 1998). Another Ethiopian site, Konso-Gardula, has very ancient (1.8 million years old) fragmentary *H. erectus* fossils and the oldest known *H. erectus*-associated stone tools. The Bouri lineage in particular will prove significant for understanding the evolution of genus *Homo*, because it also contains fossils of the earliest *H. sapiens* (see Chapter 13). As early as 1.8 million years ago in Africa, *H. erectus* making a new type of tool as well (Lepre et al., 2011).

The First African Diaspora: Republic of Georgia

About 50 miles southwest of Tbilisi, the capital city of the Republic of Georgia, lies the village of Dmanisi. Nearby, beneath a medieval village built at the confluence of two rivers, a stunning series of finds in the 1990s changed our understanding of when humans left the cradle of Africa (Figure 8.11 on page 241). Excavations by an international team headed by Leo Gabunia, Abesalom Vekua, and David Lordkipanidze discovered evidence of early *H. erectus*-like hominins outside Africa at approximately 1.7 million years ago and associated with Oldowan-like stone tools. Since 1991, at least five crania and some postcranial remains have been found in a small area (16 m^2) beneath the medieval village (Figure 11.16 on page 352).

The Dmanisi hominins are very similar to early African *H. erectus*, or so-called *H. ergaster* (Table 11.4 on page 352). They are small brained (less than 546–750 cc) but differ in cranial and dental anatomy from *H. habilis*. The Dmanisi hominins are linked to *H. erectus* by their premolar and molar tooth structure, the development of their browridges, and the shape of their braincase. They are markedly more similar to the early African *H. erectus* fossils than they are to early Asian *H. erectus* (Gabunia et al., 2000). But compared with early African *H. erectus*, the Dmanisi hominins are small (Rightmire et al., 2006). They are also interesting because a number of individuals

Figure 11.15 *Homo erectus* from Bouri Formation of the Middle Awash, Ethiopia, is about 1 million years old.



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Figure 11.16 (a) The Dmanisi cranium (right) shows similarities to early African *H. erectus* including the Nariokotome boy (left). (b) One individual from Dmanisi lost all his teeth before he died.

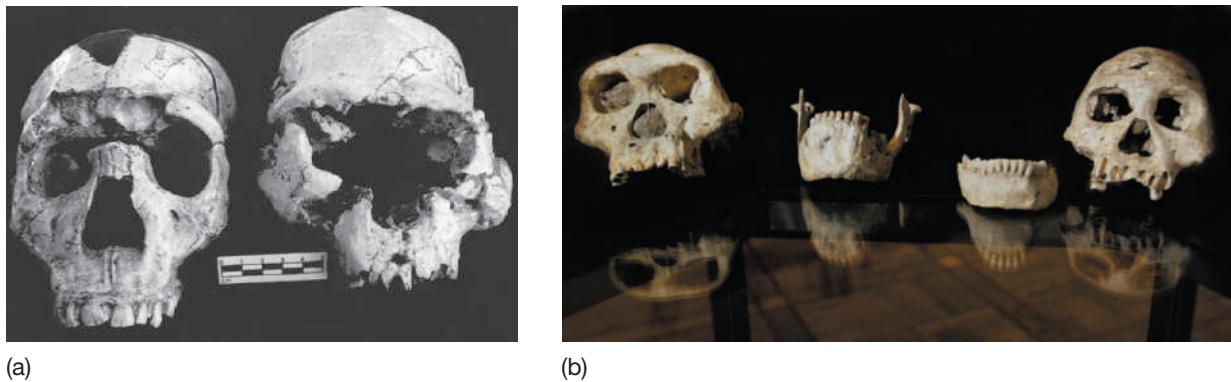


Table 11.4 Dmanisi Hominins Compared with Other Early Hominins and *H. sapiens*

| TAXON | Brain Size (cc) | Body Height (in.) | Body Weight (lbs.) |
|---------------------------|-----------------|-------------------|--------------------|
| Dmanisi <i>H. erectus</i> | 546–780 | 57–63 | 90–110 |
| African <i>H. erectus</i> | 690–1,067 | 63–71 | 120–145 |
| Asian <i>H. erectus</i> | 855–1,250 | 55–67 | 90–120 |
| Earliest <i>Homo</i> | 500–750 | 39–63 | 70–130 |
| <i>H. sapiens</i> | X = 1,350 | 60–75 | 100–200 |
| <i>A. africanus</i> | 448 | 45–54 | 66–90 |

SOURCES: Gabunia (2001), Lordkipanidze et al. (2007), and Antón et al. (2014).

show health problems not usually seen in fossil crania: one is entirely toothless, which poses questions about how he/she prepared his food and whether he could survive on his own or needed assistance from others in the group (Figure 11.16b). Other individuals show abnormalities of the teeth often seen in closely related individuals, perhaps indicating that this was a closely related group.

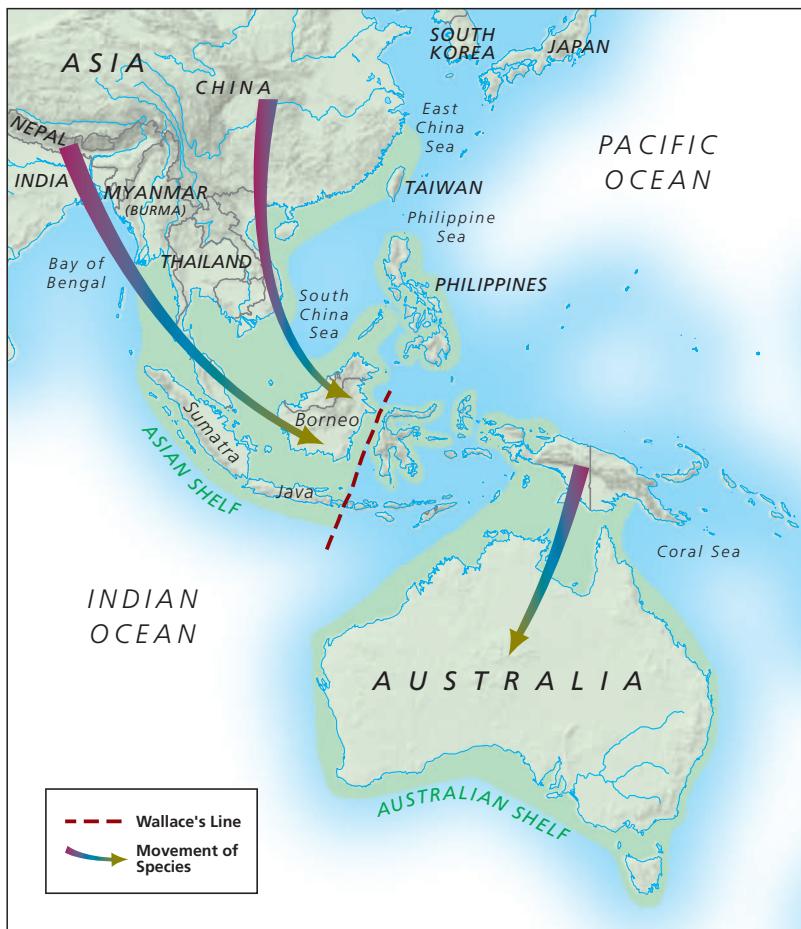
The Dmanisi skulls show conclusively that early humans had migrated out of Africa at nearly the same time that *H. erectus* first appears in Africa. Thus, shortly after the emergence of *H. erectus* in Africa, the species moved out of the African continent and into other regions and other ecosystems.

Dispersal into East Asia

The oldest Asian *H. erectus* are from island Southeast Asia, particularly the island of Java, and date to about 1.6–1.8 million years ago. The sea level was substantially lower 1.8 million years ago than it is today, and Java and nearby islands were connected to mainland Asia by landbridges (Figure 11.17). So colonizing the far reaches of Asia meant only walking a long distance, not crossing water. Although travel through continental Asia is necessary to reach Southeast Asia, so far the earliest archaeological evidence of *H. erectus* on the eastern part of the continent is only about 1.6 million years old in China.

INDONESIA The very first *H. erectus* fossil ever found, and thus the type specimen for the species, was discovered in 1891 in Indonesia (Figure 11.18). A few years earlier, a young doctor named Eugene Dubois left Amsterdam by steam ship in search of human fossils in the Dutch East Indies (now called Indonesia). Following Darwin's lead, Dubois considered the tropics a likely cradle of humankind. But he also thought that Asia was a more likely spot for the origin of humans than Africa because African apes, with their primitive appearance and robust facial features, seemed to

Figure 11.17 Landbridge connections between continental Asia and Indonesia during glacial periods (and low sea level) extend as far as Wallace's line.



him unlikely human antecedents, whereas the slender-bodied, monogamous Asian gibbons and seemed more similar to modern humans (Shipman, 2001). Dubois went to Indonesia to find the missing link between the two.

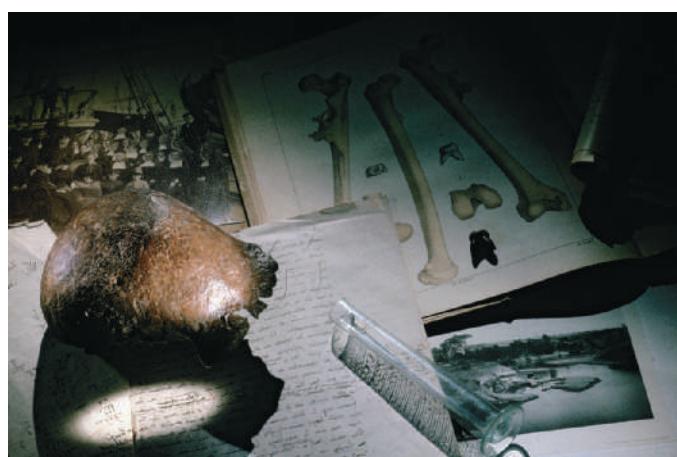
In October 1891, in the banks of the Solo River near the village of Trinil, Java, Dubois's team unearthed the **calotte** or skullcap of an early human. Although only the top of the skull was found, Dubois could see that it was hominin and that in life it possessed a large brain, in a robust braincase more primitive than that of any hominin known at that time. He named the species *Pithecanthropus erectus* ("the upright ape-man"), and this specimen, Trinil 2, also nicknamed Java Man, became the type specimen for the species. The team later found a fossilized femur that Dubois believed to be of the same individual, thereby proving to him that the creature was fully bipedal. Recent work by Chris Ruff has established, however, that the femur and skullcap are from different stratigraphic layers and do not belong to the same individual (or even the same species; Ruff et al., 2015).

Dubois' claims were met with much skepticism, however, in part because of preconceived ideas about evolution and which characters had appeared first in our evolutionary history (Insights and Advances: the Piltdown Hoax in Chapter 8, page 239).

calotte

The skullcap, or the bones of the cranium exclusive of the face and the base of the cranium.

Figure 11.18 The skullcap from Trinil, Java, is the type specimen for *H. erectus* and is about 900,000 years old.



calvaria

The braincase; includes the bones of the calotte and those that form the base of the cranium but excludes the bones of the face.

Although by the 1940s *P. erectus* was classified in our own genus as *H. erectus* and recognized as a primitive hominin intermediate between the apes and modern people, Dubois himself died well before this, embittered about his treatment by the scientific community.

The volcanic sediments of Java provide the ideal context for estimating the radiometric age of fossil hominins using the argon–argon technique (Chapter 8). The Trinil site has been dated to about 900,000 years old. A series of fossils from the Sangiran Dome were recovered from volcanic sediments ranging from about 1.7 to about 1.0 million years ago (see Figure 8.14 on page 247) (Swisher et al., 1994; Larick et al., 2001). And the most ancient specimen from Java, a child's **calvaria**, or braincase, from the site of Mojokerto, is dated to about 1.8 million years ago. There is some controversy about the precise geological ages of individual fossils because many have been discovered not by scientists but by farmers making rice fields; however, it is clear that both sites are far older than 1 million years.

The latest surviving *H. erectus* are also from Java and may represent the youngest *H. erectus* anywhere in the world. A series of partial crania and other fossilized remains were excavated in the 1930s at the site of Ngandong in eastern Java. Using uranium series and electron spin resonance (ESR) methods (see Chapter 8), Carl Swisher and colleagues redated the fauna associated with the Ngandong hominins and those from nearby Sambungmacan (Figure 11.19) to a remarkably recent 27,000 to 53,000 years ago (Swisher et al., 1996). And using a nondestructive spectrometric U-series technique two of the Ngandong hominins recently yielded ages around 70,000 years (Yokoyama et al., 2008). (Figure 11.20). Thus, *H. erectus* may have survived in this island refuge even while going extinct in other parts of the world. Recent finds on the island of Flores dating to 18,000 years ago may also support a young age for late surviving *H. erectus* (see Insights and Advances: The Little People of Flores on page 356). However, scientific work continues on the Solo River sites, and a group led by paleoanthropologists Etty Indriati and Susan Antón and dating experts Swisher, Feibel, and Grün has conducted more extensive excavation and exploration (Indriati et al., 2011). This group has found evidence of pumices dating to 550,000 years ago at Ngandong, while the fossil teeth yield U-series ages similar to those found previously. This conundrum may mean either that the pumices are not in stratigraphic position, or that the U-series ages of the teeth are recording another event that influenced uranium migration, such as a change in the level of the water table.

Figure 11.19 Outcrops near Trinil, Java.



Figure 11.20 Ngandong calottes from Java are the youngest *H. erectus* fossils, perhaps 27,000–50,000 years old.



Since Indonesia achieved independence in 1945, a series of other fossils have been recovered by Indonesian scientists Teuku Jacob, Fachroel Aziz, and Sartono. As a group, these Indonesian *H. erectus* have cranial capacities that vary between about 800 and 1,250 cc. These finds have helped us to understand the anatomy and evolution of *H. erectus*, but tools are almost entirely lacking in Indonesia. Tools of an Oldowan-like technology have been found, but they are few, and none are in association with fossil hominins.

CHINA Perhaps the most famous of the *H. erectus* remains are the so-called Peking Man fossils from China. Discovered in the 1930s, most are now dated to about 800,000 years ago, although different techniques yield ages as young as 200,000 years ago (See Insights and Advances: Dating Controversies in Chapter 8, page 251). Either way, they are younger than the African and the earliest Indonesian hominins. However, *H. erectus* almost certainly occupied China as early as they did Indonesia. Although the oldest Chinese fossil hominins, fragmentary and crushed remains from Gongwangling, are only about 1.2 million years old, sites with stone tools in the Nihewan Basin are about 1.6 million years old (Zhu et al., 2004).

The story of the famed Peking Man fossils is one of discovery and loss. Chinese paleontologist Pei Wenshong discovered the first skull in December 1929 at a quarry site, Chou Kou Tien (now transliterated as Zhoukoudian), not far from modern Beijing (Figure 11.21 on page 357). Along with Davidson Black, a Canadian anatomist, he described and initially named the fossil *Sinanthropus pekinensis* ("Chinese human from Peking"). After Black's untimely death, Franz Weidenreich, a Jewish anatomist who had fled his native Germany during the Nazi era, took over anatomical work on Zhoukoudian.

In the mid-1930s, Japan invaded China before the American entry into World War II, and work at Zhoukoudian stopped. Fear spread that the Zhoukoudian *H. erectus* fossils, objects of great cultural and historical value, would be confiscated, destroyed, or taken as gifts to the Japanese emperor, a noted naturalist. In fact, at least one of the Ngandong fossils was sent to the emperor as a birthday gift. So Weidenreich made extensive measurements, drawings, and plaster casts of the Zhoukoudian remains. The fossils were then placed in the care of the United States Marines, who guarded them on a train from Beijing to the coast, where they were to be put on a ship to San Francisco. The train arrived at the Chinese coast on December 7, 1941, the day of the Japanese attack on Pearl Harbor. The Marines were taken prisoner, and the crates of fossils have never been found (Shipman, 2001).

Insights and Advances

The Little People of Flores

Homo sapiens never coexisted with *Homo erectus*. Or did they? Conventional wisdom has held that *H. erectus* went extinct in the middle Pleistocene after giving rise to *Homo sapiens*. Controversial discoveries on the island of Flores suggest that another group of hominins may have survived until 18,000 years ago. At the cave of Liang Bua, where Indonesian archaeologists led by R. P. Soejono have been excavating since 1976, the remains of a diminutive hominin were recovered (Brown, P. et al., 2004). Analyses by Peter Brown show that the skull had a cranial capacity of 380 to 420 cc (Figure A) (Falk D. et al., 2005), and the postcranial skeleton suggests a female biped that stood just about a meter tall—the size of the *A. afarensis* skeleton “Lucy.” Stone tools at the site may be associated with the hominin.

Although some scientists call it a new species, *H. floresiensis*, Brown's description of the skull makes it difficult to distinguish from *H. erectus* except on the basis of its small size. And the shoulder skeleton is also reminiscent of *H. erectus* (Larson et al., 2007, 2009). But other aspects of the postcranial skeleton look more primitive (Morwood et al., 2005; Jungers et al., 2009a,b). The hand skeleton in particular suggests to Matt Tocheri that the hominins from Flores were more primitive than even earlier *Homo* (Tocheri et al., 2007; Larson et al., 2009). And the limb proportions appear unlike those of recent humans. Alternatively, Teuku Jacob and colleagues (2006) argue the Flores remains are just those of a short human with an abnormally small brain. And it is the case that some aspects of the skeleton are diseased—for example, one arm shows evidence of a healed fracture. Jacob's initial claim has gained support from studies of the relationship between brain and body size by Bob Martin (Martin et al., 2006) and Tom Schoenemann (Schoenemann and Allen, 2006). Their studies suggest

that the relationship between brain and body size in the Flores specimen is more similar to humans with a condition known as microcephaly, or perhaps to some kind of dwarfism, than it is to fossil hominins. And recent work by Israel Hershkovitz and colleagues (2007) argues the Flores material represents modern individuals with a congenital deficiency in insulin-like growth factor production. However, other scaling analyses suggest the Flores remains are what you would expect of a scaled-down version of *H. erectus* or some other form of *Homo* (Gordon et al., 2007; Baab & McNulty, 2009).

A common phenomenon for large mammals that colonize small islands (Flores is about 1,400 km², or 540 square miles) is to become smaller over many generations. In fact the fossil record of Flores yields the remains of a dwarfed elephant as well (Figure B). This size reduction (called insular dwarfism) is related to two selective pressures on island mammals: Fewer resources favor smaller individuals who need less food to survive, and fewer predators mean that having a small body doesn't increase the chance of being eaten. If the Flores hominin is a new species, it may represent such a process. Perhaps a few members of *H. erectus* were washed onto the island on natural rafts during a storm. Stranded there, they were isolated from other members of their species. Their isolation may explain not only their small size but also their survival. In their island refuge they did not come into competition for resources with and were not replaced by modern humans until much later than other archaic hominins.

There is so much disagreement over the interpretation of the Flores individual because only a single skull has been found, and the critical characters (such as cranial capacity) for assessing what species a hominin belongs to are found in the skull; however, most of the new studies of the postcrania all seem to support the idea that the Flores specimens are not modern humans and may be even more primitive than *H. erectus*. In the short time since



Figure A The skull from Flores is tiny, less than one-third of the capacity of a modern human skull.



Figure B Insular dwarfism commonly affects mammals isolated on islands.

its discovery, two special volumes of papers and many individual studies have been wholly or partly dedicated to its identity (Indriati, 2007; Jungers & Morwood, 2009). Yet disagreement abounds, and much about how morphology scales with very small size is not yet well understood (Holliday & Franciscus, 2009).

The growing consensus seems to favor the idea that the Flores remains are not pathological human remains

and that they represent a distinct type of hominin (Aiello, 2010). Many studies favor associations with *H. erectus*, but aspects of especially the postcranial anatomy may favor another form of early *Homo*. More evidence is needed to assess this, but for the moment the remains remind us that it may have been only a few thousand years since we last shared the earth with another hominin species.

Figure 11.21 (a) The site of Zhoukoudian outside of Beijing, China, spans several hundred thousand years and (b) yielded numerous *H. erectus* fossils.



(a)



(b)

Because of Weidenreich's careful molding and measuring of the Zhoukoudian fossils, at least we have replicas of the Peking Man fossils, comprising more than a dozen calvaria and hundreds of associated teeth and bone fragments (Weidenreich, 1943). They represent as many as forty individuals who lived nearby Zhoukoudian.

Although it was originally described as a cave where *H. erectus* lived, used fire, and cooked meals, more recent archaeological work has found that the site is a series of sediment-filled fissures in the rock and not a living site (Goldberg et al., 2001). In addition to the Zhoukoudian material, other Chinese *H. erectus* have been discovered including the more recently discovered Nanjing and Hexian crania, which are morphologically very similar to the Zhoukoudian finds (Wu and Poirier, 1994). In most ways, *H. erectus* from China looks like other *H. erectus*.

Despite their similarities, Chinese *H. erectus* also show some regional differences from the Indonesian *H. erectus* in their frontal and occipital regions (Antón, 2003). These differences may reflect the intermittent isolation of these two groups from each other during the Pleistocene. Each time sea level rose in the Pleistocene, continental and island Southeast Asia, and the hominins and land mammals living on them, were isolated from each other. These periods of separation might last 10,000 to 50,000 years—that is many, many generations of fossil hominins. Such isolation could have led to some genetic (and morphological) differences between the populations over time.

The Status of *Homo erectus* in Europe

Early humans that somewhat resembled *H. erectus* occupied Europe during the same time period that *H. erectus* occurred in Asia. However, most of the fossils discovered

so far differ from the typical *H. erectus* seen in Africa, Asia, or Southeast Asia. Many of the European fossils resemble *H. sapiens* as well as *H. erectus* and Neandertals, and they may well be transitional, or archaic, forms of *H. sapiens*. The later middle Pleistocene European fossils, those dated between 500,000 and 200,000 years ago, are likely to be ancestral only to Neandertals and are discussed in Chapter 12.

The oldest European hominin, announced in 2008, is 1.2 million years old (Carbonell et al., 2008). This partial mandible is from Sima de Elefante in the Sierra de Atapuerca, Spain (Figure 11.22a). Slightly younger are the fossils from Gran Dolina in the Sierra de Atapuerca that date to nearly 800,000 years ago, more than 200,000 years older than any other known hominins in western Europe (Figure 11.22b). The Sima de Elefante and Gran Dolina fossils were found in the oldest of a series of deposits in the Sierra de Atapuerca that were exposed when a road cut was made for a now abandoned rail line. Younger deposits from the same region are discussed in Chapter 12. The Gran Dolina fossils include young individuals, between 3 and 18 years of age at the time they died, that exhibit a mix of characteristics, some of which appear to foreshadow Neandertals, others of which seem to link the fossils to modern humans. In particular, the presence of a **canine fossa** (an indentation on the maxilla above the canine root) has been used to argue that the Gran Dolina fossils represent a previously unknown hominin species, *Homo antecessor*, which may have been the common ancestor of both Neandertals and recent humans (Arsuaga et al., 1999).

However, many researchers are skeptical of this classification because the species *H. antecessor* was based largely on characters exhibited in a child's partial cranium, characters that might have been lost as the child aged. Another adult calvaria, Ceprano, from Italy is said to be 800,000 years old and a member of *H. antecessor*, but it lacks the critical facial bones that define that species. It also differs anatomically from typical *H. erectus* and more importantly, the site has recently been re-aged to between 350,000 and 450,000 years old, so it is more likely related to the later remains from Atapuerca (Muttoni et al., 2009). Only the discovery of more complete adult fossils will settle the question of the identity of *H. antecessor*. Regardless of whether *H. antecessor* is a valid taxon or part of *H. heidelbergensis* or archaic *H. sapiens* (see Chapter 12), anatomically they cannot be classified as *H. erectus*, suggesting that this taxon may never have made it into Europe. Whatever its name, its discoverers argue that the broken bits of bone from Spain are evidence of cannibalism.

Figure 11.22 (a) The mandible from Sima de Elefante Atapuerca, Spain, is the oldest European hominin at about 1.2 million years old. (b) The Gran Dolina locality in Atapuerca Spain has yielded some of the oldest fossil hominins in Europe.



(a)



(b)

The Lifeways of *Homo erectus*

11.7 Discuss the lifeways of *Homo erectus*.

From the fossils and stone tools associated with *H. erectus* and from their own anatomy, we can begin to piece together how these early species lived. The fossils themselves are evidence of the physical adaptations of the species, and the stone tools are a window into their activities and their minds. *H. erectus* is associated with two different tool technologies that reflect advanced cognitive skills. *H. erectus* appears to have undergone a dietary shift to a more heavily meat-based diet than its predecessors, and this shift seems to have fueled both its dispersal from Africa and a slightly different pattern of growth.

Homo erectus and the Early Stone Age

From 1.8 to about 1.5 million years ago in Africa, only Oldowan tools are found with *H. erectus*. The earliest tools found outside Africa at Dmanisi in the Republic of Georgia are also Oldowan-like assemblages (Gabunia et al., 2001). However, starting about 1.76 years ago in Africa some *H. erectus* are found with a different tool technology called the **Acheulean** tradition. This tradition persists until about 250,000 years ago and is made by a number of different species of the genus *Homo*. Together, the Oldowan and Acheulean are known as the **Early Stone Age or Lower Paleolithic**.

Acheulean assemblages are characterized by specifically shaped tools called hand axes and cleavers that are worked on two sides. Both are thus **bifaces**, tools whose cutting edge is formed by the removal of flakes from opposing sides of the piece. The scars left by the removal of these flakes meet to form the sharp edge. A **hand axe** is a bifacially worked, symmetrical, teardrop-shaped tool (Figure 11.23). A **cleaver** has a broader working end where the point of the teardrop would have been in a hand axe.

For the first time in human prehistory we see hominins making standardized tools that clearly indicate they had a plan or mental template in mind. Hand axes and cleavers were highly uniform in appearance. They were made from stone cobbles or larger flakes that had been carefully selected for size and weight. The toolmaker

Acheulean

Stone tool industry of the early and middle Pleistocene characterized by the presence of bifacial hand axes and cleavers. This industry is made by a number of *Homo* species, including *H. erectus* and early *H. sapiens*.

Early Stone Age (or Lower Paleolithic)

The earliest stone tool industries including the Oldowan and Acheulean industries, called the ESA in Africa and the Lower Paleolithic outside Africa.

bifaces

Stone tools that have been flaked on two faces or opposing sides, forming a cutting edge between the two flake scars.

hand axe

Type of Acheulean bifacial tool, usually teardrop-shaped, with a long cutting edge.

cleaver

Type of Acheulean bifacial tool, usually oblong with a broad cutting edge on one end.

Figure 11.23 The Acheulean industry is typified by hand axes and cleavers.



roughed out the axe first, and then refined the product with more subtle flaking to achieve a particular shape.

Indeed, one of the most extraordinary aspects of the Acheulean industry is its persistence and uniformity over great spans of time and space. We first see hand axes at about 1.76 million years ago, and they persist almost unchanged until about 250,000 years ago. In comparison, how many of our tools do you think will still be in use 1.2 million years from now and in nearly the same form they have today? This conservatism is also found across vast geographic areas. Hand axes appear in western and northern Europe, in East and North Africa, and in the Near East. (However, as we saw, they are very rare, or absent, in the East Asian *H. erectus* sites.) The uniformity of hand axe appearance suggests that they were used for specific purposes and in standard ways.

The advantages of the hand axe and cleaver over the simple flake are their ability to hold a sharp edge for a long period of time, the greater length of their working edge, and their generally convenient size, which allows them to be used for holding and cutting without fatigue. Nick Toth and Kathy Schick think that hand axes and cleavers are best seen as tools specifically developed for the butchery of large animals (see Insights and Advances: Understanding the Meat-Eating Past through the Present on page 342). The circular pattern of flaking around the perimeter of the axe leads some scholars to consider them primitive versions of a circular saw in which more flaking was done as earlier edges became worn and dull. But other hypotheses for the use of hand axes cannot be discounted. A recent study found evidence of fossilized *phytoliths*, microscopic mineral particles from plants (see Chapter 8), on the cutting edge of some hand axes. Their presence suggests that the tool was used to scrape plant material. This could have meant the users of the tools were sharpening a wooden spear, or perhaps stripping bark from wood for building or eating. Alternatively, hand axes might also have been used as digging implements or as projectiles, thrown at prey animals or even at hominin enemies. Although it seems unlikely, it is also possible that hand axes were simply raw material, the cores from which flake tools were struck. *H. erectus* might have simply carried hand axes around and struck flakes off them until the axe core was exhausted. Whatever their use, hand axes and cleavers were clearly critical components of daily life for hominins. At some sites like Olorgesailie in Kenya (where a small *H. erectus* has been found, Figure 11.24) hand axes litter the site's surface, and evidence of large animal butchery is abundant (Figure 11.24).

Whatever their use, the Acheulean industry presents an innovative technology that extended over much, but not all, of *H. erectus*'s Old World range. As mentioned, East Asian sites yield Oldowan-like tools but no true hand axes, at least not until late in time. The division between hand axe-bearing areas and those without hand axes is called the **Movius line**, after Hallam Movius, an early archaeologist who first recognized this puzzling distribution (Figure 11.25). There are two not necessarily mutually exclusive hypotheses for the Movius line. The first suggests that the absence of hand axes reflects a loss of hand axe technology in Asia caused by differences in selective pressures and raw materials between Asia and Africa. In particular, organic materials such as bamboo are inferred to have been used by the hominins. In this view, African *H. erectus* left the continent with Acheulean technology but reverted to Oldowan technology in their new environment. Alternatively, other scientists suggest that the hominins that inhabit Asia left Africa before Acheulean tools were developed, so their absence is not so much a loss of technology as a difference in the technological paths taken in Asia and Africa. This difference may result from differences in available resources and selective pressures as well.

However, it is important to recognize that there is no one-to-one correlation between a species and a technology. Oldowan tools are used by both *H. habilis* and *H. erectus* (and perhaps any number of australopithecines), and different groups of *H. erectus* use Oldowan or Acheulean tools, or both. *H. erectus* continued to make and

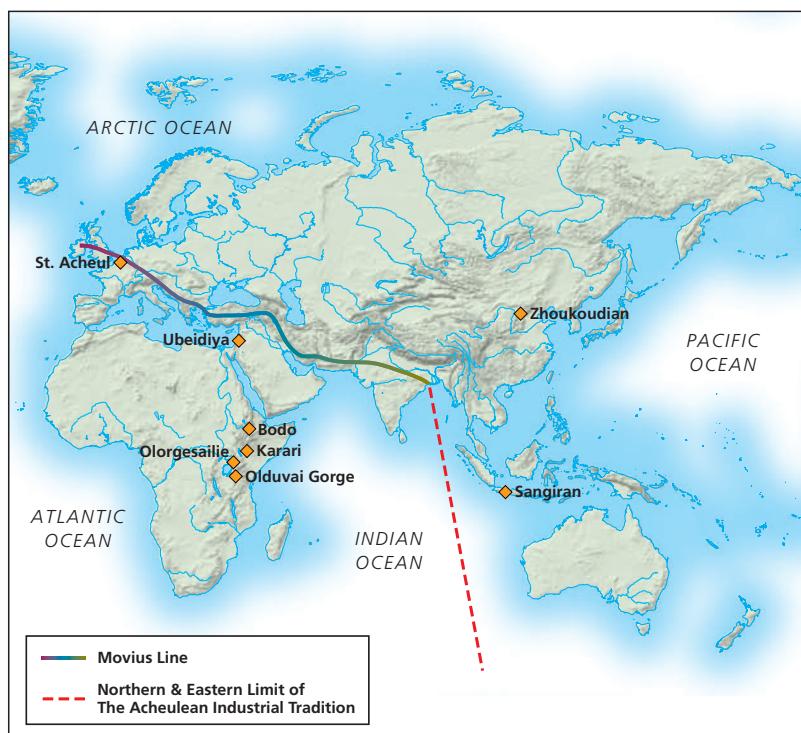
Movius line

The separation between areas of the Old World in which Acheulean technology occurs and those in which it does not; named for archaeologist Hallam Movius who first recognized the pattern.

Figure 11.24 The site of Olorgesailie, Kenya, is littered with Acheulean hand-axes dating to around 900,000 years ago.



Figure 11.25 The Movius line separates regions of the world where Acheulean hand axes were made from regions where they were not made.



use Oldowan industry tools in Africa and elsewhere even after Acheulean tools came into widespread use, and later hominins used Acheulean tools in Africa and Europe.

A Higher-Quality Diet: *Homo erectus* Subsistence

We assume that *H. erectus*, like modern foraging peoples, ate mostly plant foods, but there is no mistaking the archaeological evidence that *H. erectus* also ate meat. About 1.8 million years ago, an important biological shift apparently occurred in the hominin lineage; the human form became much more modern, a bit taller, perhaps more linear, and with a larger brain. Shortly after this time hominins left Africa and began their worldwide expansion. Both these things tell us that the shift probably was associated with a major increase in the quality of the diet, which was needed to maintain a larger body and brain (see Innovations: What's Size Got to Do with It? on pages 364–365; Leonard & Robertson, 1997; Antón et al., 2002, 2014).

Many scientists think the adaptive shift occurred when hominins became predators (Shipman & Walker, 1989). As they became carnivores, their small intestine would have lengthened while the large intestine shortened because meat takes less time in the large intestine for processing. The amount of leisure time would have increased as the time needed to forage for plants decreased. Population density would have been low because predators sit atop the food chain and must exist at low densities to avoid outstripping their prey supply. But the ability to disperse may have increased as hominins became less dependent on specific plant resources and more dependent on animal resources. Migrating herds might have led hominins to follow them, and in new areas meat is fairly safe, regardless of species, but new plants might be poisonous or inedible.

Most scientists argue that the adaptive shift happened with the emergence of *H. erectus* about 1.8 million years ago and that *H. erectus* was the first truly predatory human species. They base their assertion on the increasingly sophisticated tools associated with *H. erectus*, which may have been used for butchering prey, and on evidence that as *H. erectus* spread its range across the Old World, they lived at low population densities in the manner of a hunting species. Alan Walker and colleagues (1982) found one *Homo erectus* individual who may have died from too much vitamin A, a condition which is known to occur in modern people that eat too much internal organ meat, such as the liver, from prey animals. In addition, it seems that human-specific tapeworms share a history with tapeworms that live in hyenas but diverged from them about 1.8 million years ago. This suggests that ancient hyenas and humans were eating the same infected animals about 1.8 million years ago, further suggesting that humans had made the shift from a largely vegetarian to a more heavily meat diet. And Pete Ungar and colleagues using 3D GIS mapping methods are finding that molar tooth topography in early *Homo* (including *H. habilis*) differs from *Australopithecus* in the way that would be predicted, to allow them to shear or slice through tough foods more easily but to be less efficient at crushing brittle foods than were australopiths (Figure 11.26). Meat as well as other food items have properties that differ in this way from the brittle food items that we think *Australopithecus* ate.

Once meat and marrow was obtained, there is only equivocal evidence that *H. erectus* was the first hominin to cook it. Archaeologists working in East Africa at Koobi Fora and Chesowanja have found hominin and animal fossils associated with burnt earth that suggests the possible use of fire as early as 1.6 million years ago (Bellomo, 1994). However, it is unclear whether this was hominin-controlled fire, perhaps collected from a natural fire, or hominin-made fire, or even just a natural fire. To date, most researchers think this may be evidence of brush fires that were not human made. The best unequivocal evidence of hominin-controlled fire comes much later in time during the middle Pleistocene. Although the evidence of *H. erectus*

controlling fire is questionable, some researchers hypothesize that the advent of cooking created whole new adaptive niches for *H. erectus*. They suggest that eating potato-like tubers rather than meat could have provided the higher-quality diet necessary for expansion of the human brain (Wrangham et al., 1999). Wrangham and colleagues suggest that lightning-set fires on the African savanna created an opportunity for early humans to see the effects of fire on the charred underground tubers that survive wildfires (Wrangham et al., 1999). Nonetheless, during this time period, evidence of meat eating is overwhelming, whereas the evidence of tuber cooking is scanty.

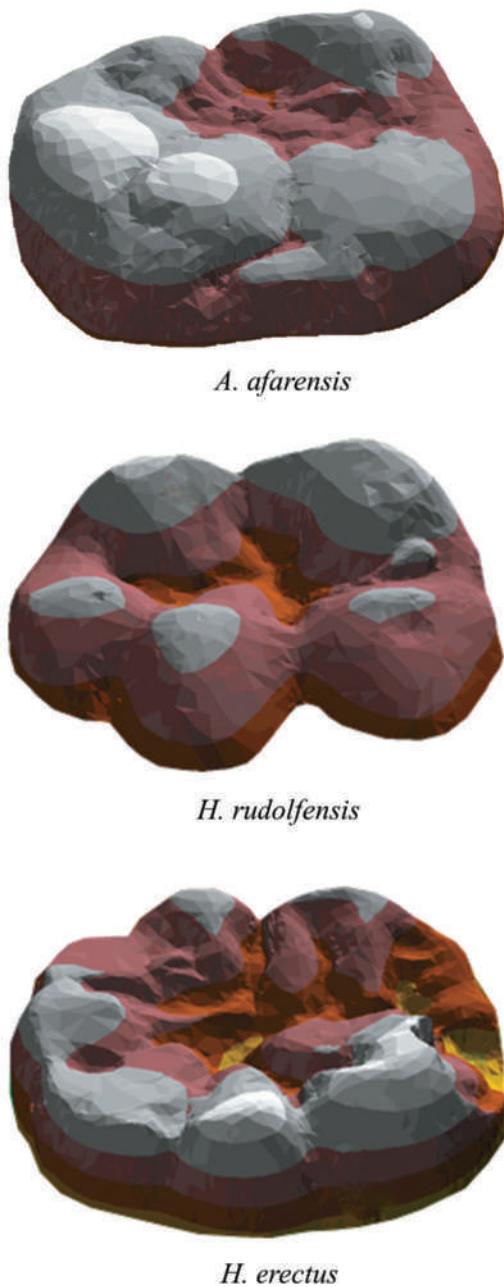
Homo erectus Life History

As adults, modern humans and *H. erectus* look remarkably different, but are they more similar as children? The discovery of the Nariokotome boy (KNM-WT 15000), the remarkably complete *H. erectus* youth discussed earlier, highlighted how little we know about growth in fossil hominins (see Chapter 10 Innovations: Dikika and Development on pages 312–313). At first this may seem unimportant, but consider this basic fact: Evolution often proceeds by modifying the developmental pattern. In small ways and in larger ways, modifications of this pattern produce the differences we see in adults. So understanding the developmental pattern is critical to understanding hominin evolution.

As you saw in Chapter 5 and will explore further in Chapter 15, because of our large brain, humans grow slowly and mature late compared with nonhuman primates, even chimps. During this long development, human maturation is characterized by two growth spurts. The first occurs in the middle of childhood, around the age of 5, and the second is the adolescent growth spurt that occurs in humans in the teenage years (see Chapter 15 and Figure 15.8 on page 477 and Figure 15.9 on page 479). Neither exists to the same degree in chimpanzees, posing the question of when during hominin evolution they arose and what their behavioral implications are.

Teeth have been the most informative structures from which we learn about development because their internal structure forms by layers deposited in cyclical patterns in daily increments during dental development. As the crown develops, a number of bands are formed, and by looking at these bands we can glean something about the age and rate of development. Work on dental microstructure by Chris Dean and colleagues suggests that early development in *H. erectus* was fast compared to our standards. Based on these data, Nariokotome boy would have been no more than about 8 years old at the time of death even though a modern human of similar development would be more like 11 or 12 years old (Dean & Smith, 2009). And *H. erectus* probably reached adulthood earlier than we do, perhaps around the age of 15 years. Although this seems remarkably fast by our standards, we need to remember this growth rate is actually slower than that of *Australopithecus*. So in fact, *H. erectus* had taken a step in our direction. Having a somewhat slower growth rate than *Australopithecus* may signal some changes in selection pressures in *Homo* populations. In humans, the tempo of maturation (and overall size) is sensitive to nutritional challenges and increased mortality rates (Stearns & Koella, 1986). So differences in growth rate in *Homo* may be yet another piece of evidence pointing to higher diet quality.

Figure 11.26 Dental topography differs between *A. afarensis* and *H. erectus*, suggesting that the australopithecine teeth were better suited to breaking brittle food objects.



Innovations

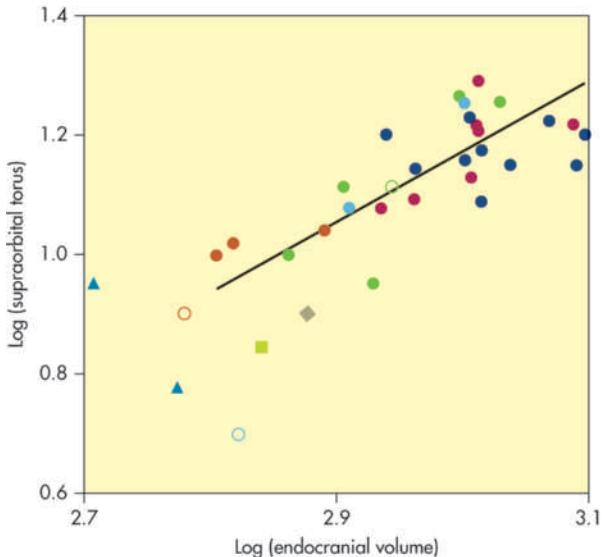
What's Size Got to Do with It?

Homo erectus were bigger, in some cases much bigger, than *H. habilis*. On average, they had bigger brains and bigger bodies, an increase perhaps due to their ability to access a higher-quality diet. However, there was also a lot of size variation in *H. erectus*, and a number of new fossils suggest that some *H. erectus* individuals were no bigger than some of the larger members of *H. habilis*, and one new *Australopithecus afarensis* is somewhat larger than expected (Haile-Selassie et al., 2010).



Fossil Size

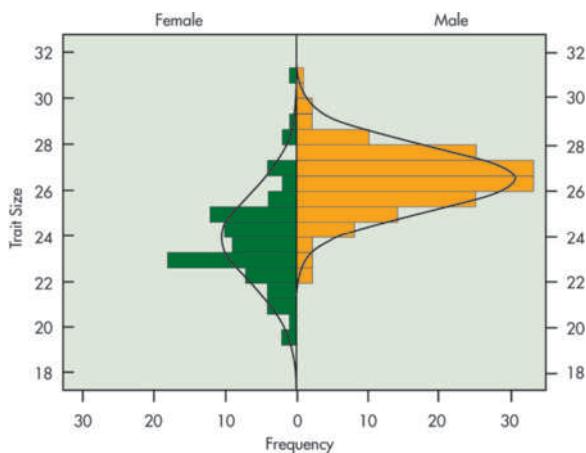
The smallest of the new fossil crania is a recently discovered calvaria from Ileret, Kenya, that, at 1.5 million years old, is about the same geological age as the largest of the African *H. erectus*, OH 9 from Olduvai Gorge, Tanzania (Spoor et al., 2007). The Ileret specimen, discovered by Meave and Louise Leakey's Koobi Fora Research Project, has a cranial capacity of just 690 cc, and external vault dimensions that are even smaller than those of the Dmanisi fossils (see Figure 11.16 on page 351). The Ileret specimen is even tinier in comparison with the largest of the early African *H. erectus* Olduvai Hominin 9 (see Figure 11.13). Yet the specimen has all the cranial characters typical of *H. erectus*: cranial superstructures, an angulated vault, and so on. In fact, the Ileret specimen is more similar to some Asian *H. erectus*



than are other Koobi Fora specimens. And this makes a good argument for Asian and African specimens belonging to a single species.

Scaling of Size to Other Traits

The Ileret and Dmanisi specimen are examples of small, early *H. erectus*; however, there appear to have been small individuals through the entire time range of the species (see Figure 11.8 on page 345). At the younger end of the *H. erectus* range in Africa lived some relatively small individuals at Olduvai (OH 12; Antón, 2002) and at Olorgesailie (Potts et al., 2004), which are both larger than the Ileret specimen. With all these specimens, we can test to see whether some anatomical features are more exaggerated in larger crania. Larger-brained *H. erectus* have thicker cranial walls, and their brow ridges are larger as well. But other anatomical characters, such as keels and



dental proportions, do not vary with overall size, and these differentiate even small-brained *H. erectus* individuals, like Ileret and Dmanisi, from *H. habilis*.

Sexual Dimorphism

The new fossils change our understanding of size variation in *H. erectus*. Until recently, size variation wasn't considered to be that great, and the amount of sexual dimorphism in *H. erectus* was thought to be less pronounced than in earlier hominins and about the same as that seen in our own species (Aiello & Key, 2002). In living humans, males tend to be larger on average than females, but their size range overlaps substantially (see graph). *Australopithecus* is more dimorphic than humans and perhaps *H. erectus* and this has implications for social structure (see Chapter 10). Because the decrease in dimorphism in *H. erectus* compared to *Australopithecus* was thought to be due mostly to the larger size of female *H. erectus*, this had important implications for the size and costs of bearing newborns. However, the new fossils expand the size range of *H. erectus*. Taken as a group, the amount of cranial variation in African *H. erectus* is larger than that seen in living humans or chimpanzees, but smaller than that seen in gorillas today and in earlier hominins like *A. afarensis* (Spoor et al., 2007). And a new pelvis from Gona, Ethiopia, which has been said to be a female *H. erectus* is very small and would also suggest great dimorphism for this species if indeed it is correctly assigned to the species (Simpsons et al., 2008). If *H. erectus* had a lot of sexual dimorphism, then their reproductive patterns may not have been as similar to our own as previously thought. They might even give us clues about a nonmonogamous mating system in *H. erectus* (see Chapter 5). But, especially for the cranial fossils, we do not know for sure which fossils are male and female, so perhaps other causes of size difference might explain the variation.



Regional, Populational, or Nutritional Size Differences

Size differences may not reflect differences between male and female *H. erectus* but may instead be the result of individual differences in genetic background, diet, or other factors such as predation levels. We all know that individuals of a species vary in size even if they are all adults of the same sex—the vast number of dire wolves recovered from the La Brea Tar Pits offer a great example of this individual variation. And we know that differences in diet can influence body size; for example, over the past several decades humans in industrial societies dramatically increased in height due to improvements in nutrition (see Chapter 15). Additionally, body size and proportions in humans and other mammal populations vary with climatic and other selective factors as well (see Chapter 5). So the size variation in *H. erectus* may also reflect intraspecific (within species) variation in body size based on regional conditions influencing different populations. There is some evidence for this because it appears that both males and females are present in the best preserved of the small populations, the fossils from Dmanisi, Georgia (Lordkipanidze et al., 2007), yet all the individuals are small for *H. erectus*. Small size in human groups can come about from food scarcity (too few calories) as well as increased mortality rates due to disease and predators. Possibly the size differences in the Dmanisi group tell us about local resource scarcity in the early Pleistocene and/or increased predation rates rather than sexual dimorphism.

Homo erectus Leaves Africa

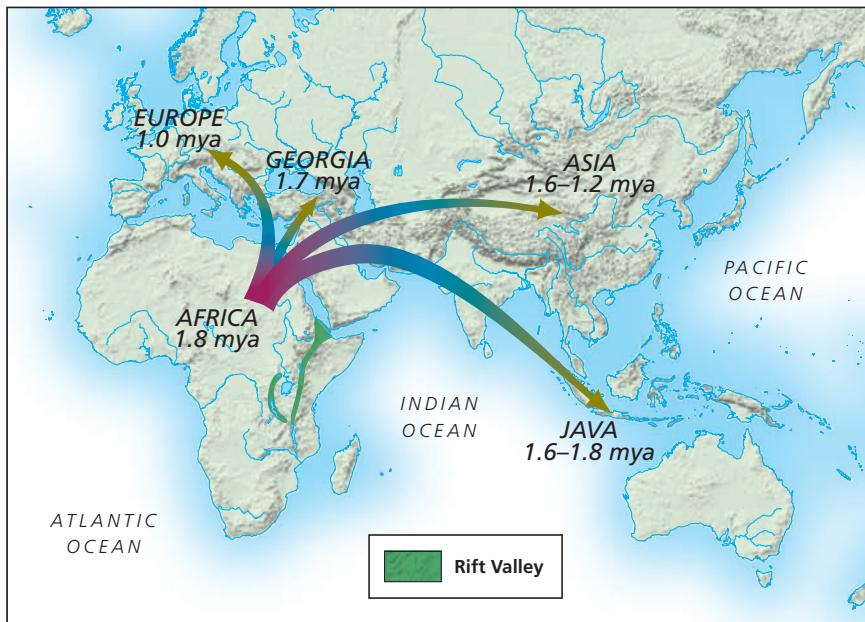
The most important adaptive shift *H. erectus* made was the first migration out of Africa (Figure 11.27). This emigration meant moving across a variety of ecosystems, climates, and ecological settings. Each of these would have presented *H. erectus* with new challenges never encountered by a hominin. Most important was the move from tropical and subtropical Africa into the more seasonally cold regions of the Northern Hemisphere in Eurasia and the Far East. This change alone demonstrates the remarkable adaptability and behavioral flexibility our lineage had evolved by just under 2 million years ago. The ability to adapt to a wide range of novel environments is a hallmark of the human species.

One question remains: Why did hominins remain in Africa for 3 to 4 million years, only to disperse relatively quickly after the origin of *H. erectus*? Some of the likely causes we have suggested in this chapter form a web of ecological and morphological advantages that facilitated *H. erectus* dispersal. First recall that world climate was beginning to undergo some severe fluctuations slightly before the rise of *H. erectus*. The African area was cooling and drying around 2 million years ago, leading to diminished forests with larger grasslands between them. The rise of grasslands saw the increase in the quantities of grass-eating animals like antelope and the evolution of a new niche for animals (including hominins) that could eat them.

H. erectus seems to have taken advantage of these opportunities by using Oldowan tools to access animal foods it was not physically adapted to acquire. The higher-quality animal diet that resulted allowed the growth of larger bodies, and if they had a more linear body shape it may have allowed greater midday activity because they coped better with the heat. Larger bodies allowed greater ranging (home range, the area an animal traverses over a year, is positively correlated to body size in mammals). As animals such as antelope migrated, hominins may have followed.

In the late Pliocene, at about the time that we see other African fauna migrating into the Near East and western Asia, we also see *H. erectus* migrating. Were they following this food resource? Earlier hominins had not migrated during earlier faunal migrations out of Africa. Perhaps they remained in place because of their greater reliance on plant foods. It does seem that at this point *H. erectus* was able to do something that earlier hominins were not capable of doing. It seems reasonable to assume that tool use and the

Figure 11.27 *H. erectus* migrated out of Africa beginning about 1.8 million years ago and is first known from Georgia and Java.



access to previously inaccessible resources it allowed were fundamental to the ability to migrate. However, a complex web of factors must have been involved in dispersal.

And remember, there is unlikely to have been a single directional dispersal event from Africa to Asia. Rather, random movements of multiple hominin groups over time probably led to the eventual dispersal of the species across the Old World, and some back migrations probably also occurred. Even though the entire dispersal seems a long one, consider that an average change in home range of just 1 km a year (less than a mile), over a period of 10,000 or 15,000 years, would have led to a slow dispersal that would look geologically instantaneous.

Having moved into many parts of the Old World using a combination of technology and physical adaptation, and having made a shift in foraging strategy to a higher-quality diet, early *H. erectus* was poised to begin the brain size expansion and intellectual development characteristic of the genus. Through time, *H. erectus* continued a gradual development of physical and cultural evolution. However, more recent species of genus *Homo* exhibited even more dramatic changes. Intelligence is a survival strategy of enormous evolutionary importance to the human lineage. In *H. erectus*, we see the beginning of what intelligence meant for the hominin lineage. Now we turn to *H. sapiens*, in which cognition and culture take on far more importance.

Summary

CLIMATE AND THE EVOLUTION OF *HOMO* IN THE PLIOCENE AND PLEISTOCENE

11.1 Detail the climate and the evolution of *Homo* in the Pliocene and Pleistocene.

- Climate fluctuates dramatically in the plio-pleistocene.
- The genus *Homo* may be adapted to climatic fluctuations

DEFINING THE GENUS *HOMO*

11.2 Discuss the anatomical characteristics used in defining the genus *Homo*.

- Members of *Homo* differ from *Australopithecus* by increases in brain and eventually body size, and decreases in tooth and jaw size.
- Brain size ranges from 500 to 750 cc.

EARLIEST GENUS *HOMO*

11.3 Discuss the arguments surrounding the earliest genus *Homo*, including those for recognizing one species of early *Homo* versus those for recognizing two.

- Many scholars divide the species into *H. habilis* and *H. rudolfensis*.
- *H. rudolfensis* has a more derived face, but the species overlap in size.
- Other scholars argue that only one species *H. habilis* encompasses all the variation and that some of it is attributable to sexual dimorphism.
- So far, early *Homo* is restricted mostly to eastern Africa.
- *Homo* may appear as early as 2.8 million years ago, with the *H. rudolfensis* group appearing about 2.1 million years ago.
- The last early *Homo* not belonging to *H. erectus* is dated to 1.44 million years ago.

EARLY TOOL USE, HUNTING, AND SCAVENGING

11.4 Understand and explain the relationship among early tool use, hunting, and scavenging, including how Oldowan stone tools are made and used.

- Early *Homo* is associated with Oldowan stone tools.
- The Oldowan industry consists of flakes struck from cores have sharp edges useful for cutting.

- Hammerstones were used for flaking and to smash open animal bones to access marrow.
- Oldowan tools are made by *H. habilis*, *H. erectus*, and possibly some *Australopithecus* species.
- Stone tool use is ubiquitous by 2 million years ago.
- Animal bones with cutmarks show that hominins were eating meat.
- Broken and cutmarked bones found at butchering sites provide evidence that early hominins were sometimes eating meat and marrow.
- We do not know whether those animal resources were hunted or scavenged, but we do know that they provide high-quality resources.
- Studies of modern carnivores suggest that scavenging carcasses would have been a possible source of nutrition for early hominins.

WHO WAS *HOMO ERECTUS*?

11.5 Explain who *Homo erectus* was, including the anatomical differences between *H. erectus* and *H. habilis*.

- *Homo erectus* has larger average brain and body size than early *Homo*; however, there is a great deal of size variation in *H. erectus*.
- Members have long, low, and relatively angular cranial vaults, often with well-developed supraorbital and occipital tori and other superstructures.
- *H. erectus* teeth suggest a different diet than *Australopithecus* and a slightly different diet than earlier *Homo*.
- *Homo erectus* first appears about 1.8 to 1.9 million years ago and persists until perhaps 100,000 years ago.
- Some *H. erectus* use Acheulean tools others use Oldowan tools.
- Some scholars divide the species into two—*H. ergaster* in Africa and *H. erectus* in Asia—based on cranial anatomy.

HOMO ERECTUS AROUND THE WORLD

11.6 Discuss the distribution and characteristics of *Homo erectus* around the world.

- Initially an African species, *H. erectus* disperses into Asia and Southeast Asia by about 1.7 million years ago.
- There was a great deal of variation in body size, which may be related to sexual dimorphism, regional differences, or differences in nutrition or climate.
- A web of interrelated factors, including a shift to greater animal resource use, larger ranging, and body size, may be related to this hominin's ability to disperse from Africa.

THE LIFEWAYS OF *HOMO ERECTUS*

11.7 Discuss the lifeways of *Homo erectus*.

- The archaeological record suggests that meat and marrow became a more consistent part of the diet of *Homo* and *H. erectus* providing a high-quality resource in addition to gathered plants.
- Dental evidence suggests that *H. erectus* grew more quickly than we do but more slowly than do living African apes or *Australopithecus*.
- Acheulean tools include bifacial handaxes and cleavers.
- Acheulean tools retain their cutting edges longer and are easier to hold than simple flakes.
- *Homo erectus* used both Oldowan and Acheulean tools.
- The Acheulean industry may be an adaptation to carcass processing and is made by *H. erectus* and archaic *H. sapiens*.

- Teeth suggest *H. erectus* grew more slowly than *Australopithecus*. This, along with larger brain sizes, suggests they must have had a high quality diet.
- Many scenarios of the evolution of genus *Homo* consider these new animal resources important (but not necessarily exclusively responsible) for brain expansion and dispersal from Africa.

Review Questions

- 11.1 How does climate change in the Pliocene and Pleistocene and what opportunities does that present?
- 11.2 What anatomical characters would you use to define genus *Homo*?
- 11.3 Why do some scientists recognize two or more species of early *Homo* but others recognize just one?
- 11.4 What do Oldowan tools look like and what were they used for?
- 11.5 How does *H. erectus* differ from other early *Homo*?
- 11.6 Where does *H. erectus* go first when it leaves Africa and how do populations of *H. erectus* differ from one another in space and time?
- 11.7 Why is *H. erectus* the first hominin to move out of the African continent and colonize the old world.

Key Terms

| | | |
|-------------------------|--|--------------------------------|
| Acheulean, p. 359 | Early Stone Age (or Lower Paleolithic), p. 359 | Oldowan, p. 339 |
| angular torus, p. 344 | flake, p. 339 | platycnemic, p. 346 |
| bifaces, p. 359 | hammerstone, p. 339 | platymeric, p. 346 |
| butchering site, p. 339 | hand axe, p. 359 | quarrying site, p. 340 |
| calotte, p. 353 | home base, p. 340 | sagittal keel, p. 344 |
| calvaria, p. 354 | metopic keel, p. 344 | shovel-shaped incisors, p. 345 |
| canine fossa, p. 358 | Movius line, p. 360 | supraorbital torus, p. 344 |
| cleaver, p. 359 | occipital torus, p. 344 | tool industry, p. 339 |
| core, p. 339 | | |

Chapter 12

Archaic *Homo sapiens* and Neandertals



Learning Objectives

- 12.1** Explain the transitions that took place during hominin evolution in the middle to late Pleistocene including the anatomical characteristics that distinguish modern *H. sapiens* from earlier hominins.
- 12.2** Describe the anatomy and distribution of archaic *Homo sapiens*.
- 12.3** Describe the behavior of archaic *Homo sapiens* as inferred from the evidence preserved in the archaeological record.

12.4 Outline the history, anatomy, health, geographic distribution, and temporal range of the Neandertals.

12.5 Compare Neandertal behavior with earlier hominins.

12.6 Discuss the phylogenetic and taxonomic issues related to understanding relationships among the many late-middle and late Pleistocene hominins.

In an open coal pit in Schoeningen, Germany, a huge mechanical shovel grinds away at the earth, stripping away not only vast amounts of coal but also Holocene and Pleistocene deposits. Over the years, archaeologists have identified a number of Lower Paleolithic sites in the pit. The sites are several meters below ground and date to about 400,000 years ago: the middle Pleistocene. The material found includes flint tools and flakes, combined with the remains of extinct elephants, bovids, deer, and horses. No hominin remains are found, which is unfortunate given the scarcity of fossils from this critical period in human evolution. But after several years of excavation, archaeologist Hartmut Thieme discovered something that was even more scarce, and perhaps more significant, than additional fossil remains: four large wooden spears.

The spears are impressive: Two of them measure more than 2.25 m (7 ft.) in length. Three of them are sharpened at one end. They are carefully shaped and their weight is distributed to make them aerodynamically efficient when thrown. It is also possible that they could have been used as lances and thrust at prey. The fourth, perhaps a throwing stick or small thrusting spear, is smaller (less than 1 m long) and sharpened at both ends. Three smaller wooden implements, made from the branches of trees, were also found. Although the function of these implements is not clear, they each had a groove cut into one end that could have been used to hold flints, perhaps creating a composite cutting or chopping tool.

These wooden tools show us how hominins of the middle Pleistocene made use of organic materials and provide us with a window to the past that is typically shuttered. They remind us that hominin behavior may have been much more sophisticated during this period than we may sometimes think.

Today, one species of hominin, *Homo sapiens*, occupies the globe. As a species, we share a common origin that should be traceable back to a population that existed at a certain time and place: but which time and place? Hominins definitely have an African origin. We do not find hominins outside Africa until after 2 million years ago. But because *Homo erectus*, the presumed ancestor of all later hominin species, lived throughout the Old World in regions that were later occupied by modern humans, it is not immediately clear which *H. erectus* populations, if any, are directly ancestral to us. In addition, the tools these populations made and the behaviors they record become more complicated throughout the Pleistocene. The discovery of tools made from organic material, such as the wooden spears at Schoeningen, reminds us just how much information is missing from the archaeological record of early humans. To understand the evolution of our genus during the Pleistocene, we need to consider both the anatomical and behavioral traits of our ancestors.

In this chapter, we look at the anatomy and behavior of the hominins of the middle to late Pleistocene. Hominin fossils from this evolutionarily dynamic period have been found throughout much of the Old World, but taxonomic assignments for the fossil specimens remain controversial. How many hominin species were present? What constitutes enough variation to differentiate them from one another? Are the famous Neandertals simply another type of human or something more distinct? How did they behave and what does that tell us about the selective pressures and evolutionary changes that led to the origin of our own species?

Hominin Evolution in the Middle to Late Pleistocene

12.1 Explain the transitions that took place during hominin evolution in the middle to late Pleistocene including the anatomical characteristics that distinguish modern *H. sapiens* from earlier hominins.

The beginning of the Pleistocene epoch (1.8 million years ago) is marked by the intensification of glacial cycling, and significant latitudinal variation in climate. At the start of the Pleistocene, as hominins began to move out of Africa and into western Asia and ultimately the northerly latitudes of Europe, climatic conditions in some instances were quite harsh. This harsh climate appears to have kept hominins from moving too far north permanently until they had sufficient cultural means of buffering the conditions. Not until Neandertals and their ancestors was there permanent settlement in Europe.

In about the middle of the Pleistocene we begin to find fossils that exhibit features often interpreted as being more “advanced” or derived in the direction of *H. sapiens* than was *H. erectus*. These specimens often are informally labeled “archaic *Homo sapiens*” or “advanced *H. erectus*,” designations that distinguish them from anatomically modern *H. sapiens* and classic *H. erectus*. Such informal labels indicate the transitional nature of these fossils between *H. erectus* and *H. sapiens* and the difficulty of elucidating their relationships to other hominins. In addition to archaic *H. sapiens*, classic *H. erectus* survived in China and Indonesia until at least the middle Pleistocene and maybe later (see Chapter 11). The earliest representatives of the Neandertals make their first appearance in Europe, and it is possible that the earliest modern humans may also have first appeared in Africa at the very end of the middle Pleistocene (see Chapter 13).

Defining Anatomically Modern *Homo sapiens*

Archaic *H. sapiens* are intermediate between classic *H. erectus* and anatomically modern *H. sapiens*. To understand what this means, let us consider the features that distinguish modern humans from other hominins (Clark, 1975).

Compared with other members of genus *Homo*, the skull of recent *H. sapiens* is large (average capacity 1,350 cc), bulbous, and gracile (Figure 12.1). Muscular ridges on the cranium are not strongly marked. Supraorbital (brow) ridges are not well developed or are absent altogether. The occipital region of the cranium is rounded, lacking development of an occipital torus and usually without an **occipital bun** (a backward-projecting bulge on the occipital part of the skull). The forehead is rounded and more vertical than in other groups of *Homo*. Seen from behind, the maximum breadth of the skull is high (in the *parietal* region), and the vault is parallel-sided in rear view. The **mastoid process**, a protrusion from the temporal bone of the skull that you can feel behind your earlobe, is large and pyramidal in shape. The jaws and teeth are small. The third molars (wisdom teeth) sometimes are poorly developed or even absent. Following jaw size, the face is smaller and retracted under the braincase to a greater degree than in previous hominins because the cranial base is more flexed. A *canine fossa* (a depression in the maxilla above the root of the upper canines) is present. There is marked development of a chin. The limb bones are straight and slightly built, with the lower limb much longer than the upper.

Archaic *H. sapiens* tend to exhibit a mosaic of *H. erectus* (see Chapter 11) and *H. sapiens* features, in many cases retaining the robustness of classic *H. erectus* but with a larger cranial capacity and a shape more similar to recent *H. sapiens*. This intermediate or transitional nature of archaic *H. sapiens* poses problems for classifying these fossils.

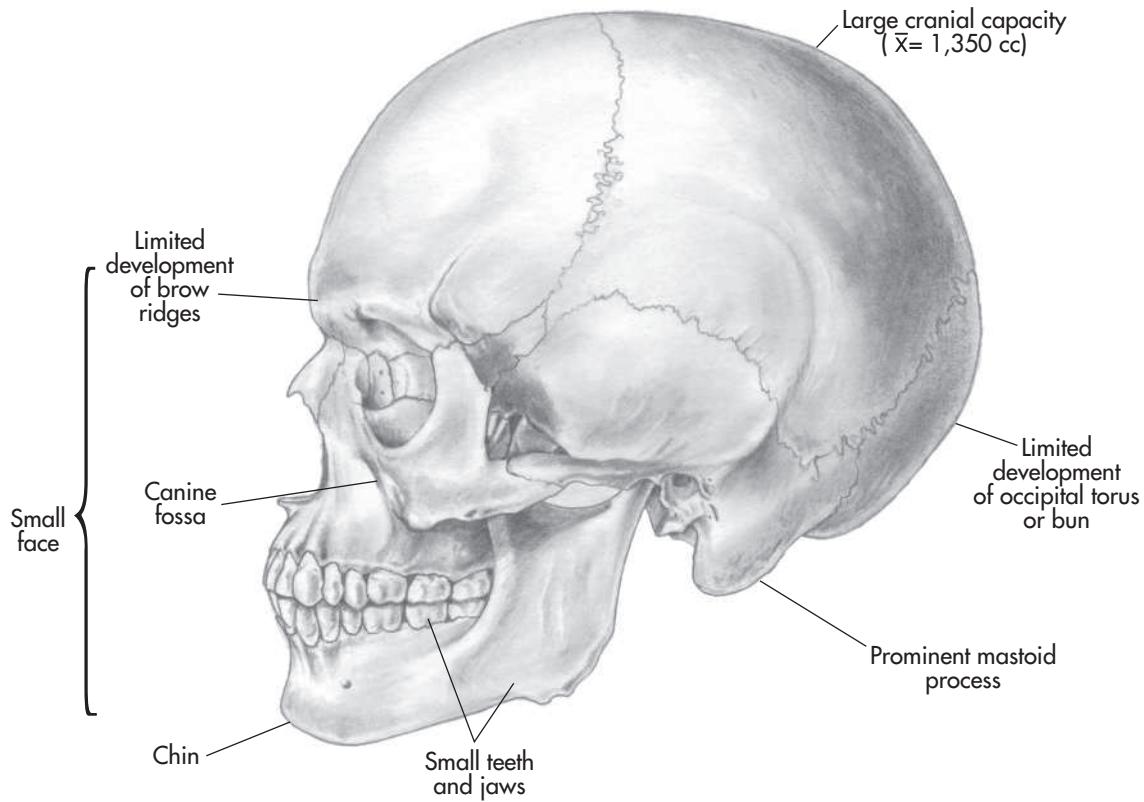
occipital bun

A backward-projecting bulge of the occipital part of the skull.

mastoid process

A protrusion from the temporal bone of the skull located behind the ear.

Figure 12.1 Features of the skull of anatomically modern *Homo sapiens*.



Archaic *Homo sapiens*

12.2 Describe the anatomy and distribution of archaic *Homo sapiens*.

Archaic *H. sapiens* fossils reflect an important transitional period during human evolution. As we review the individual fossils, keep in mind that although we may call them archaic *H. sapiens*, that does not mean we consider them ancestral to later *H. sapiens* (although that may be a reasonable hypothesis), nor do they necessarily all represent the same species, although many scientists argue that they do. Anatomically the group is diverse, but it seems to differ consistently from *H. erectus* by having larger brains (1,000–1,400 cc), more parallel-sided, taller, and less angular cranial vaults, robust but arching rather than straight supraorbital tori, and in some instances, wide nasal apertures (Figure 12.2 on page 374). Archaic *H. sapiens* differ from modern humans by retaining robust supraorbital tori, large faces, and thicker-walled, lower cranial vaults.

European Archaic *Homo sapiens* (*H. heidelbergensis*)

The first archaic *H. sapiens* to be discovered in Europe was a mandible found in 1907 in a sandpit in the village of Mauer, near Heidelberg, Germany (Figure 12.3 on page 374) (Schoetensack, 1908). Based on ESR/U-series dating (see Chapter 9), the mandible was assigned an age of 600,000 years (Wagner et al., 2010). Because the Mauer mandible is clearly not modern—it is quite robust and lacks a chin—it was correctly identified in 1908 as a hominin species distinct from our own. Because *Homo (Pithecanthropus) erectus* was not a generally accepted taxon at that time, the Mauer mandible was given the name *Homo heidelbergensis*.

Although its anatomy is largely primitive, the Mauer mandible differs from classic *H. erectus* in both its bony anatomy and its dentition and resembles several more

Figure 12.2 Features of the skull of archaic *Homo sapiens*.

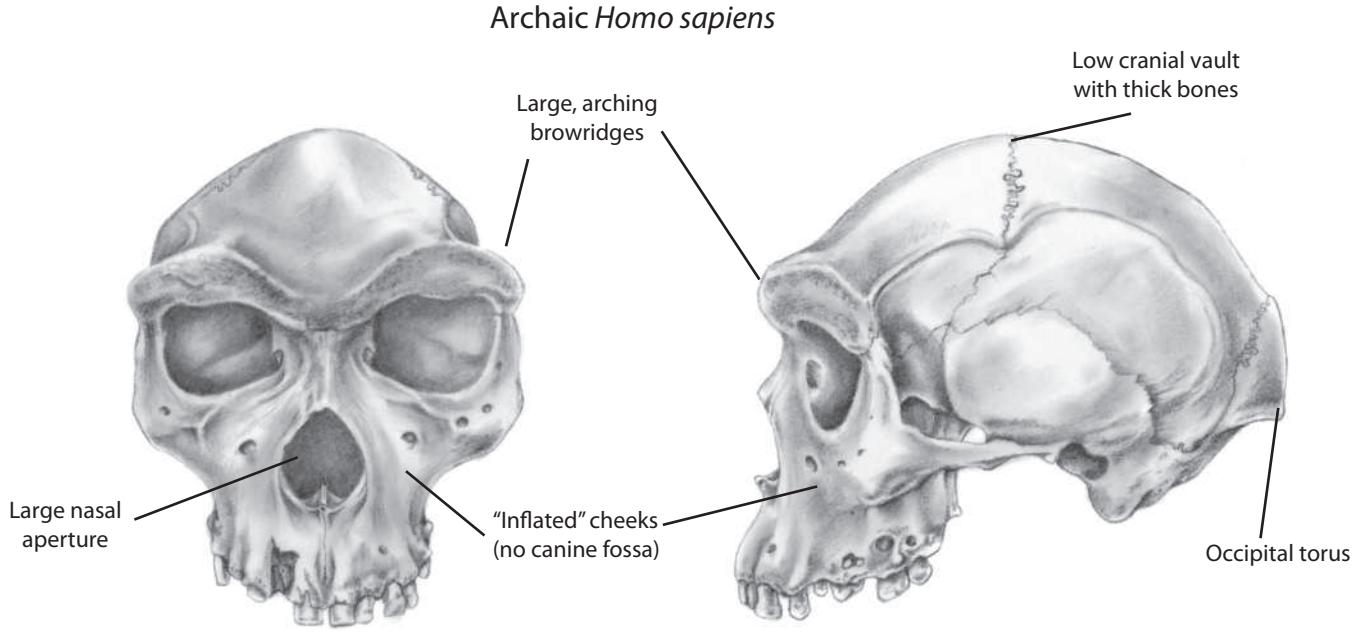


Figure 12.3 The Mauer mandible, discovered in Germany in 1907.



midfacial prognathism

The forward projection of the middle facial region, including the nose.

complete specimens that were discovered later and are often called archaic *H. sapiens*. However, mandibles are notoriously hard to classify, and so the debate continues. For the many researchers who think that the informal label “archaic *H. sapiens*” should be replaced with a formal species designation, the name *H. heidelbergensis* would have priority because the Mauer mandible was the first of this group to be discovered and named.

More complete fossils provide a more detailed picture of European hominins in the middle Pleistocene (Figure 12.4). In general, these fossils are less primitive than the Mauer mandible and include the Petralona cranium from Greece (of uncertain age but likely 150,000–300,000 years ago), the Steinheim cranium from Germany (300,000–350,000 years ago), the Arago 21 partial cranium from France (>350,000 years ago), and the back of a cranium from Swanscombe, England (350,000–450,000 years ago). Less complete remains of archaic *H. sapiens* are known from several other sites in Europe, such as Bilzingsleben and Véretesszöllös in Hungary.

The greatest number and the oldest of the archaic *H. sapiens* fossils recovered from a single locality come from a younger part of the same cave system in which *H. antecessor* was discovered, the Sierra de Atapuerca, Spain (Arsuaga et al., 1997, 2014; Arsuaga, 2002) (Figure 12.5). This cave (or pit) known as “Sima de los Huesos” (literally, the “bone pit”) is about 430,000 years old based on a variety of techniques including U-series dating (Bischoff et al., 2007; Arsuaga et al., 2014). The pit yielded at least 28 individuals ranging in age from 4 to 35 years.

All these archaic *H. sapiens* specimens resemble *H. erectus* in having thick cranial bones and less round cranial vaults and similar postcranial skeletons, but they differ from classic *H. erectus* in vault shape and size, browridge shape, and facial morphology. Their cranial capacities range between about 1,050 and 1,390 cc, making them larger brained than typical *H. erectus* specimens. They have taller vaults with the greatest cranial breadth higher on the parietal than in *H. erectus*, yet their braincase is lower than ours. The extensive postcranial remains from Sima de los Huesos and the 500,000-year-old tibia from Boxgrove in southern England, suggest that like other

Figure 12.4 (a) The Petralona cranium from Greece. (b) The Steinheim cranium from Germany.



(a)



(b)

premodern *Homo*, archaic *Homo sapiens* were robust with strong muscle markings and thick cortical bone, large joint surface areas, and strongly buttressed, broad pelvis (Stringer et al., 1998; Arsuaga et al., 2014).

These middle Pleistocene European hominins are too primitive to be considered Neandertals by most researchers, but especially those from the Sima de los Huesos exhibit several cranial and dental features that are very Neandertal-like. These include a double-arched supraorbital torus and **midfacial prognathism**, the forward projection of the middle facial region, including the nose. The nasal bones actually form a shelf projecting from the face, and the cheek bones gradually recede from these rather than being perpendicular to the nose, as in our face. The nasal aperture is also quite wide. The dental features include an asymmetrical lower fourth premolar and specific crests of the lower molars and P4. These characteristics suggest that the Sima de los Huesos hominins and other European archaic *H. sapiens* may be directly ancestral to the later Neandertals. We will discuss this phylogenetic model and others later.

African Archaic *Homo sapiens* (*H. rhodesiensis*)

The African continent has yielded at least four crania that are generally regarded as archaic *H. sapiens* because of their large cranial capacities, massive but more arching, non-barlike supraorbital tori, and less angular vaults, with their greatest width higher on the cranium. Two are perhaps large males (Figure 12.6). The oldest of these is the partial cranium from Bodo, Ethiopia, which preserves the face and anterior braincase, has a cranial capacity of 1,300 cc and dates to as much as 600,000 years ago (Conroy et al., 1978; Clark et al., 1994). Its most extraordinary features are cut marks on the face that appear to be made by stone tools that may reflect a burial or ritual practice (White, 1986). The Kabwe cranium and

Figure 12.5 Cranium from the Sima de los Huesos, Sierra de Atapuerca, Spain.



Figure 12.6 The Kabwe cranium (left) and the Bodo cranium (right) from Ethiopia, which show signs of having been defleshed with stone tools.



Figure 12.7 Dali, a Chinese archaic *Homo sapiens*.



several postcranial elements were discovered in northern Rhodesia (present-day Zambia) at the Broken Hill limestone mine in 1921. Also known as Rhodesian Man or Broken Hill for their find spot, Kabwe is more complete but slightly smaller (1,280 cc) than the Bodo cranium. Dating of the site is uncertain with ages of 400,000–600,000 and of 125,000 years ago having been suggested (Klein, 1999; Stringer 2011). Both Kabwe and Bodo have large nasal apertures and somewhat prognathic midfaces with massive, arched brows. The previous classification of Broken Hill as an African Neandertal, although now discarded, may indicate an ultimate ancestry to the Neandertal lineage.

Two smaller archaic *H. sapiens* crania also exist in Africa. The Ndutu partial cranium from Lake Ndutu near Olduvai Gorge in Tanzania has a cranial capacity of about 1,100 cc (Rightmire, 1990). The Salé partial cranium from Morocco has a smaller cranial capacity (900 cc). Both crania may be about 400,000 years old (Hublin, 2013). Like the Steinheim cranium from Germany, these crania may be from small females, with similarly small cranial capacities. Although not particularly large, Ndutu and Salé share features of the cranial vault with other archaic *H. sapiens*, including a high maximum cranial breadth and rounder vaults.

The European and African archaic *H. sapiens* specimens share many features and have a similar overall appearance. However, unlike the Sima de los Huesos hominins from Spain, so far no African archaic *H. sapiens* possess the specific derived features that the Sima de los Huesos hominins and other European fossils are claimed to share with later Neandertals.

Asian Archaic *Homo sapiens*

Archaic *H. sapiens* from Asia differ from *H. erectus* in vault size and shape and suprorbital toral shape. Reasonably complete crania from the sites of Dali, Maba, and Jinniushan, China, range in age from 130,000 to 280,000 years old (Figure 12.7). The finds from Jinniushan also include some postcrania. Two other crania from Yunxian probably also represent archaic *H. sapiens* based on the shape of the browridge. However, both are heavily distorted and difficult to interpret (Li & Etler, 1992). The oldest hominin remains on the Indian continent come from the Narmada Valley, where a partial calvaria dates to perhaps 125,000 to 150,000 years ago. The Narmada cranium was initially classified as belonging to *H. erectus*; however, later analyses established its transitional character, indicating that it was more similar to archaic *H. sapiens* (Kennedy et al., 1991). It has an estimated cranial capacity of 1,150 to 1,400 cc, more vertically sided vault walls, and an arched browridge.

Although dating is a problem for the Chinese and Indian archaic *H. sapiens*, evidence indicates that archaic *H. sapiens* probably were present in Asia by 200,000 years ago. Given some of the late dates for some classic *H. erectus* in Asia (see Chapter 11), if you accept that archaic *H. sapiens* is a different species than *H. erectus*, it is possible that two distinct hominin species were present in Asia at this time. Most scientists assign the Asian fossils to archaic *H. sapiens*, but the new Denisovan DNA raises the intriguing possibility that they may instead be related to the Denisovans.

Behavior of Archaic *Homo sapiens*

12.3 Describe the behavior of archaic *Homo sapiens* as inferred from the evidence preserved in the archaeological record.

Reconstructing the behavior of archaic *Homo sapiens* poses a somewhat different problem from reconstructing the behavior of earlier hominins. Given their large brain size and probable close relationship to modern humans, we are compelled to consider archaic *H. sapiens*

behavior from the perspective of what we know about the behavior of contemporary humans. Unfortunately, the material culture of archaic *H. sapiens* doesn't provide a comprehensive rendering of late middle Pleistocene behavior. Nonetheless, archaeological excavations at many sites in the Old World dating from 150,000 to 500,000 years ago indicate this was a period of evolutionary, although perhaps not revolutionary, change in behavior.

Stone Tools

Middle Pleistocene archaeological sites still yield the same stone tool types as seen in the early Pleistocene. In Africa and Europe Acheulean traditions—including production of bifaces (hand axes)—continued until about 150,000 years ago. In China, where hand axes were never associated with *H. erectus*, archaic *H. sapiens* are found in association with simple flake tools and cores. Together the Oldowan and Acheulean industries are known as the *Lower Paleolithic* in Europe or the *Early Stone Age* in Africa.

But in addition to the Lower Paleolithic, **Middle Paleolithic (Middle Stone Age)** industries that used *prepared core* technologies originated in the middle Pleistocene as well (Figure 12.8). Prepared core technologies require that the toolmaker modify the original core by a number of flake removal steps in order to prepare it to produce a flake of a prescribed size and shape. Although wasteful of raw material in one sense, prepared core technology allows great control of production of a main tool type, the so-called *Mousterian* point.

Such preparation in pursuit of a particular flake indicates increasing forethought and abstract thinking. Prepared core techniques include the **Levallois technique** that was developed in Africa between 200,000 and 300,000 years ago. In addition to prepared cores, Middle Paleolithic industries also used other flaking methods, characterized by a greater prevalence of soft hammer techniques (in which materials such as bone, antler, or soft stone were used to remove flakes), more retouched tools, and a larger variety of possibly stylized tool shapes. Tools include a number of different kinds of scrapers, made from flakes, and the previously mentioned points. The advantage of Middle Paleolithic industries, beyond the predictability of flake size and shape, is that from a given amount of raw material they produce more cutting surface than Early Paleolithic techniques.

Middle Paleolithic (Middle Stone Age)

Stone tool industries that used prepared core technologies.

Levallois technique

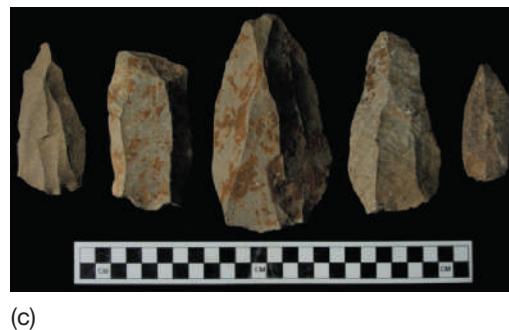
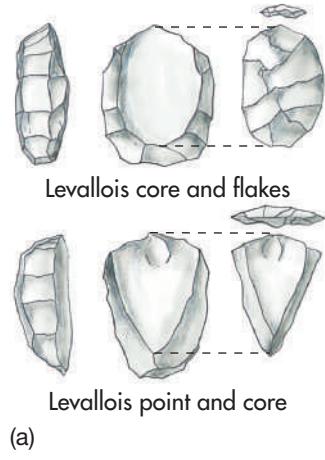
A Middle Paleolithic technique that made use of prepared cores to produce uniform flakes.

Biodegradable Tools

Based on the behavior of living nonhuman primates and humans, we assume that hominins also used tools made from organic materials that would rarely be preserved

Figure 12.8 (a) The Levallois technique for making uniform flakes from a prepared core. (b) A levallois core from Kapedo Tuffs, Kenya dates about 130,000 years ago. (c) Levallois points and flakes from Kapthurin, Kenya date to between 200,000 and 280,000 years ago.

THE LEVALLOIS TECHNIQUE



in the archaeological record. Chimpanzees fashion tools from twigs and leaves, and it is likely that early hominins did as well. Although we have seen evidence of bone tool use by the robust australopithecines (see Chapter 10), modified bone or antler tools are missing from the archaeological record of archaic *H. sapiens*. There is, however, indirect evidence, from flake scars on stone, that bone and antler were used as “soft” hammers to produce stone tools (Stringer et al., 1998).

In addition, the wooden spears, throwing stick, and worked branches from Schoeningen, Germany, described at the beginning of the chapter, provide important evidence of the use of wood by at least 400,000 years ago. The three worked branches may be as significant as the spears, since they may have been the handles of stone-wood composite tools, a technologically advanced technique. Because the tools were found in close association with numerous animal remains, they could be evidence of large game hunting. Some researchers believe these pointed wooden sticks were not spears but only thrusting lances or that, if they were spears, they would not have been very effective for large-game hunting (Klein & Edgar, 2002). Regardless of their use, the well-crafted wooden implements suggest that wood was a common medium, at least for this archaic *H. sapiens* population in Germany.

Big Game Hunting

There is little doubt that big game hunting would have been advantageous for some archaic *H. sapiens* (or *H. erectus*) occupying northern latitudes in Europe or Asia. In those locations, there probably would have been a seasonal dependence on animal food, and the ability to hunt big game would have made it easier to expand into colder areas, even if scavenging were still done. In the 1960s and 1980s Clark Howell and Les Freeman excavated at the Spanish sites of Ambrona and Torralba, dated between 200,000 and 400,000 years ago, and found the remains of large game in association with Acheulean artifacts (Howell, 1966; Howell et al., 1991) (Figure 12.9). Critics point out that associations such as this do not constitute proof of hunting because they could have resulted from the activity of other animals or other nonhominin depositional forces. Perhaps the Ambrona and Torralba animals were scavenged not hunted; the sites were in a swamp, and some investigators think the animals could have died while stuck in the mud and then have been scavenged (Shipman & Rose, 1983). Others argue that finding both large animals and artifacts at watering spots simply means that water was important for both hominins and other animals and does not indicate a reliance on big game by either hunting or scavenging (Klein & Edgar, 2002).

Figure 12.9 F. Clark Howell excavates remains at Torralba, Spain.



However, excavations at two sites in the 1990s provide increasing evidence in support of the hypothesis that hominins hunted big game by the middle Pleistocene. The Schoeningen spears were found in direct association with the butchered remains of 10 horses and flake tools that could be used to deflesh the carcasses. Although it is impossible to be certain that the spears were used to bring down the horses, it seems reasonable to conclude they were made to be thrown at large, living animals. Excavations at the Boxgrove site in England (Figure 12.10) provide further evidence of big game hunting (Stringer et al., 1998; Roberts & Parfitt, 1999). In addition to a hominin tibia and tooth, numerous remains of small and large animals in association with stone tools,

mostly hand axes, have been meticulously excavated. Mark Roberts and his colleagues argue that big game hunting rather than scavenging explains how these animals and tools came to be deposited together: Taphonomic analysis indicates that hominins defleshed the remains before carnivores or scavenging animals; stone tool cut marks always underlay carnivore teeth marks, and butchering marks indicate that eyes and tongues were removed by hominins ahead of bird scavengers. Furthermore, butchered rhinoceroses at the site were all healthy midlife adults with no apparent disease or defect, and a horse scapula (shoulder blade) recovered from the site has a projectile wound, a hole about 50 mm (2 in) in diameter; just the kind of wound you would expect from spears like those found at Schoeningen.

Thus, evidence seems to be mounting that archaic *H. sapiens* were capable of bringing down large game and that they did so in a cooperative manner, using Acheulean technology. At this point, however, it seems that these middle Pleistocene hominins did not have a great impact on the populations of large game animals they hunted. We do not, for example, see any evidence of animals driven to extinction by archaic *H. sapiens*, as we would see in some regions of the world in the later part of the epoch when modern *H. sapiens* overhunted their large game species. This may indicate that big game hunting occupied a less important role in the subsistence strategies of archaic *H. sapiens* than it did for anatomically modern *H. sapiens*. It may also speak to differences in population size between the hominins.

Fire, Campsites, and Home Sites

Evidence of the use of fire and campsites by archaic *H. sapiens* is rare. No proper hearths have been discovered, but ash deposits and charred bones recovered from a number of sites indicate that fire may have been used by archaic *H. sapiens*. Archaic *H. sapiens* did not leave a particularly obvious imprint on the landscape. Although it is reasonable to assume that they had campsites and home bases, there are few signs of them in the archaeological record. No postholes or storage pits have been found, for example. The use of caves as shelter was also limited. Evidence of Acheulean “beach huts” at the site of Terra Amata in the South of France has been claimed. However, disruption of the “living floor” of the site and the somewhat random scatter of bone and stone remains make this interpretation difficult to accept (Stringer & Gamble, 1993).

Figure 12.10 Evidence for big game hunting by archaic *H. sapiens* is suggested by the excavations at the Boxgrove site, England. Here the stratigraphic layers of the site that have been meticulously excavated can be seen.



The Neandertals

12.4 Outline the history, anatomy, health, geographic distribution, and temporal range of the Neandertals.

Compared with the little we know of archaic *H. sapiens*, we know much more about the anatomy and behavior of the later Pleistocene hominins informally known as Neandertals. The complete or partial remains of several hundred Neandertal individuals have been discovered from sites dating between about 35,000 and 150,000 years ago in Europe, the Near and Middle East, and western Asia (Figure 12.11 on pages 380–381) (Stringer & Gamble, 1993; Trinkaus, 1995). As you will recall from Chapter 8, this time period is one of extreme oscillations in temperature caused by strong glacial and interglacial cycles (see Figure 8.18, on page 254). As a result latitudinal variation in climate became quite significant (remember that temperature varied little

Hominin Evolution in the Mid to Late Pleistocene

Figure 12.11 Beginning about 600,000 years ago in Africa, hominins who were somewhat larger brained than classic *H. erectus* but still cranially robust appeared in Africa, and then later in Europe and Asia. This group is usually referred to as archaic *Homo sapiens* (or by some as *H. heidelbergensis*). In Europe and western Asia, a distinct type of hominin, the Neandertals, appeared about 140,000 years ago. Their antecedents may be represented among the archaic *H. sapiens* specimens of Europe, dating up to 400,000 years ago.



BOXGROVE Evidence of big game hunting by archaic *H. sapiens* is hinted by hand axes and deer bones at the Boxgrove site, England.

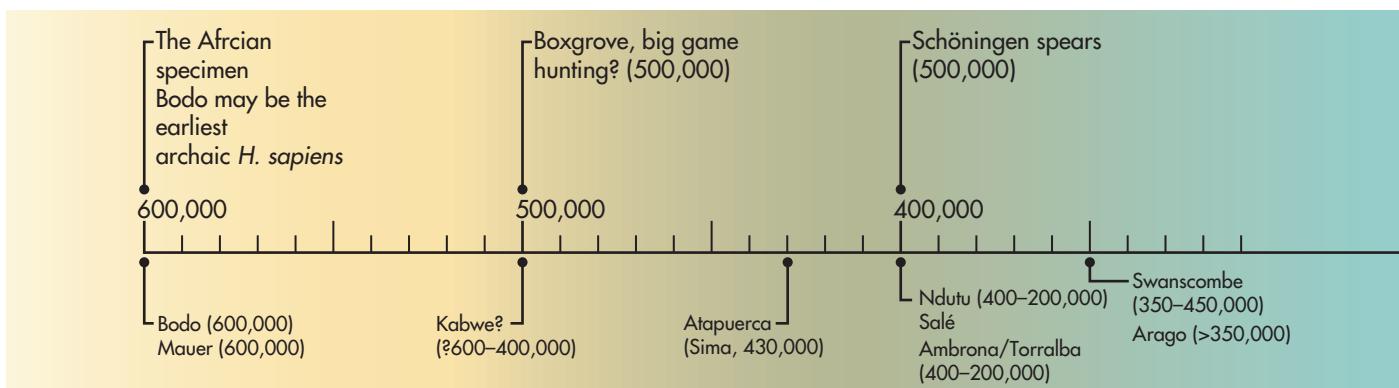
NEANDERTALS Neandertal specimens are numerous enough that we can begin to understand developmental changes across their lifespan.

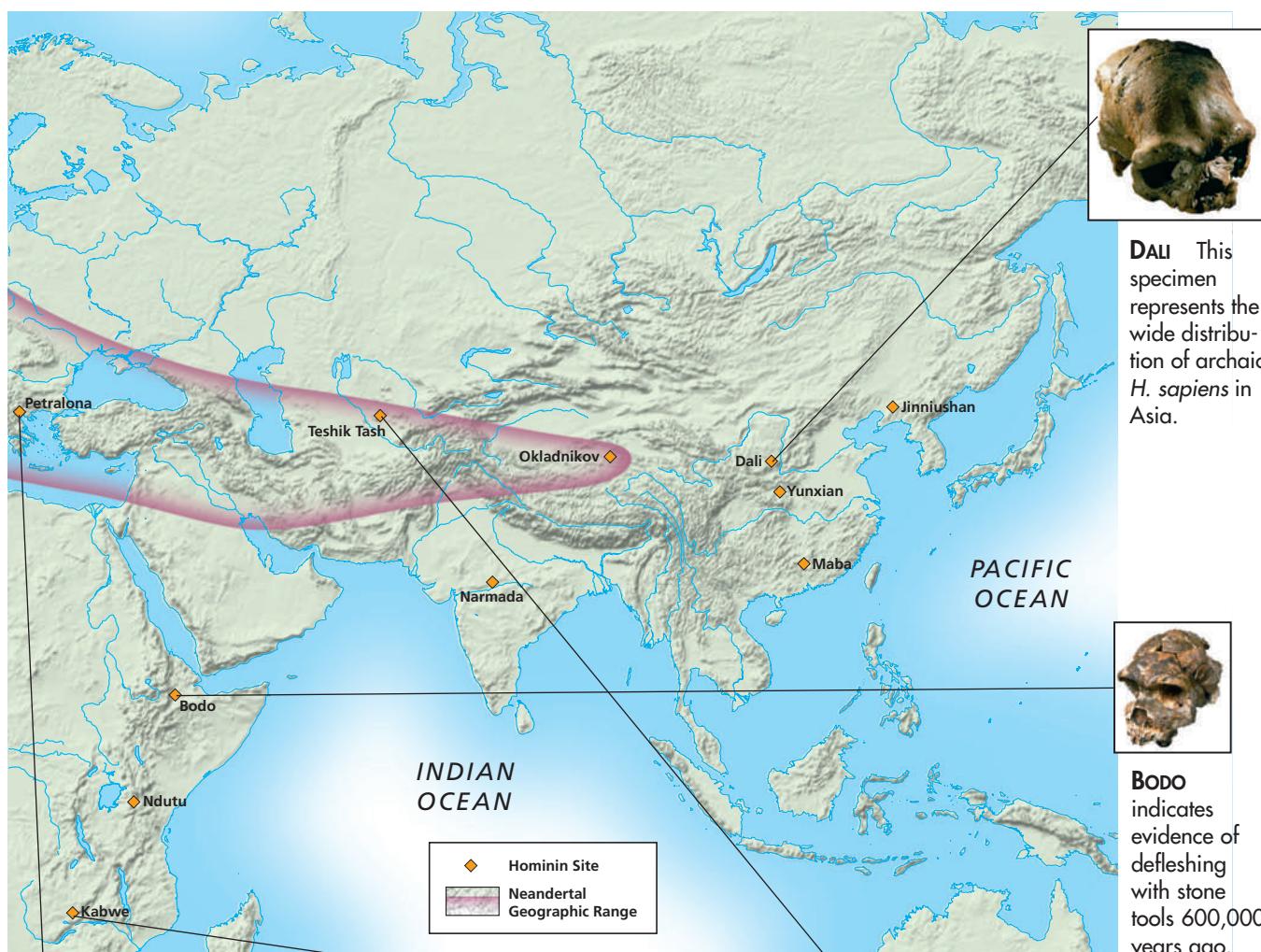


ATAPUERCA Remains of more than 30 archaic *H. sapiens* individuals have been found in the Sima de los Huesos at Sierra de Atapuerca, Spain.



STEINHEIM is a possible contemporary of Petralona.





PETRALONA is a typical archaic *H. sapiens* specimen, but some argue that it has pre-Neandertal characteristics.

KABWE (OR BROKEN HILL) was once thought to be an "African Neandertal" but is now considered to be an archaic *H. sapiens*.



Origins of levallois technique in Africa signals beginning of MSA (300–200,000)

300,000

Steinheim
(300,00–350,000)

Petralona
(300–150,000)

Approximate end of the Acheulean in Europe and Africa (150,000)

200,000

Dali (200–130,000)
Maba (200–130,000)
Jinniushan (200–130,000)
Yunxian (200–130,000)

Earliest appearance of classic Neandertals (140,000)

Narmada (150–125,000)

Kabwe (?125,000)

Latest appearance of classic Neandertals (39,000)

Present

from north to south early in primate evolution). Yet some Neandertals lived fairly far north, and thus climate is a particularly important variable for understanding the origin and evolution of this group (Howell, 1964). At the end of their existence Neandertals and anatomically modern *H. sapiens* overlap in time and space. How they share the landscape, and indeed the relationships between them, are points of some debate.

Scientists disagree as to whether Neandertals should be considered a species within the genus *Homo* (*H. neanderthalensis*) or a subspecies within *H. sapiens* (*H. s. neanderthalensis*). As was the case for archaic *H. sapiens*, choosing a taxonomic name for the Neandertals depends on how we define a species and on the phylogenetic model for the emergence of anatomically modern *H. sapiens* to which we subscribe. There is little disagreement that “classic Neandertals” are an anatomically distinct group of hominins that lived during a short period of time and occupied a circumscribed portion of the Old World. However, there is much disagreement as to whether or not these anatomical differences mean that Neandertals are a separate species or simply a geographic variant of *H. sapiens*.

Geographic and Temporal Distribution

Neandertals occupied a circumscribed portion of the old world (Figure 12.12). The largest number of Neandertal sites, including the oldest (more than 150,000 years ago) and the youngest (perhaps 35,000 years ago, but certainly to 40,000 years ago), are located in Western Europe. Fossil-bearing sites are plentiful in Germany (Neandertal, Ehringsdorf), Belgium (Spy, Engis), Spain (Zafarraya, Gibraltar), Italy (Guattari), and France (La Quina, La Ferrassie, St. Cesaire, La Chapelle). However, the Neandertal range extends into Central Asia at the site of Teshik Tash in Uzbekistan and based on DNA evidence Okladnikov in Siberia, into the Near East (Kebara, Amud, and Tabun, Israel; Dederiyeh, Syria), and into the Middle East (Shanidar, Iraq). In addition to fossil-bearing localities, archaeological sites of the same ages span the entire

Figure 12.12 Distribution of Neandertal sites in Europe and western Asia.



region, telling us about site distribution and Neandertal movements relative to time and climate.

Most Neandertal fossils are found in caves, indicating extensive use of these areas as living sites. However, most Middle Paleolithic archaeological sites are open air localities. Cave use results in better preservation of remains and thus the better fossil record for Neandertals than for earlier hominins.

History of Neandertal Discovery

From the mid-1800s until the 1930s, when *H. erectus* became a more widely accepted taxon and the South African australopithecines started to come to light, Neandertals were the core of the hominin fossil record. In the popular imagination, “Neandertal” and “caveman” became synonyms. But as the best-known representative of our evolutionary past, Neandertals also became the focus of negative portrayals and feelings (see Insights and Advances: Neandertal Image Makeover on pages 385–386). Ideas about progress along with anxiety about our animal origins cast the Neandertal in the loser’s role in the evolutionary game.

The significance of the first Neandertal finds was not fully appreciated at the time of their discovery. The first Neandertal discovered, the cranium of a small child aged 2 to 3 years, was found in 1830 at the Engis cave site in Belgium. Even at that young age the Engis child shows incipient development of a double-arched Neandertal browridge. The second Neandertal discovery, in 1848, was a nearly complete cranium from the British colony of Gibraltar on the southern coast of Spain. It took nearly 20 years for the Gibraltar cranium to be recognized as a Neandertal; although considered from the time of its discovery to be an ancient specimen, the Engis child was not “rediscovered” to be a very young Neandertal for more than a century. Perhaps they were not appreciated because both were discovered well before Darwin published his theory of evolution by means of natural selection in 1859, and thus the framework necessary for understanding them was not in place.

The original Neandertal specimen (for which the group was named) was found in 1856 in a limestone quarry in the Neander Valley (in German, the word for valley is *tal*) near Düsseldorf. The quarry was dotted with caves filled with clay and debris that had to be removed before the limestone could be mined. The Neandertal remains, including a skullcap and partial skeleton, were discovered in such clay deposits that had been thrown 20 m (60 ft.) down a hill (Figure 12.13). The owner of the quarry saw large bones in the deposit and, thinking that they were from cave bears, contacted a local schoolteacher and natural historian, Johann Carl Fuhlrott who identified them as human. Recognizing the potential significance of the find, Fuhlrott contacted noted anatomist Professor Herman Schaafhausen, who led the scientific analysis. Although the original cave was destroyed by commercial quarrying, the deposits removed from the cave were recently rediscovered through study of the archives of the mining company (Schmitz et al., 2002). More than 140 years after the initial find, additional bones and artifacts from the Neander Valley indicate that there were at least three individuals in the cave. Almost unbelievably, additional remains of the original Neandertal specimen were discovered. This re-excavation allowed dating of the finds for the first time, giving them an age of 40,000 years.

Professor Schaafhausen presented his initial analyses of the Neandertal remains in 1857, a full 2 years before Darwin published *On the Origin of Species*. Schaafhausen noted the long and low shape of the skullcap, the large browridges, and the development of an occipital bun. All

Figure 12.13 The original Neandertal remains from the Neander Valley, Germany.



these features distinguished this specimen from modern humans. Furthermore, the postcranial bones were very robust and marked with strong ridges for the attachment of large muscles; the ribs were rounded, indicating a barrel-chested individual. One of the bones of the lower left arm (the ulna) had clearly been broken and healed awkwardly; it is likely that the arm was not usable in life, and it showed some signs of atrophy due to disuse. Schaafhausen concluded, however, that the left arm was the only pathological aspect of a skeleton that otherwise reflected the normal development of a race of men (or perhaps a species) who lived in Europe long before the Romans or Celts. Critics argued the remains were simply those of an odd or pathological human: perhaps a Cossack who had died during the Russian invasion of Germany in 1814, or possibly an unfortunate individual who suffered from a variety of pathological conditions, thus explaining his obviously injured left arm.

Thomas Henry Huxley, who was known as “Darwin’s bulldog” for his vociferous defense of natural selection (see Chapter 1), provided one of the first evolutionary analyses of the Neandertal specimen, in 1864. Although Huxley was impressed with the “pithecoid” (apelike) nature of some aspects of the skull, such as the thickness of the bones and the browridges, he concluded that the Neandertal was no ape-man or “missing link.” The cranial capacity clearly exceeded that of any ape and was in the human range, and the postcranial skeleton, though robust, was essentially human. Huxley placed the Neandertal at an extreme end of variation seen in modern humans. While Huxley was presenting his analyses, British anatomist George Busk recalled the odd-looking skull from Gibraltar he had seen years before. In 1864, he presented the Gibraltar cranium as the second Neandertal specimen.

Arguments that the Neandertal specimen represented only a diseased modern human rather than a distinct fossil ancestor would not be disproven until more fossils were discovered. By 1915, Neandertals were known from sites in Germany, Spain, Belgium, Croatia, and France. In the 1920s and 1930s, they were discovered in sites in the Middle East and as far as Uzbekistan in Central Asia. We now have the remains of hundreds of Neandertal individuals recovered from dozens of sites.

Besides modern humans, Neandertals are by far the most thoroughly represented hominins in the fossil record. Given the relatively large number of Neandertal fossils, it is possible to study aspects of their growth and development and demography, population-level variables that are impossible to realistically examine in earlier hominins. It is likely that compared with earlier hominins, the cultural behavior of Neandertals was more complex, so it is more difficult to interpret in the context of the archaeological record.

Neandertal Anatomy and DNA

Neandertals possess some derived features that are not present in either anatomically modern humans or archaic *H. sapiens* such as *H. heidelbergensis* (Figures 12.14 and 12.15 on page 386). Therefore, many scientists think that they represent a unique evolutionary trajectory. Some of their derived features seem to be anticipated by the anatomy of some archaic *H. sapiens*, especially those from Sima de los Huesos, perhaps suggesting that Neandertals descended from these populations.

Although the Neandertal vault is long and low, its size and shape are quite different from that of *H. erectus*. The Neandertal cranium is larger than that of *H. erectus* or *H. sapiens*; the species average is 1,520 cc. Research on Neandertal brains (as studied from endocasts) suggests they were fully modern in their organization and that the large size of the brain was a function of large body size and adaptation to the cold environments in which they evolved (Holloway, 1984).

In addition to these size differences, vault shape differs in important ways. The maximum cranial breadth in Neandertals tends to be in the middle of the

Insights and Advances

Neandertal Image Makeovers

It is definitely not a compliment to be called a Neandertal, and most of us are familiar with the stereotype of the brutish caveman. Although the origins of the stereotype have their roots in early negative portrayals of Neandertals presented by scientists, it is safe to say that the scientific appraisal of Neandertals over the past several decades has been far more positive than negative, despite debates about their status vis-à-vis anatomically modern *H. sapiens* (Figure A). So why does the negative connotation of Neandertals remain in the popular culture?

Erik Trinkaus and Pat Shipman (1992, pp. 406–407) chronicled the ambivalence of popular and scientific images over the years, writing “They [historical Neandertal images] testify to an ongoing struggle between our willingness to accept Neandertals as close relatives and yet our abhorrence at having anything so potentially inhuman so close at hand. It is the age-old struggle between the god-like and the bestial in humans restated.” According to Trinkaus and Shipman the oldest illustration of a Neandertal from a popular magazine article published in 1873 was a picture of a Neandertal couple and their dogs that has an almost romantic quality. The Neandertal male is portrayed as a kind of “noble savage,” ready to meet head-on anything that might appear at the mouth of their cave to challenge them. The woman’s portrayal, on the other hand, constitutes a stereotype of Victorian notions of female passivity. Clearly, this view of Neandertals is not wholly negative or bestial, although it reflects Victorian mores.

However, later reconstructions see-sawed between beast and gentleman. The discovery of the French La Chapelle-aux-Saints Neandertal led to reconstructions of Neandertals in the popular press that were clearly not of the noble savage type. Instead, an image from a popular French publication (1909) reveals a feral and bestially Neandertal who is very unlike a modern human (Figure B). Not long after this, scientist Marcellin Boule depicted Neandertals as stooped and hulking. Their brawn was emphasized over their brains. By the 1930s, anthropologist Carleton Coon produced a drawing of a Neandertal dressed in modern clothing, making the point that a Neandertal could ride on the New York subway with little notice if he were dressed correctly and



Figure A A scientific reconstruction of a Neandertal family.



Figure B Historical reconstruction.

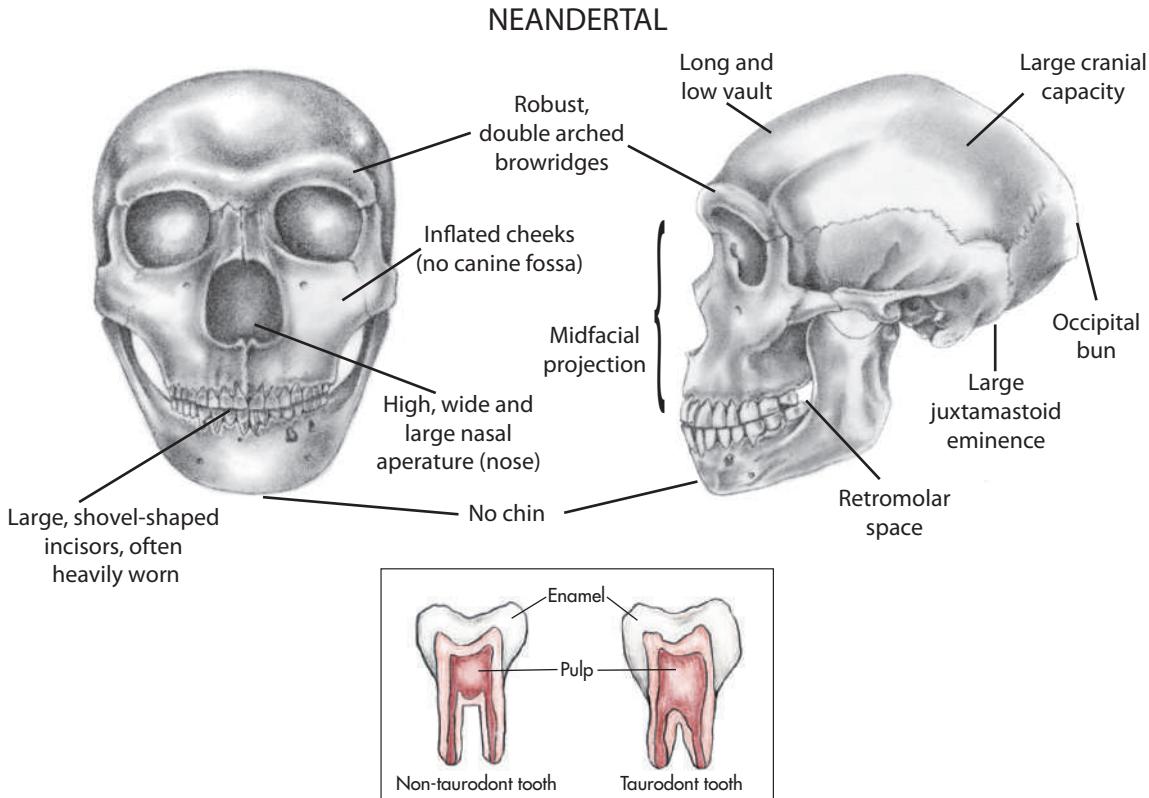
given a good shave. And the paleoanthropologist Milford Wolpoff considers his own appearance quite similar to that Coon representation. Yet a 1950s horror movie, *The Neanderthal Man*, indicates that the more beastly view was easier to sell to the moviegoing public. (Figure C)

Popular views of Neandertals reflect not only deep-seated tensions about the conflict between humanity and bestiality, as Trinkaus and Shipman suggest, but also feelings about racial inferiority and superiority. After all, humans have a long history of considering those who do not come from their own particular group as being something less than human, even when they most obviously are. In his novel *Dance of the Tiger*, which dramatizes the demise of the Neandertals in northern Europe some 40,000 years ago, noted paleontologist Björn Kurten makes a point of depicting the Neandertals as light-skinned and destined to be replaced by darker-skinned modern humans from the south. Although these skin color assignments are justifiable based on scientific grounds, from a literary standpoint Kurten was also using race as a device to make an ancient species-level conflict more poignant for twentieth-century readers.

Recently, a series of car insurance commercials have played on this ambivalence about Neandertals, promoting their product as “so easy a caveman could do it,” but then showing the astute and sensitive caveman as traumatized by this stereotyping.



Figure C Bestial reconstruction from the 1950's movie Neandertal man.

Figure 12.14 The Neandertal skull and teeth. Neandertals have taurodont molars.

juxtapamatoid eminence

A ridge of bone next to the mastoid process; in Neandertals, it is larger than the mastoid process itself.

cranium, giving it an oval appearance when viewed from the rear. In contrast, in humans, the maximum cranial breadth is higher on the skull, and the side walls are parallel. In *H. erectus* maximum breadth is low on the vault, and the side walls slope inward, forming a pentagon in rear view (Figure 12.16). At the back of the Neandertal cranium, the occipital bone bulges posteriorly, forming the occipital bun. The mastoid process in Neandertals is smaller than in modern humans, but a ridge of bone just next to it, the **juxtapamatoid eminence**, is larger than the mastoid process.

Figure 12.15 The faces of Neandertal (left) and anatomically modern *H. sapiens* (right) display anatomical differences including a double-arched brow and absence of a canine fossa in Neandertals.

The face of the Neandertals also differs from those of *H. erectus* and modern humans. Among the most important of the derived characters of the Neandertals is their midfacial prognathism (Figure 12.15). The middle part of the face, around the nose, projects strongly anteriorly, and the cheek region is placed far posteriorly, with an even grade between the two. It is almost as if someone has grabbed the Neandertal nose and pulled it away from the cheeks, forming a smooth transition from cheek to nose. Therefore, the cheeks of Neandertals are often described as "swept back." The face as a whole is also quite tall. Probably related to the anterior position of the midface (and upper dentition) is the presence on the rear of the mandible of a *retromolar space* between the third molar and the ascending ramus. Like earlier hominins, Neandertals show no development of a chin.

Figure 12.16 Posterior views of *H. erectus*, Neandertal, and modern *H. sapiens* show differences in vault shape.



There are also important differences between the inner ear anatomy of Neandertals and that of modern humans and *H. erectus*. The semicircular canals of the inner ear assist in maintaining balance, but there is variation in their structure even between closely related species. Although modern humans and *H. erectus* do not differ in inner ear anatomy, work by Fred Spoor and his colleagues using three-dimensional CT scans shows that Neandertals have a different and probably derived inner ear anatomy (Figure 12.17 on page 388); (Spoor et al., 2003). The differences are so clear that they have been used to definitively identify the infant temporal bone from Arcy-sur-Cure, France, as a Neandertal, an important identification for this site that had otherwise nondiagnostic fossil remains (Hublin et al., 1996). More recent detailed analyses of the teeth from the site also support a Neandertal affinity for the remains (Bailey & Hublin, 2006). Arcy-sur-Cure is one of only two sites in which Neandertals are associated with an Upper Paleolithic (blade-based) technology known as the Châtelperronian and may also show association with symbolic remains including personal ornaments. These clear-cut differences in ear anatomy also support the idea that the Neandertals may be a species separate from modern humans.

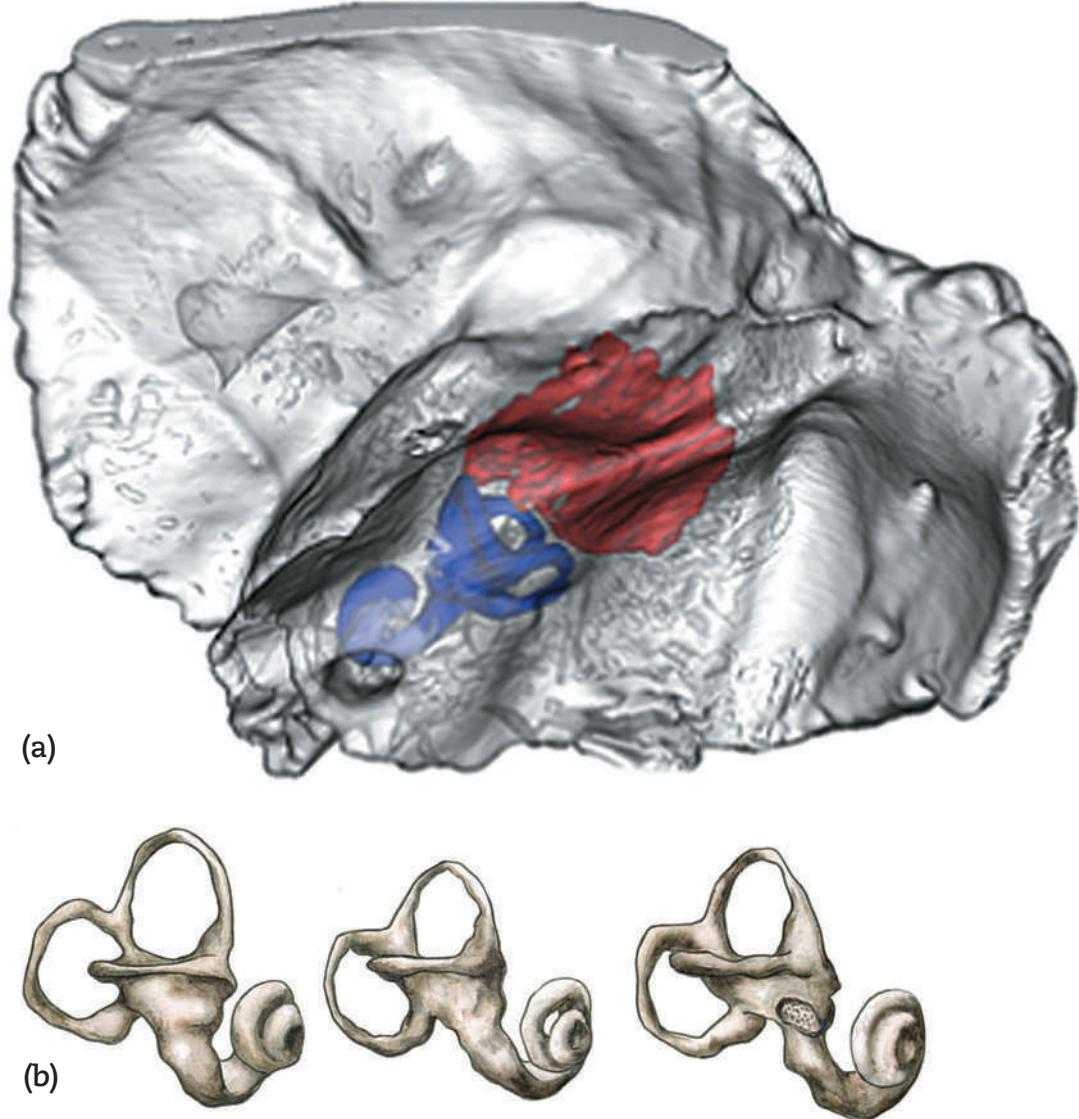
Several prominent features characterize Neandertal teeth. The anterior teeth are large compared with modern humans and they show an unusual amount of wear that is much greater than that on the molars and is greater than among modern human populations, even those who extensively use their anterior teeth. Neandertal upper incisors were more curved than those of modern humans and had built-up ridges of enamel on the side nearest the tongue (lingual surface), giving the tooth a *shovel-shaped* appearance. Shovel-shaped incisors generally are considered to provide greater resistance to wear. Lower fourth premolars are perhaps the most distinctive difference between Neandertals and modern humans; Neandertals have extra subcusps that modern humans lack and are very asymmetric. Neandertal molars also tended to have extra cusps and specific crests more frequently than modern humans, and the molars had expanded pulp cavities and fused roots, a feature known as **taurodontism** (Figure 12.14 on page 386). Taurodont teeth can sustain more wear than nontaurodont teeth because they maintain a broader base for wear after the enamel of the crown has been worn away. Both taurodont molars and shovel-shaped incisors are found in modern human populations at various frequencies.

Many have speculated about why Neandertals had such prognathic faces, large noses, and heavily worn teeth. A popular idea is that the nose warmed cold air before it reached the respiratory system and brain. Among modern humans, however, cold-dwelling populations tend to have long and narrow noses to restrict cold airflow to the brain, whereas broad noses are found in more tropically adapted humans and

taurodontism

Molar teeth with expanded pulp cavities and fused roots.

Figure 12.17 Neandertal inner ear anatomy is distinctive from modern humans. The inner ear is figured in blue in this temporal bone from Engis images by Antoine Balzeau (a). The size and shape of the canals differ between the Neandertal ears (on the right) and the modern human ear on the left (b).



facilitate heat dissipation (Stringer & Gamble, 1993). Others argue that the prognathic midface (and the large nose associated with it) helps dissipate heavy bite loads on the anterior dentition. However, in animals and hominins that produce large bite forces, the face typically is retracted, not prognathic (remember the adaptive suite of the robust australopithecines, for example), and Neandertal muscle forces may not have been much greater than in modern human fossils with very different facial morphologies (Antón, 1996; O'Connor et al., 2004). No convincing argument for an adaptive function for the large Neandertal face and nose has yet to be generally accepted, and it may be that Neandertal facial morphology results from a variety of phylogenetic trends or evolutionary forces. We would also do well to remember that although Neandertal facial features are striking compared with modern humans, as Erik Trinkaus (2003) points out the large faces of Neandertals reflect continuation of a trend seen in archaic *H. sapiens*; thus, modern humans should be thought of as having small faces. Similarly, large nose size and other features in the nasal region of the Neandertals also reflect well-established evolutionary trends observed in a

wide range of middle and late Pleistocene hominins (Franciscus, 1999, 2003). In particular, genetic isolation in glacial environments may have produced the Neandertal face via genetic drift from an already prognathic ancestor as Clark Howell proposed many years ago. Tim Weaver, Charles Roseman, and Chris Stringer have used population genetic models to convincingly argue that the Neandertal face is likely the result of gene drift (Weaver et al., 2007).

The postcranial skeleton of the Neandertals was massive compared with that of modern humans, although Neandertals were shorter on average than we are (Figure 12.18, on the left). Neandertal males are estimated to have stood about 169 cm (5 ft. 6.5 in.) tall, with a weight of 65–78 kg (143 lbs.), whereas females were 160 cm (5 ft. 3 in.) and 50–66 kg (110 lbs.) (Stringer & Gamble, 1993). The chest was barrel-shaped and the limbs, especially the forearm and shin, were short. These characteristics are consistent with a body designed to conserve heat in a cold climate (see Bergman's and Allen's rules in Chapter 5), and Neandertals have been described as having "hyper-polar" bodies (Holliday, 1995). The long bones and major joints were all larger and more robust than those found in modern humans, features that Neandertals may have shared with earlier hominins and that indicate a physically demanding lifestyle.

The Neandertal skeleton shows evidence of having had very large, powerful muscles. Erik Trinkaus suggests that this powerful build indicated high levels and possibly even long hours of physically difficult activity. The energetic costs of such activity have been estimated by Mark Sorenson and Bill Leonard (2001), who suggest that Neandertals would have had daily energy needs much higher than those of modern human hunter-gatherers and more similar to those of trained athletes and subsistence farmers.

Neandertal and modern human postcranial skeletons differ in several other respects. One of the most striking differences appears in the anatomy of the *pubic bone*, which forms the front part of the pelvis. The upper, anterior part of the pelvis, formed by the *superior pubic ramus*, was longer and more gracile in Neandertals than in modern humans. This is in direct opposition to the pattern established by the rest of the skeleton. Much speculation about the function of the Neandertal pubis has been offered. However, the complete Neandertal pelvis discovered at Kebara, Israel, shows that the lengthened pubis does not result in a larger pelvic outlet (Figure 12.19). This suggests that pubis size is not related to either increased birth efficiency or increased gestation time, as has been previously argued. The broader pelvis may simply have been the Neandertal way of establishing greater body breadth (and greater volume relative to surface area) to aid in heat retention. Despite some obvious examples of adaptation to cold-climate, the estimates of Neandertal heat retention still suggest that they would have required some clothing and shelter to live in most of their known range (Aiello and Wheeler, 2003).

In the late 1990s, the original Neandertal remains again came to the attention of the scientific world when it was announced that DNA from this specimen had been successfully extracted, amplified, and sequenced (Krings et al., 1997). DNA from the recently discovered Mezmaiskaya subadult and a number of other individuals has also been extracted and analyzed (Schmitz et al., 2002). Attempts to extract DNA from fossils this old (hominins or other animals) often are unsuccessful, but the cold climate the Neandertals lived in

Figure 12.18 These articulated skeletons suggest that Neandertals were much more heavily built than anatomically modern humans.



Figure 12.19 The Kebara remains from Israel had a complete innominate that shows that the birth canal was no larger in Neandertals than in modern humans.



may have helped to preserve their DNA. Initially scientists had only small snippets of Neandertal mitochondrial DNA that is quite different from that of living peoples. Recently two groups of scientists have isolated nuclear DNA (Noonan et al., 2006; Green et al., 2006) and a draft of the Neandertal genome was published in 2010 (Green et al., 2010; see Innovations: Neandertal Genes on pages 392–393). The phylogenetic implications of these results are discussed in Chapter 13.

Growing Up Neandertal

Neandertals are the only fossil group to be reasonably well represented by children's remains of nearly all ages from fetal to just short of adult. In Belgium, the first Neandertal ever discovered was the 2- to 3-year-old Engis child, and the site of Spy also yielded deciduous (baby) teeth. In France, at La Ferrassie, remains of six children ranging in age from not much older than newborn to about 12 years of age were found, and at another French site, La Quina, an important cranium of an 8-year-old child was discovered. Devil's Quarry on the island of Gibraltar yielded a 2- to 5-year-old child's cranium. And of the thousands of bone fragments at Krapina in Croatia, many of the 25 individuals were subadults. In the northern Caucasus, northeast of the Black Sea, a partial skeleton of a Neandertal neonate or fetus (estimates of age range from 7 months gestational age to 2 months neonatal age) was recovered from Mezmaiskaya Cave and has yielded important DNA (Ovchinnikov et al., 2000).

The easternmost Neandertal, Teshik Tash from Uzbekistan, is also a child, the skeleton of a 9-year-old (Figure 12.20). In the Near East, several infants have been found at Amud Cave, including a 10-month-old who clearly bears Neandertal features in its cranial anatomy (Rak et al., 1994). And excavations under the direction of Takeru Akazawa at the cave of Dederiyeh in Syria have yielded partial remains of two toddlers who died about 50,000 years ago. Both toddlers were about 17 to 19 months of age when they died—based on dental microstructure. Although they are similar in age, the more complete skeleton (Dederiyeh 1) is also more robust than the more fragmentary one (Figure 12.21; Kondo et al., 2000; Akazawa & Muhesen, 2002). Despite their young ages, the Dederiyeh children and the other fossils discussed are clearly identifiable as Neandertals rather than modern humans.

Figure 12.20 Remains of a Neandertal child from Teshik Tash. Neandertals grew at a similar, if slightly faster, tempo than do modern humans.



In the 1950s, Clark Howell argued that understanding the ontogenetic pattern of Neandertals was critical for understanding their relationships to one another and to living humans. He proposed that the Neandertals from Europe and the Near East/Asia presented different populations with different trends in growth. While the details of the argument may no longer apply given changes in our understanding of the geological ages of particular Neandertals, the concept of understanding growth patterns to illuminate the meaning of adult morphology, as well as considering the importance of local adaptation in particular subgroups of fossil hominins, is an important organizing principle in fossil studies.

With a relative abundance of subadult remains, the Neandertals are the only fossil hominin group for which most developmental stages are known and for which detailed studies of growth can be made. Recall the work by Chris Dean (see Chapter 11) that indicated *H. erectus* had a faster dental developmental rate than modern humans; this same study found Neandertals had a dental developmental rate more similar to humans. More recent studies suggest that some Neandertals may have grown even more quickly. Studies of mandibular growth, including the Dederiyeh toddlers, indicate that early in development Neandertal children may have grown faster than modern human children but that growth rates are generally similar between the two (Kondo et al., 2002). Recent synchrotron “virtual histology” has allowed

dental anthropologists to see inside teeth without sectioning them and to compare dental growth rates between Neandertal and human children. Both Neandertals and contemporaneous *H. sapiens* had a prolonged period of dental development but the humans have an even greater elongation of development than Neandertals (Smith et al., 2010). Likewise, growth in the postcranial skeleton of the Dederiyeh toddlers suggests similar processes as in modern humans, albeit some may occur earlier in Neandertals than in modern humans (Sawada et al., 2004). Neandertals thus seem to show, for the first time in hominin evolution, growth patterns similar to our own.

Health and Disease

The history of Neandertal research has been strongly influenced by the recognition and interpretation of pathological conditions in bone. Recall that the type specimen from the Neander Valley, Germany, was at the center of an argument over whether it was a pathological human or a distinct species or subspecies. For many years the common perception of Neandertals as primitive creatures came from reconstructions produced by Marcellin Boule from a Neandertal skeleton from La Chapelle, France. The “Old Man” of La Chapelle-aux-Saints was found buried in a small cave in the Dordogne region of France and dates to about 40,000 years ago. The skeleton is clearly that of an older male, although in this context *old* means about 40 years of age. He suffered from numerous pathological conditions: a deformation in the pelvis, a crushed toe, severe arthritis in several of the vertebrae, and a broken rib sustained not long before death. He was missing many teeth, and the mandible and maxilla showed a significant amount of bone loss (Figure 12.22).

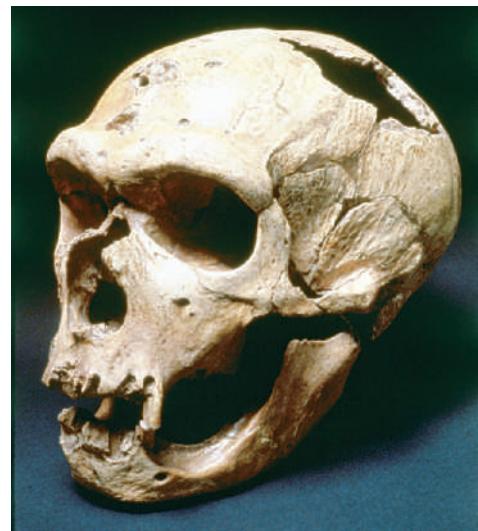
Boule reconstructed the Old Man as having a stooped posture and a shuffling gait, far from the upright stride of modern humans. In part, Boule may have been misled by the numerous pathological conditions in the skeleton, but recent investigators who have examined the skeleton and Boule’s work also believe that his interpretation of the skeleton was biased by his preconceptions about the “primitive” Neandertals (to be fair to Boule, the excavators of the Spy Neandertals also interpreted the skeletons as having a stooped posture). Nonetheless, Boule’s appraisal and interpretation of the Old Man of La Chapelle-aux-Saints was very influential, and it formed the “scientific” basis for the negative image of Neandertals for decades (Insights and Advances: Neandertal Image Makeovers on pages 385–386).

Other Neandertal skeletons provide abundant evidence of traumatic injuries. Nearly all the Shanidar remains from Iraq, dated to about 40,000 to 50,000 years ago, provide evidence of the hard lives that Neandertal individuals led (Trinkaus, 1983). Shanidar 1, a male between 30 and 45 years old, had a healed fracture of his left eye socket, and he may have been blind in that eye. The right side of his body had suffered even more extensive trauma: The lower right arm and hand were missing (the skeleton was otherwise intact and well preserved), perhaps because of an extensive injury that led to atrophy of the upper right arm and shoulder; he also showed signs of injury in the right leg and foot. It is possible that this individual could not have survived such injuries without help from other Neandertals, although drawing such a conclusion based on paleopathology alone is problematic (Dettwyler, 1991).

Figure 12.21 The Dederiyeh 1 infant from Syria preserves nearly the entire skeleton of a 17- to 19-month old Neandertal. Another, more fragmentary, toddler of the same age was also found at the site.



Figure 12.22 The “Old Man” from La Chapelle shows evidence of extensive tooth loss and bone resorption.



Innovations

Neandertal Genes

Ancient DNA (aDNA) recovered from fossils provides a direct window into the genetics of past populations. Unfortunately, only a small percentage of fossils actually preserve any DNA. Several factors influence whether DNA will be preserved. Age is a critical factor. Although in the early days of ancient DNA research (the late 1980s and early 1990s) many claims were made for the recovery of DNA from samples more

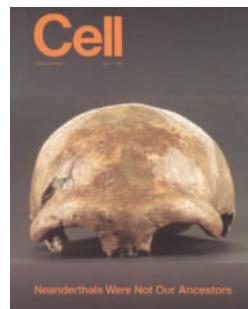


than 1 million years old, subsequent studies indicate that recovering usable DNA from fossils older than 100,000 years is extremely unlikely (Wayne et al., 1999). Temperature and humidity are also critical to whether DNA will be preserved: Cold and dry is better than warm and wet. For example, late Pleistocene mammoths preserved in arctic permafrost and Ötzi the ~5,000 year old “Tyrolean Iceman” discovered in the Alps preserve DNA quite well (Rollo et al., 2006). In terms of hominin fossils, this suggests those from northern Europe and northern Asia are the most likely to provide intact DNA, whereas hominins in the tropics such as portions of Africa and Southeast Asia are least likely.

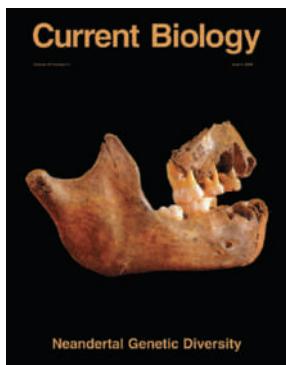
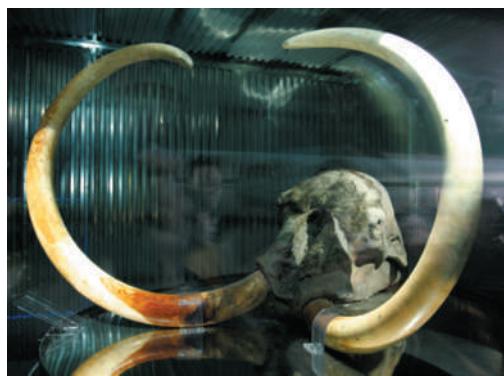
Ancient DNA from more than 20 Neandertals and modern humans has been recovered and analyzed. Ancient samples from known archaic *H. sapiens* specimens have not yet been obtained, but there is some ancient DNA from a hitherto unknown hominin from Denisova (see Insights and Advances: The Denisovans on pages 400–401). The Neandertal samples include samples from the Feldhofer Cave, Germany, the original site of the Neandertal’s discovery (Krings et al., 1997; Schmitz et al., 2002); from Vindija Cave in Croatia (Krings et al., 2000; Serre et al., 2004); Mezmaiskaya Cave in the northern Caucasus (Ovchinnikov

et al., 2000); Engis and Scladina in Belgium (Serre et al., 2004; Orlando et al., 2006); El Sidrón in Spain (Lalueza-Fox et al., 2005, 2006); Monte Lessini, Italy (Caramelli et al., 2006); Rochers de Villeneuve and La Chapelle-aux-Saints in France (Serre et al., 2004; Beauval et al., 2005); Teshik Tash in Uzbekistan and Okladnikov in Siberia (Krause et al., 2007). These samples cover much of the Neandertal geographic and temporal range including some of the youngest Neandertals and some of the older Neandertals (the Scladina site is about 100,000 years old). The modern human samples come from Mladec in Czechoslovakia, Cro-Magnon, Abri Pataud, and La Madeleine in France (Serre et al., 2004), and sites in Italy (Caramelli et al., 2003), Romania (Fu et al., 2015) and Siberia (Fu et al., 2014).

Most of the DNA extracted from Neandertals is ancient mitochondrial DNA, some of it from the hypervariable region 1. Remember that mtDNA is passed down only through the maternal lineage, and represents a fairly small part of the whole genome (see Chapter 2 for a review). The snippets of mtDNA recovered from Neandertals are all fairly similar to one another. They cluster together as a group to the exclusion of DNA from fossil *H. sapiens* and from living humans. The amount of variation between Neandertals and ancient *H. sapiens* is about 200 bases greater than the difference amongst living humans, but it is much less than the variation seen among chimpanzees and gorillas. Like living humans, Neandertals have even less diversity in their mtDNA than living humans—who themselves are fairly invariable compared to chimpanzees. This restricted variation suggests that Neandertals, like modern humans, underwent a population bottleneck sometime from 50,000–100,000 years ago (Disotell, 2012).



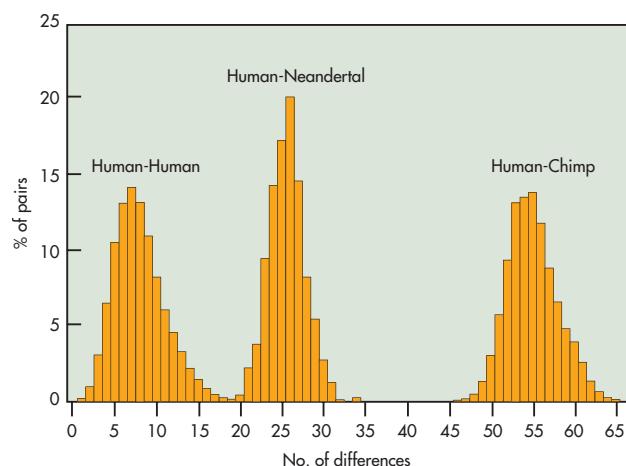
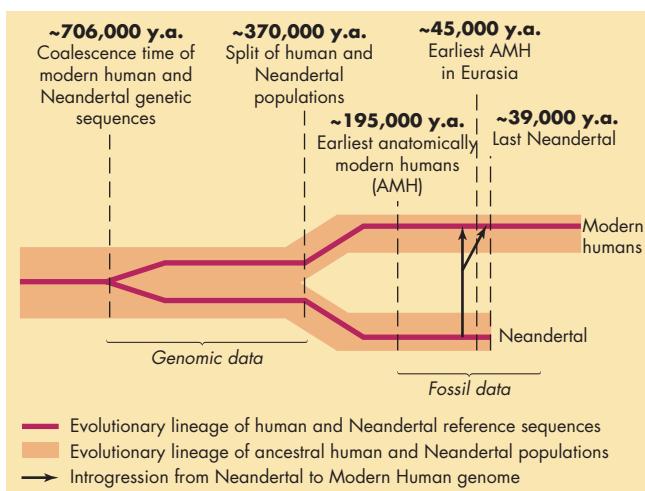
Neandertals Were Not Our Ancestors



Recent studies of both mitochondrial and nuclear DNA have yielded some surprises. DNA analyses have extended the geographic range of Neandertals into Siberia at a site called Okladnikov. And nuclear DNA from Neandertals at El Sidrón in Spain has suggested that, like living humans, some Neandertals had pale skin and red hair (Lalueza-Fox, 2007). This suggests that Neandertals had evolved phenotypic adaptations to low UV radiation, including skin depigmentation, as modern human populations have. However, the adaptations are not identical. The mutation in the Neandertal DNA differs from that seen in modern humans and this means that the two groups evolved these adaptations separately, rather than having gained it from a common ancestor or by interbreeding.

The date for the most recent common ancestor (MRCA) of *H. sapiens* and Neandertals is between 365,000 and 853,000 years ago. Using mitochondrial DNA, an MRCA date for the western (Feldhofer and Vindija) and eastern (Mezmaiskaya) Neandertal samples has been estimated to be between 151,000 and 352,000 years ago.

Nuclear DNA has been sequenced as well (Green et al., 2006; Noonan et al., 2006). Originally, nuclear DNA came from just a single fossil from Vindija and was sequenced by two different research groups using two different techniques that yielded similar results (Green et al., 2006; Noonan et al., 2006). DNA was also isolated from cave bear fossils from the same site and compared to modern carnivores to test the technique. Now the entire nuclear genome of Neandertals is available, having been spliced together from fragments of multiple individuals from Vindija with comparisons to smaller sequences from El Sidrón, Neander, and Mezmaiskaya (Green et al., 2010). This was no small job because the fossil bones also included DNA of fungi and bacteria from the soil in which the remains were buried, and aDNA is always highly



degraded. The results are the product of the Neanderthal Genome Project, a joint collaboration between the Max Planck Institute for Evolutionary Anthropology and 454 Life Sciences. You can browse the results of the project at <http://neandertal.ensemblgenomes.org/index.html>. These data indicate a date for the split between Neandertal and *H. sapiens* of between 270,000 and 440,000 years, a range that is compatible with that produced by mtDNA. And they also suggest that there was a small genetic contribution from Neandertal nuclear DNA into the modern human gene pool. The earliest modern human mandible (Oase 1 from Romania) shows 6–9% Neandertal contribution, or the equivalent of some Neandertal input to his lineage four to six generations (about 200 years) before he lived. A Siberian femur shows somewhat more distant contributions. Living humans show much less input, perhaps around 1–3%. And the availability of this information has led genetic testing companies like 23andMe to include a comparison of the percentage of your nuclear DNA that is from a Neandertal source. Interestingly, there is currently little evidence of mtDNA contributions from Neandertals to humans. The researchers of the Neanderthal Genome Project also found evidence of uniquely human genetic traits, the implications of which we discuss in Chapter 13.



In fact, so many Neandertals exhibit healed fractures that their cause has been sought. Some scientists think the fractures, especially the high incidence of head and neck fractures, indicate that Neandertals were routinely getting close to dangerous prey while hunting (Berger & Trinkaus, 1995). But the spears from Schoeningen suggest that Neandertals should have been able to hunt from a distance, although whether that practice continued with Neandertals (or in all Neandertal groups) is

unkown. Other scientists suggest that fracture rates may vary by geographic region according to the ruggedness of the terrain.

Neandertal Behavior

12.5 Compare Neandertal behavior with earlier hominins.

When we reconstruct past human behavior based on the archaeological record, we make inferences based on direct observation of living humans. We can be fairly certain that modern humans do not provide a perfect model for Neandertal behavior, but we do not know how bad the fit is. Take something as fundamental to human behavior as language. It is not unreasonable to assume that the Neandertals possessed some fairly sophisticated form of communication, but how did it compare to language in its ability to transmit ideas and information (see Chapter 14)? The Neandertals' large brains indicate that they were among the most cognitively sophisticated species that have ever lived, but what exactly did they do with these abilities?

Material Culture

Upper Paleolithic (Later Stone Age)

Stone tool industries that are characterized by the development of blade-based technology.

Châtelperronian

An Upper Paleolithic tool industry that has been found in association with later Neandertals.

blades

Flakes that are twice as long as they are wide.

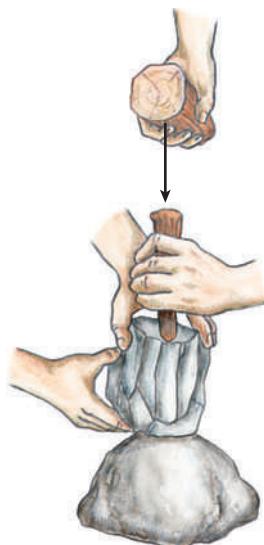
Most Neandertal fossils have been found in association with the Middle Paleolithic tools. This tool industry builds on earlier tool cultures such as the Acheulean by using some similar tools, like bifaces, and adding prepared core technologies. There is a greater reliance on small flaked tools and systematic variation in tool complexity in the Middle Paleolithic industries. For example, the late Neandertals of Mezmaiskaya Cave possessed a Middle Paleolithic technology that made extensive use of bifaces, a feature more commonly associated with the Acheulean. Likewise, all early Neandertals and contemporaneous anatomically modern humans (such as those from Skhūl and Qafzeh in Israel) are associated with Mousterian tools. This indicates that there is no reason to expect that stone tool traditions will correlate with anatomical differences between hominins.

All later anatomically modern humans and a few later Neandertals are found with the **Upper Paleolithic (Later Stone Age)**, which we discuss in more detail in Chapter 13 (Figure 12.23). The Saint-Césaire and Arcy-sur-Cure Neandertals from France are associated not with the Middle Paleolithic but rather with tools from an Upper Paleolithic industry, the **Châtelperronian** (Hublin et al., 1996). Upper Paleolithic industries are characterized by the development of blade-based technology. **Blades** are flakes that are twice as long as they are wide. In addition, Upper Paleolithic technologies use more refined flaking techniques, and an increase in the variety of flaked tools. Saint-Césaire and Arcy-sur-Cure demonstrate that Neandertals were capable of producing Upper Paleolithic technology. At some archaeological sites without hominins we find Châtelperronian and another Upper Paleolithic industry, the *Aurignacian* (which is associated with modern humans), interstratified through time in the site as if the groups were taking turns using the area. Given that most Neandertals produced Middle Paleolithic tools and only a few, late Neandertals produced Upper Paleolithic tools it is possible that this technology may have been adopted from anatomically modern groups.

Middle Paleolithic assemblages have few bone or antler tools. Although there have been no wood tool discoveries directly associated with Neandertal remains, a wooden spear dated to 130,000 years old from Lehringen, Germany, suggests that Neandertals, like earlier archaic *H. sapiens*, must have made extensive use of wood. Additionally, many smaller Mousterian points probably were hafted to wooden shafts to form spears or lances.

The anterior teeth of the Neandertals may be their most unusual tool (Figure 12.24). As mentioned earlier, the anterior teeth of Neandertals are large and heavily worn compared with their back teeth, indicating that they were used in a viselike manner. Wear patterns on the teeth indicate that both animal and vegetable matter were held

Figure 12.23 Upper Paleolithic stone tools include blade-based tools as seen here being produced from a blade core.



in the front teeth. This may indicate that Neandertals used these teeth to hold objects. Cut marks on the teeth further indicate that Neandertals held objects with their front teeth while cutting what they held, perhaps hide or pieces of meat, with stone tools. It is possible to imagine—but difficult to prove—any number of tasks that the Neandertals might have accomplished using their front teeth. All we can say for certain is that most Neandertals regularly used their front teeth as tools. And new research on the archaic *H. sapiens* from Atapuerca Sima de los Huesos, Spain, show these hominins also had cutmarks on their teeth and probably used them like a vise (Lozano et al., 2008).

Coping with Cold

Neandertal bodies are typical of cold-adapted populations, and their archaeological sites also give indications of behavioral adaptations to cold. Fire is one way to cope with cold and charcoal deposits and ashy dump spots are commonly found in Middle Paleolithic sites attributed to Neandertals. True hearths are rare, but they have been identified in a 60,000-year-old Middle Paleolithic site in Portugal. It is also very likely that Neandertals used animal skins and hides to protect themselves from the cold. No sewing tools, such as awls or bone needles, have been found in the Middle Paleolithic; so if they did use hides there is no evidence that they were sewn. In Molodova in the Ukraine, a Middle Paleolithic site has yielded a ring of mammoth bones, approximately 5×8 m (15×24 ft.) in size, which encloses a dense concentration of artifacts, bones, and ash. Although it could be a natural deposition, many scientists think that this site represents a living space of some kind, a wind-sheltering structure, or perhaps even a tent. If this is the case, the walls of structure probably were constructed from animal hides. As yet, there is no evidence of more substantial Neandertal structures.

Another way to cope with cold is to avoid it, either by seasonally migrating over long distances or by moving permanently as overall conditions get colder (or warmer) during all parts of the year. Middle Paleolithic archaeological deposits indicate that Neandertals were a mobile people seasonally occupying sites for short periods of time. In general, their sites served as temporary spots for camping, hunting, or food processing, but their mobility seems to have been limited. Most of the raw materials they used for stone tools came from within 5 km (3 miles) of where they were found, with a maximum distance of 80 km (Stringer & Gamble, 1993). Thus Neandertals did not move over a large enough area to avoid seasonal cold altogether, but rather probably moved locally to exploit scarce resources within a small area. The distribution of Neandertal sites through time indicates that they did migrate in and out of areas over longer periods of time depending on whether glacial or interglacial conditions persisted. For example, across the eastern Russian plain presumed Neandertal sites are found far north only during interglacial periods and are located farther south during glacial periods, as if the Neandertals were retreating in the face of the harsh glacial climate. Neandertals probably never, even during interglacials, lived as far north as anatomically modern humans eventually would.

Similarly, Neandertals appeared to move south into the Near East during glacial times, and modern humans occupied the region during warmer interglacials. Five prominent cave sites located on Mount Carmel in Israel have been the focus of much attention over the years (excavations in this area began in the late 1920s) because they possess either Neandertal or anatomically modern human fossils. Three of these sites have produced classic Neandertals: Tabūn (dating to about 110,000 years ago), Kebara (60,000 years ago), and Amud (35,000–40,000 years ago). And two, Skhūl and Qafzeh,

Figure 12.24 The heavily worn, and sometimes cutmarked, anterior teeth of Neandertals suggest that these teeth were used as a third hand for holding items while being cut and perhaps also for working items such as hides.



have yielded anatomically modern human fossils dated to about 90,000 to 110,000 years ago. All these hominins, Neandertal and modern human, were found in association with Mousterian (Middle Paleolithic) stone tools, which are more typically found in association with Neandertals, at least in Europe.

Scientists long thought that the anatomically more modern-looking Skhūl and Qafzeh specimens were younger than the Neandertals, but electron spin resonance and U-series dates turned that idea on its head. Neandertals clearly occupied the region for a long time, but the current evidence for occupation by modern-looking humans is more limited. If you accept Neandertals as a separate species, then it is likely that Neandertals and modern humans were alternatively using the region during varying climatic times: Neandertals during cold spells, modern humans during warmer spells. Others argue that Neandertals and modern humans could be representatives of a single, highly variable species. The Middle Eastern hominins as a group would be considered a variant on the classic Neandertal form, and the more modern features seen in some of the specimens would simply reflect local population variation. In a crossroads region (at the intersection of Africa, Europe, and Asia), it might not be surprising that this population would vary more than isolated populations.

Hunting and Subsistence

Stable isotope ratios of carbon and nitrogen indicate that Neandertals ate a lot of meat (Richards et al., 2000). They undoubtedly used all the hunting strategies known by archaic *H. sapiens* and earlier hominins. Different Neandertal sites indicate that they used a variety of subsistence strategies depending on local conditions and the game available in a given area. Although they may have scavenged meat opportunistically, there is little evidence that Neandertals engaged in scavenging on a broad scale (Marean & Assefa, 1999).

An in-depth study of Neandertal subsistence has been undertaken at the site of Kebara in Israel. John Speth and Eitan Tchernov (2001) looked at faunal remains found in Middle Paleolithic deposits dating from 48,000 to 60,000 years ago, concentrating on a collection of 21,000 ungulate bones. Most of these bones came from two species, the mountain gazelle and the Persian fallow deer, but other kinds of deer, wild boar, and aurochs (the precursor to domestic cattle) were also hunted. Speth and Tchernov found little evidence in the processing of the bones to indicate that they were scavenged rather than hunted. In fact, a high percentage of the animals were healthy adults, indicating that the Kebara Neandertals were very capable hunters. A consistent distribution of burned bones indicates that they were cooked rather than accidentally burned after consumption. Speth and Tchernov found evidence of a *midden* located along one wall of the cave, indicating that the Neandertals cleared waste and debris from the area in a consistent way. In general, these studies support the conclusion that Neandertals were competent hunters and in some cases large game hunters.

Zooarchaeological (animal bone analysis) and stone tool evidence from sites in western France show that by the end of the Middle Paleolithic Neandertals were accomplished hunters who used seasonal and selective strategies to hunt large game, including red deer. Anne Delagnes and Will Rendu argue that Neandertals moved their campsites seasonally in a way that suggests they were adjusting to the migration schedules of these herd animals that would be expected only if they were exploiting the animals throughout the year (Rendu, 2010; Delagnes & Rendu, 2011).

Cannibalism

Many human cultures have engaged in cannibalism. Although it is generally thought to have been undertaken in a political or ritualistic context, cases of subsistence cannibalism are also known. Because there is little evidence of ritual behavior in Neandertals, cannibalism is perhaps better classified as a kind of specialized subsistence strategy.

Early claims for Neandertal cannibalism came from Italy based on a cranium (known as Guattari 1) discovered in 1939 at the cave of Monte Circeo near Rome and dated to about 60,000 years ago. The cranium is reasonably complete, but there is a large hole in its base. Early researchers thought that it was likely that the hole in the base of the cranium had been deliberately made to facilitate access to the brain during some sort of cannibalistic rite, which was indicated by the supposed placement of the skull in a circle of stones. However, the base of the cranium is a weak part of the skull, often broken by natural forces; thus its absence is not direct evidence of cannibalism.

More substantial evidence of cannibalism can be found in the fragmentary remains from Krapina, Croatia, dated to about 130,000 years ago (Figure 12.25). D. Gorjanović-Kramberger, who excavated the site in the early twentieth century, pointed out that among the thousands of fragmentary hominin bones almost no intact long bones were present, a sign that the bones may have been split open to access the marrow within. He also thought that the bias toward juveniles at the site was an indication of cannibalism. Furthermore, many of the bones showed signs of burning. More recent research has established that some of the bones show cut marks as well, although this is not in itself evidence of cannibalism (Russell, 1987).

The recently excavated Mousterian cave site of Moula-Guercy in France, dating to about 100,000 years ago, provides an even better case for Neandertal cannibalism (Defleur et al., 1999). Seventy-eight hominin bone fragments are mixed in with several hundred animal bone fragments (mostly from red deer). Diagnostic Neandertal anatomy is apparent in several of the fragments. The hominin remains from Moula-Guercy display numerous cut marks; these are consistent with expected defleshing and butchering patterns. All crania and long bones have been broken, presumably to gain access to the brain and marrow. A key piece of evidence indicates that these remains were processed for access to meat rather than for some other purpose: The deer and other animals from the site were treated in the same manner as the hominin remains. Because it is unlikely that the game species were being treated to some sort of mortuary processing that did not involve being eaten, Alban Defleur and his colleagues conclude that the Neandertals were also being eaten by other Neandertals. This seems like a reasonable conclusion because only Neandertals are known in this area at this time. However, recent genetic revelations about another non-Neandertal hominin group in Siberia, the Denisovans, whose ancestors left Africa in the middle Pleistocene urge caution in assuming that Neandertals were entirely alone until modern humans arrived (see Insights and Advances: The Denisovans on pages 400–401).

Burials

The notion that some Neandertals may have buried their dead goes back to the discovery of the Spy skeletons in Belgium in the 1880s (Stringer et al., 1984). Unlike the earlier discoveries from Gibraltar and the Neander valley, the Spy remains were carefully excavated. The two Spy adult skeletons were found complete and fully articulated, suggesting that they may have been intentionally buried in the cave. Since that time, numerous Neandertals have been found in caves; most scientists interpret these remains as deliberate burials. Often these Neandertal skeletons have been recovered in situ and fully articulated, and many were in a flexed position. Although the sites may be littered with disarticulated animal bones, only the Neandertal bones remain in anatomical position, protected from the effects of geology or scavengers. For example, at La Ferrassie in southern France (excavated in the early 1900s) several adults and subadults, are interpreted by many researchers as forming an intentional

Figure 12.25 The Krapina remains may provide evidence of cannibalism by some Neandertals.



burial complex. In 1938, the skeleton of a 9-year-old child found in the small cave of Teshik Tash in Uzbekistan was claimed to have been interred surrounded by six pairs of upright goat horns, reflecting some sort of ritualistic activity. Although there is no doubt that the goat horns were found near the child, researchers today are skeptical that they were distributed in a “meaningful” way.

In the 1950s, the idea of burial and compassionate Neandertals was further supported by the remains from the 40,000- to 50,000-year-old Iraqi site, Shanidar, excavated by Ralph Solecki (1971). The Shanidar 4 individual may have been buried on, or perhaps covered by, a bed of wildflowers. The claims were based on the position of the skeleton and a large quantity of wildflower pollen associated with this individual. There is no certainty, however, that wildflowers were placed there deliberately by Neandertal mourners. The same pollen exists in the region today and could have been blown into the cave. Nonetheless, both the “flower burial” and the obvious survival of badly injured individuals at Shanidar led to a softer and more humanized perspective of Neandertals in the 1960s and 1970s.

However, some investigators argue that it is possible to account for the deposition of articulated Neandertal skeletons in caves by natural forces (Gargett, 1989, 1999). One criticism is that many Neandertal sites were excavated decades ago, before the development of modern excavation techniques or accurate recordkeeping. Without a clear rendering of the excavation context, it is difficult to assess the status of a claim of deliberate burial. Recent excavators of Neandertal sites, mindful of the need to provide evidence for burial rather than simply assume it, have gone to some effort to prove what was once considered obvious. Recently excavated Neandertal infants from Amud (Hovers et al., 2000), Mezmaiskaya Cave (Golovanova et al., 1999), and Dederiyeh (Akazawa & Muhesun, 2002) are all argued to be from deliberate burials, and the context of these discoveries strongly indicates that such small and delicate remains probably were preserved because they were shielded from damage by deliberate burial (Figure 12.26).

Neandertal burials represent a novel behavioral development of the Middle Paleolithic. Before that time we may have evidence of mortuary practices in the defleshing of the Bodo cranium and the possibly deliberate deposition of remains in the bone pit of Sima de los Huesos at Atapuerca. But there is currently no evidence of deliberate burial of archaic *H. sapiens* remains, but Neandertal burials are significantly different from Upper Paleolithic burials of anatomically modern *H. sapiens* that begin to appear around 40,000 years ago. Neandertals have not been found to be interred with grave goods, objects placed with the corpse at the time of burials. On occasion a stray animal bone or horn has been found in association with a Neandertal burial, but it is very difficult to demonstrate that they were placed there deliberately. In contrast, grave goods often are found in Upper Paleolithic burials, sometimes in great abundance. Another difference between Neandertal and Upper Paleolithic burials is that the Neandertal burials always occur in cave sites, whereas burials at open air sites are common in the late Upper Paleolithic. Because it is presumed that Neandertals lived and died in open areas as well as in caves, they must not have buried their dead in those regions or, if they did, they did not do so in a way that prevented the disruption of the corpse by other forces.

Extrapolating from the cultural behavior of modern humans, it is easy to assume that Neandertal burial indicates some kind of ritualistic belief or significance, but the context of Neandertal burials is equally indicative of “corpse disposal” as it is of ritualized internment (Stringer & Gamble, 1993). It is clear, however, that

Figure 12.26 The Dederiyeh infant burial from Syria.



some Neandertals dedicated a significant amount of time and energy to the burial of the dead, selecting an appropriate site, placing the body in a certain position, and covering the body with a large stone. Furthermore, chimpanzees and other mammals can show attachments to the remains of deceased infants or individuals with whom they have had a long-term relationship, even though they ultimately abandon the body. Elephants have been reported to stand vigil over dead relatives and to revisit the site of the death and handle their skeletal remains (Poole, 1996). And Jane Goodall and others have reported instances of chimpanzee mothers carrying their infants with them long after they had died and exhibiting behaviors that may indicate compassion toward dying individuals (Anderson et al., 2010; Biro et al., 2010). In addition, studies of other primates including gelada baboons, macaques, and gorillas found dead-infant carrying and grooming to be relatively common, although evidence of compassion to the dying may be unique among chimpanzees (Fashing et al., 2011).

Ritual and Symbolic Behavior

If burials cannot be seen as evidence of ritualistic or symbolic behavior, then there is very little else in the Neandertal archaeological record to indicate such behaviors. A small number of incised bones have been recovered from Mousterian sites, but what these scratches might mean is beyond the scope of scientific inquiry. If Neandertals possessed something like human language, then obviously they were capable of symbolic behavior because language is reliant on symbolic representation. But there is no direct evidence of this in the archaeological record. The strongest evidence of symbolism comes from items of personal adornment. Pierced animal teeth from Arcy-sur-Cure in France may be pendants. Other engraved or incised items include a plaque or incised plate of a mammoth tooth, from the site of Tata, and an incised flint from Quneitra in the Golan Heights (Marshack, 1996; White, 2001). All of these occur late in Neandertal times, with the most secure—those from Arcy-sur-Cure and Quneitra—being 55,000 years old or younger. Even if we accept these few finds as symbolic behavior by Neandertals, they are qualitatively different from the systematic evidence of such behavior, including extensive personal adornment, in Upper Paleolithic sites associated with modern humans (Chapter 14).

Phylogenetic and Taxonomic Issues: An Overview

12.6 Discuss the phylogenetic and taxonomic issues related to understanding relationships among the many late-middle and late Pleistocene hominins.

Our interpretations of taxonomic and phylogenetic relationships between middle and late Pleistocene hominins depend largely on how we view the origins of anatomically modern *H. sapiens*. However, we can have a preliminary discussion based on the archaic *H. sapiens* and Neandertal fossil records.

The labels “archaic *H. sapiens*” and “Neandertal” are not taxonomically formal designations. We use informal labels because there is no consensus as to what the formal labels should be. Archaic *H. sapiens* include a widely distributed group of hominins who lived from about 150,000 to 800,000 years ago (Figure 12.11 on pages 380–381). Neandertal refers to a predominantly European and western Asian group of hominins who lived about 35,000 to 200,000 years ago. Both these groups possess features that clearly distinguish them from *H. erectus* and anatomically modern *H. sapiens*. Yet many researchers argue that either the differences are not profound enough to warrant species designations or that using such designations would arbitrarily impose separations on a continuous evolutionary lineage and thus be highly misleading (Figure 12.27 on page 402).

Insights and Advances

The Denisovans

You might call the child Pinky, because just a finger bone was discovered from a cave in southern Siberia in 2008 (Figure A). Yet that nondescript finger bone yielded a complete mitochondrial DNA sequence that stunned the paleoanthropological community. The finger was found in a layer dating to between about 30 and 48,000 years ago, and the researchers from the Neanderthal Genome Project hypothesized that they would find either Neandertal or *Homo sapiens* DNA. The site of Okladnikov, also in Siberia, had recently yielded Neandertal DNA, so the team was hopeful that Pinky would prove to be a Neandertal as well. Surprisingly, Pinky's mtDNA differs by 385 bases from that of modern humans—more than Neandertals do. And it also differs from Neandertals. In fact, Pinky's mtDNA suggested a third hominin was living in Siberia in the late Pleistocene (Krause et al., 2010; Reich et al., 2010).

The cave, known as Denisova, is situated in the Altai mountains. Since the initial discovery, it has also yielded a very large, upper third molar, the anatomy of which is clearly neither Neandertal nor modern human (Figure B). And the mtDNA from the tooth matches the finger bone, suggesting the two shared a similar matriline. Initial comparisons of the finger mtDNA suggested that the occupants of Denisova cave were the descendants of a hominin who had left Africa around 500,000 years ago and were equally

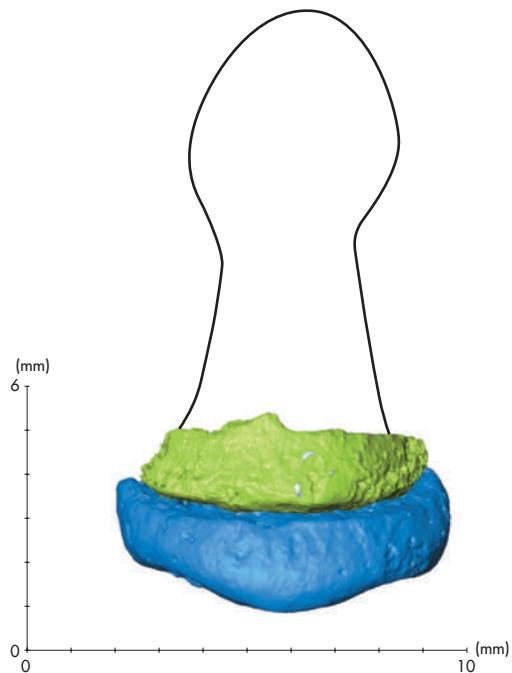


Figure A Dorsal view of a scan of the hand phalange of a child from Denisova that yielded mtDNA that differs from modern humans and Neandertals. We know that it is a child because of the unfused epiphyses (shown in blue).

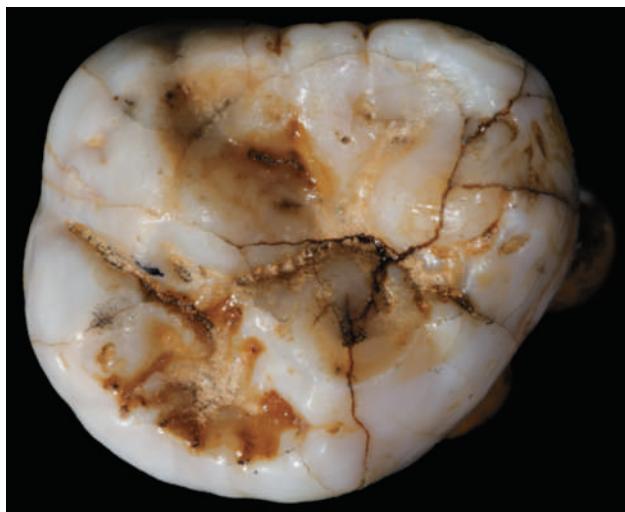


Figure B A third molar from Denisova differs anatomically from Neandertals and modern humans and has similar DNA to the finger bone.

distant from Neandertals and modern humans (Figure C). Perhaps they could have been a relict group of archaic *H. sapiens* or a late dispersing *H. erectus*, neither of which we have DNA from. But more recently the complete mtDNA sequence and a nuclear DNA sequence have been analyzed, and these results now indicate that the Denisovan is more closely related to Neandertals, and that the last common ancestor of the two lived after their common ancestor with modern humans (Figure C). Other alternatives might include that the archaic sections of the DNA came into the Denisovan population via gene flow from a more archaic hominin (like *H. erectus* perhaps).

So far, the researchers have resisted naming a new species, preferring to call these new fossils Denisovans. Reasonably, they want to wait for additional nuclear and mtDNA from other known species of hominin as well as from the Denisovans themselves. Additionally, although the single molar is anatomically different than Neandertals, it would not be the best type specimen for a species. Thus, more anatomically informative skeletal parts would be welcome before naming a species. Whether a new species or not, the Denisovans, like Neandertals, seem to have shared at least some of their DNA with some modern human groups—in the case of Denisovans their DNA shows up in modern humans from Melanesia. In addition, specific Denisovan genes are shared by other human groups—as we learned the high-altitude version of *EPAS1*, which makes Tibetans less prone to chronic mountain sickness, is shared with Denisovans (see Chapter 5). Denisovans are a tantalizing clue that up until quite recently, we were not the only hominin on the planet.

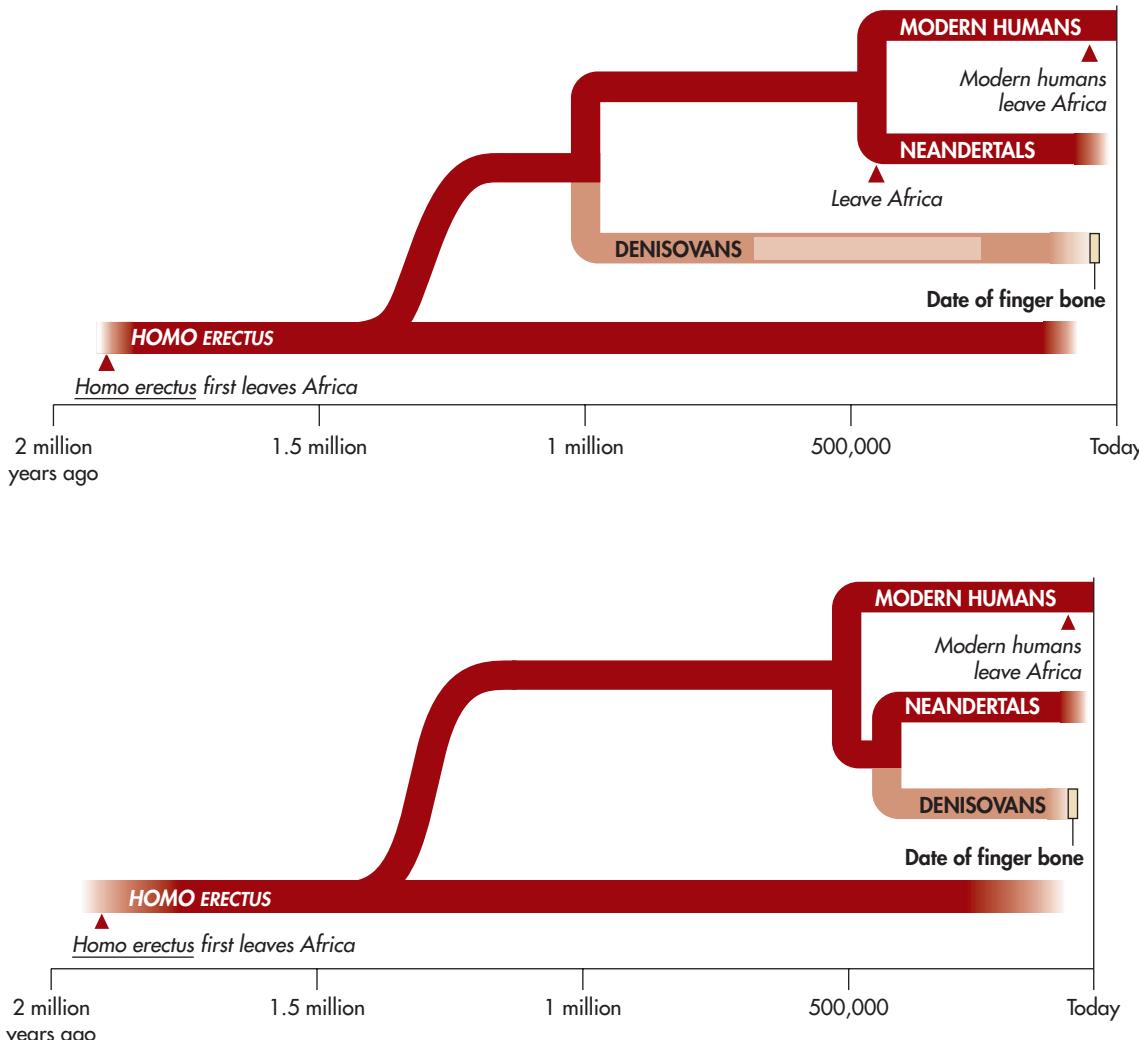


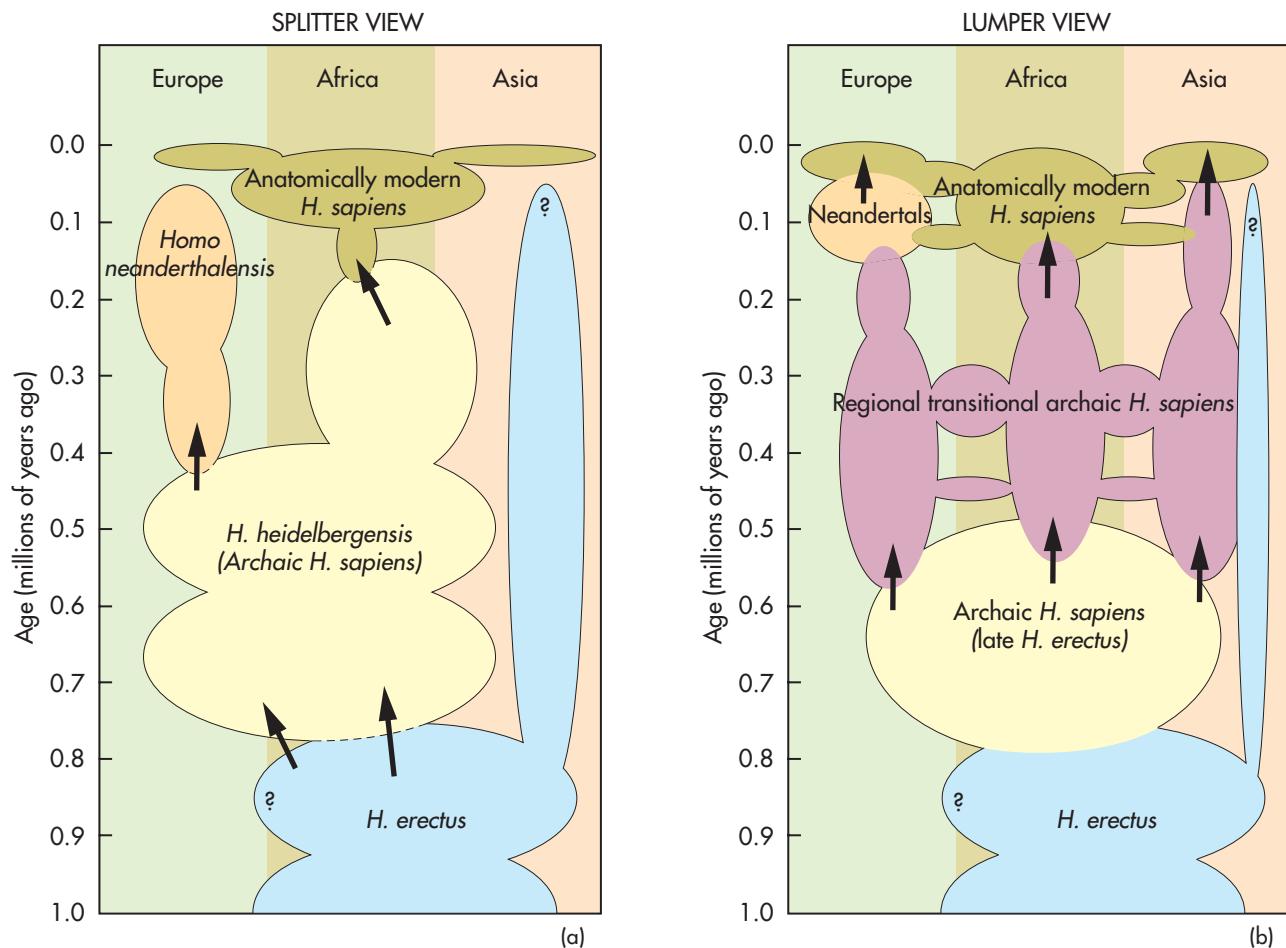
Figure C (a) Initial mtDNA results suggested modern humans and Neandertals were equally distantly related to Denisovans. (b) A more complete genome links Denisovans to Neandertals.

From the “lumper’s perspective,” the informal, subspecific labels for these groups of hominins provide an acceptable solution to the problem. In this view, archaic *H. sapiens*, Neandertals, and anatomically modern humans were all part of one potentially interbreeding species. Obviously, there was regional variation within the species, and variation across time as well, but lumpers see all the larger-brained hominins of the last half of the Pleistocene as part of a *single evolving species*.

The “splitter’s perspective” begins with recognizing the Neandertals as a separate species: *H. neanderthalensis*. They argue that the distinctive anatomy and limited distribution of the Neandertals indicate a specialized hominin taxon fundamentally different from anatomically modern *H. sapiens*. The species designation means that Neandertals and modern humans did not or could not interbreed or did so very infrequently; it suggests that Neandertals represent an extinct type of hominin, which was ultimately replaced across its entire range by modern humans. As we have seen from the genetic evidence, it does look like interbreeding happened, but infrequently.

In the splitter’s view, archaic *H. sapiens* also gets a species designation: *H. heidelbergensis*. *H. heidelbergensis* is considered a species distinct from *H. erectus*, based on the anatomical features we discussed earlier. In the simplest view, *H. heidelbergensis* becomes the stem species for both Neandertals and anatomically

Figure 12.27 Two views of the phylogenetic relationship between Neandertals and modern *H. sapiens*. (a) The splitter view and (b) the lumper view.



modern *H. sapiens*. In Europe, *H. heidelbergensis* specimens such as Petralona and those from Sima de los Huesos are seen to be proto-Neandertals, extending the Neandertal lineage back hundreds of thousands of years. In Africa, *H. heidelbergensis* specimens such as Bodo and Kabwe are thought to be early representatives of a population from which anatomically modern *H. sapiens* evolved. Indeed, some researchers argue that it is hard to encompass both African and European archaic *H. sapiens* into a single species and they split the group even further. The European fossils are included in *H. heidelbergensis*, the African fossils into *H. rhodesiensis*, and the younger Asian fossils may perhaps be linked to the Denisovans (Hublin, 2013).

At the same time that Neandertals were living in Europe and western Asia, hominin evolutionary developments were also taking place in other parts of the world, most significantly the evolution of anatomically modern *H. sapiens*. In Chapter 13, we will more fully explore the evolutionary connections between our own species and these earlier forms using paleontological, archaeological and genetic data.

Summary

HOMININ EVOLUTION IN THE MIDDLE TO LATE PLEISTOCENE

12.1 Explain the transitions that took place during hominin evolution in the middle to late Pleistocene including the anatomical characteristics that distinguish modern *H. sapiens* from earlier hominins.

- From the Middle to Late Pleistocene a transition from *H. erectus* to Neandertal and recent human anatomy takes place.
- Modern humans have larger, more globular crania and small faces.
- However, middle Pleistocene *Homo* has a large face and large double arched supraorbital region

ARCHAIC *HOMO SAPIENS*

12.2 Describe the anatomy and distribution of archaic *Homo sapiens*.

- Middle Pleistocene fossils, from about 800,000 to 200,000 show intermediate morphology between *H. erectus* and recent humans.
- Some scholars classify all of these into archaic *H. sapiens*.
- Other scholars use the species name *H. heidelbergensis* for the European fossils and *H. rhodesiensis* for the African fossils.
- Archaic *H. sapiens* are likely ancestral to later hominins in their regions. Ancestral to Neandertals in Europe and modern humans in Africa.

BEHAVIOR OF ARCHAIC *HOMO SAPIENS*

12.3 Describe the behavior of archaic *Homo sapiens* as inferred from the evidence preserved in the archaeological record.

- Archaic *H. sapiens* are usually associated with Middle Stone Age and Early Stone Age tools.
- Bone tools are also known from these time periods.
- These technologies suggest they may have hunted big game.

THE NEANDERTALS

12.4 Outline the history, anatomy, health, geographic distribution, and temporal range of the Neandertals.

- Earliest Neandertals appear in western Europe around 150,000 years ago and disappear around 39,000 years ago, overlapping for a few thousand years with *H. sapiens*.
- Many Neandertals lived around the Mediterranean, with some found as far east as Uzbekistan and Siberia and as far south as the Near East.
- The brain case is large, but long and low. From behind, the brain case is oval shaped, with the greatest breadth in the middle of the parietal. The mastoid processes are small and juxtamastoid eminences large. A suprainiac fossa and an occipital bun are present, but an occipital torus is lacking.
- The midface is prognathic, with a swept back cheek region and large nasal aperture. Browridges are large and double-arched. A retromolar fossa is present on the mandible. Neandertals have no chin.
- Postcranially, Neandertal bodies follow both Bergmann's and Allen's rules.
- Neandertal newborns had large brains similar to those of modern humans.

- Their teeth indicate that they had delayed development similar but somewhat quicker than modern humans, and some parts of their skeleton may have matured more quickly.
- Neandertal DNA is relatively distinct from modern humans, suggesting that they did not contribute much to the recent human gene pool.

NEANDERTAL BEHAVIOR

12.5 Compare Neandertal behavior with earlier hominins.

- Archaeological hearths indicate that Neandertals routinely used fire.
- Animal skins and hides were probably also used for protective shelters and cloaks.
- Neandertals migrated seasonally, and during long-lasting glacial events their range seems to extend further south and not so far north.
- Most Neandertals are found with Middle Paleolithic tool industries, which are characterized by prepared-core technologies, in which multiple steps are required to release a flake with specific characteristics (e.g., Levallois technique, disk cores etc.).
- A few later Neandertals are associated with an Upper Paleolithic industry, known as the Châtelperronian.
- Neandertals possessed thrusting spears and may have had projectile technology.
- Neandertals left relatively little evidence of symbolic behavior in the form of beads or artwork.
- They are likely to have buried their dead either for ritual or practical purposes. Few if any grave goods have been found with these burials.
- Neandertals were probably hunters rather than scavengers.
- A few sites suggest that Neandertals practiced cannibalism, at least occasionally.

PHYLOGENETIC AND TAXONOMIC ISSUES: AN OVERVIEW

12.6 Discuss the phylogenetic and taxonomic issues related to understanding relationships among the many late-middle and late Pleistocene hominins.

- Neandertals likely evolved from archaic *H. sapiens* (*H. heidelbergensis*), who preceded them in Europe.
- Archaic *H. sapiens* may represent two species, *H. heidelbergensis* and *H. rhodesiensis*
- Neandertals are either seen as a separate species, *H. neanderthalensis*, or sometimes as a subspecies of *H. sapiens*.

Review Questions

- 12.1 What anatomical characters can we use to recognize the crania of recent humans?
- 12.2 How do archaic *Homo sapiens* differ from region to region and from recent human skeletons?
- 12.3 What kinds of tools and sites did archaic *Homo sapiens* have?
- 12.4 Based on anatomy and DNA how do Neandertals differ from recent humans and do you think they should be called their own species?
- 12.5 What kinds of tools and sites did Neandertals have and how does their behavior differ from earlier hominins?
- 12.6 How are Neandertals, archaic *H. sapiens*, and recent *H. sapiens* related to each other?

Key Terms

blades, p. 394
Châtelperronian, p. 394
juxtamastoid eminence, p. 386
Levallois technique, p. 377

mastoid process, p. 372
Middle Paleolithic
(Middle Stone Age), p. 377
midfacial prognathism, p. 374

occipital bun, p. 372
taurodontism, p. 387
Upper Paleolithic
(Later Stone Age), p. 394

Chapter 13

The Emergence and Dispersal of *Homo sapiens*



Learning Objectives

-
- 13.1** Discuss the anatomical characteristics that identify the emergence of modern humans compared to earlier hominins.
 - 13.2** Compare and contrast the Replacement and Multiregional models of modern human origins; review the archaeological and molecular genetic evidence for modern human origins; and review how paleontology, archaeology, and genetics are interpreted.

13.3 Discuss the anatomy and distribution of early humans around the world.

13.4 Describe the archaeology of modern human origins including how the upper paleolithic or later stone age differs from middle and early stone age tool technologies and describe the behavioral differences and role of symbolism in the Upper Paleolithic.

13.5 Explain the role of molecular genetics and human origins, including the role of mitochondrial, Y-chromosome, nuclear, and ancient DNA in testing models for human origins.

13.6 Use the data from this chapter to help in interpreting models of human origins.

13.7 Discuss the settlement of the New World and the Pacific Islands.

Behind the building, a chaotic scree of cobbles, flakes, and deer antlers—the residue of years of experimental archaeology—were shaded by the branches of an old-growth redwood tree. A new crop of twenty-somethings in jeans, goggles, and leather gloves stood tentatively round the edges of the pile while their instructor demonstrated simple knapping techniques. She didn't flinch as the flakes parted from the underbelly of the cobble with each strike of her hammerstone. Her strikes were easy and confident—as theirs would grow to be over the semester. Some minutes later, the instructor presented the roughed out form of a hand axe to the class and invited them to try their hands.

The students moved in, each selecting a likely cobble of fine-grained basalt or chert. As they worked, fingers were pounded, and not a little blood was shed. Eventually, over days and weeks, they grew more agile and confident. As they worked they would gather in small groups, exchanging stories about their lives, their worries, their successes. They would go on weekend expeditions to gather stone from the beach or from the mountains. They became connoisseurs of form and angle—stones of just the right material, size, and shape were coveted.

By semester's end everyone could make choppers, flakes, and hand axes that resembled, at least vaguely, the Oldowan and Acheulean. Some students became specialists in more complex forms—one mastered the multistep process toward producing a Levallois core and flake, the heart of many Middle Paleolithic assemblages. Blades, beads, and microliths—the heart of the Upper Paleolithic—were more elusive still. They demanded talent and patience, and only one student mastered these.

Using a pile of soft greenish stone gathered on their last expedition, this student formed a series of oblong blanks from which would emerge several beads. She rounded one end of each blank, and then with another stone she began chipping flakes out of the center of the blank, working first on one side and then on the other. She kept chipping and listening to her classmates' stories. An hour later, the two indentations merged forming a hole that she slowly and carefully enlarged. Happy with its size, she spent the next hour polishing the bead to a lustrous finish and then dropped it onto a growing pile of similar beads. She had spent some hours now fashioning just a few beads. Yet, Upper Paleolithic sites yielded hundreds of similar beads representing thousands of hours of work. Those beads showed signs of having been carefully sewn onto garments. She wondered if these Paleolithic sequins had signaled clan affiliations and trade networks critical in some way for survival. Because of the amount of time each bead took to craft, the student knew that the advantage that such symbols conferred must have been great enough to outweigh the time lost to other critical pursuits such as foraging or hunting. She didn't have to choose between making a bead and

eating a meal, but for her Paleolithic counterparts she knew the benefit of the bead must have outweighed its cost in some important way.

Modern human origins are not simply a matter of anatomy but also of behavior. No matter how cognitively sophisticated our close cousins the Neandertals or archaic *Homo sapiens* were or how close the size of their brains was to our own, they did not attain the same level of technological achievement. The bead described in the vignette is not much of an artifact; it is not even a tool. But it provides material evidence of personal decoration and symbolic representation. Such evidence is abundant in the archaeological record of modern humans and all but absent from the records of Neandertals and archaic *H. sapiens*.

In this chapter, we review the three distinct sources of evidence used to reconstruct the critical events surrounding the emergence of modern people. Paleontological and geological data chart the distribution in time and space of anatomically modern *H. sapiens*. Archaeological data shed light on the changes in behavior that allowed modern humans to exploit the natural world in a way that would ultimately make us the dominant species on the planet. Genetic data provide information on the web of biological relationships between us and our closest relatives. By synthesizing data from these interrelated realms, biological anthropologists attempt to address the fundamental question of our field: How did human beings evolve?

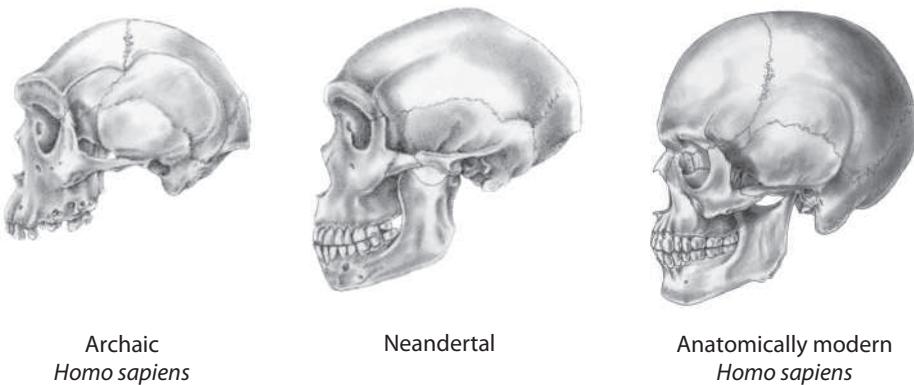
The Emergence of Modern Humans

13.1 Discuss the anatomical characteristics that identify the emergence of modern humans compared to earlier hominins.

The emergence of modern humans can be seen anatomically in a combination of cranial features that distinguish us from archaic *H. sapiens* and Neandertals (see Chapter 12). These features include a gracile skull and postcranial anatomy; limited development of browridges and other cranial superstructures; a rounded cranium with its maximum breadth high on the vault and parallel sides in rear view; a prominent mastoid process; a retracted face with a canine fossa; small teeth and jaws; and development of an obvious chin (Figure 13.1). However, large brain size does not set us apart from archaic *H. sapiens* or Neandertals. Many middle and late Pleistocene hominin fossils have cranial capacities that are easily within the modern human range (whose average is about 1,350 cc), and a number of them exceed the human mean by a substantial amount.

Despite the fact that there is no significant difference in absolute brain size, when we look at the archaeological record associated with modern humans—the Upper

Figure 13.1 Variations on a theme: archaic *Homo sapiens*, Neandertal, and anatomically modern *Homo sapiens* skulls.



Paleolithic or Later Stone Age—we find evidence of substantial behavioral differences between our close relatives and us. Whether these differences signal a difference in intelligence is hard to say, but there are many hypotheses about why brain size increased in the human lineage and the role that culture and technology may play (see Insights and Advances: Primate Intelligence: Why are Human Brains So Big? on pages 410–411). It seems likely that the rapid pace of change and the appearance of symbolic behavior, two of the hallmarks of the Upper Paleolithic revolution, are likely the culmination of this process. Some scientists think a behavioral “revolution” occurred with the sudden appearance of anatomically modern humans (Klein & Edgar, 2002). Other scientists think that different aspects of Upper Paleolithic culture appear at different times during the later Middle Stone Age (MSA), thus indicating a more gradual evolution of behaviorally modern humans (McBrearty & Brooks, 2000).

Models of Modern Human Origins

13.2 Compare and contrast the Replacement and Multiregional models of modern human origins; review the archaeological and molecular genetic evidence for modern human origins; and review how paleontology, archaeology, and genetics are interpreted.

In the past two decades, two basic frameworks have been debated for the origin of modern humans: the replacement and multiregional models. Both assemble anatomical, behavioral, and genetic data into comprehensive models. And both agree that there was an initial dispersal of *H. erectus* (or *H. ergaster*) from Africa into the rest of the Old World. However, they disagree as to what happened next.

Multiregional and Replacement Models

The **replacement models** suggest that modern humans had a localized origin—usually thought to be in Africa—and then dispersed into areas already occupied by *H. erectus* and its descendants. Replacement models thus require a second hominin dispersal from Africa. These models often are called “Out of Africa” models or “Out of Africa II,” in recognition of the earlier *H. erectus* dispersal. As the word *replacement* implies, these models predict that anatomically modern humans did not interbreed substantially (or at all) with the indigenous hominins whom they ultimately replaced. One implication is that all geographic variation seen in modern humans today evolved recently, after the origin of anatomically modern humans.

Multiregional models propose that our origins cannot be pinned down to a single population or area. Instead, gene flow, via repeated population movements and intermixing, is thought to have been extensive among Old World hominin populations. Thus the appearance of anatomically modern humans throughout the Old World resulted not from replacement of many populations by one but from the transmission of alleles underlying the modern human phenotype between populations that were in genetic contact. Therefore, multiregional models do not suggest the later dispersal of a second hominin species from Africa. Note that the multiregional models do not call for separate and multiple origins for modern humans; rather, they suggest that modern humans originated in the context of gene flow between multiple regions.

It is not entirely true that multiregional and replacement models are irreconcilable. Certainly, any proof of genetic contributions from regionally dispersed populations means that total replacement could not have happened. But population expansion from a single region could have been the dominant event in recent human evolution, with genetic contributions from other populations being trivial. Conversely, it is very likely that over the past 500,000 years, hominin populations in some regions have

replacement models

Phylogenetic models that suggest that modern humans evolved in one location and then spread geographically, replacing other earlier hominin populations without or with little admixture.

multiregional models

Phylogenetic models that suggest that modern humans evolved in the context of gene flow between middle to late Pleistocene hominin populations from different regions, so there is no single location where modern humans first evolved.

Insights and Advances

Primate Intelligence: Why Are Human Brains Big?

Although elephants and whales have absolutely bigger brains, no mammalian group rivals the anthropoids for the ratio of brain to body size—a ratio that later *Homo* took to the extreme. Because of the high cost of growing and maintaining brains, there had to have been survival benefits to the evolution of intelligence. While the term *intelligent* has little precise meaning when we speak of animal behavior, problem-solving capacity is often considered a good proxy. In recent years, three competing schools of thought for the origins and evolution of primate intelligence have emerged.

The ability to use tools to extract food and other resources from the natural environment is called **Technical Intelligence**. Not all tool-using primates make their own tools. But the ability to use tools does require cognitive skills like foresight, planning, and the flexibility to apply the tool to a variety of contexts. Additionally, each generation must observe and master the style and technique of use. For example, juvenile capuchins play at breaking open nuts with stones, but adults are far more efficient, suggesting that this skill takes years to perfect.

Producing tools, as chimpanzees do, may be another cognitive leap that could lead to culture, or the sharing of learned traditions in a group. Chimpanzees make and use a variety of types of tools in the wild including stones, sticks, and leaves. But their use varies across populations. Bill McGrew (1992) concluded that different cultural traditions best explained the diversity of chimpanzee tool use across Africa because tool cultures do not map onto genetic distances among populations and the availability of resources didn't predict tool types. For example, in the rock-strewn landscape



Figure A A chimpanzee eating figs.

of Gombe National Park the chimpanzees do not use rocks as tools, but in the lowland rain forests of western Africa the chimpanzees search for scarce stones to use as tools. In addition to tool cultures, 38 cultural features including styles of grooming among other behaviors differed across populations and were not environmentally determined (Whiten et al., 1999).

Many scientists think that tool use, production, and transmission over generations indicate a level of sophisticated cognitive skill in primates that ultimately was enhanced and expanded in humans.

Models of **Ecological Intelligence** suggest that the key impetus for the expansion of the brain was the selective advantage of being able to navigate and find food in a highly complex environment. A tropical forest, with its patchy, temporary availability and distribution of fruit, placed a premium on the evolution of large brains, especially in frugivorous species that had to remember fruiting locations and timing. Although many animals forage in

been replaced by others without interbreeding, but this does not preclude gene flow from having occurred between other populations in the species.

Predictions of the Two Models

Replacement models predict that we should first see modern human fossils in Africa and then at least two anatomically distinct lineages of hominins in each region of the Old World: Neandertals and modern humans in Europe, *Homo heidelbergensis* (archaic *H. sapiens*) and modern humans in mainland Asia, and possibly relict populations of *H. erectus* and modern humans in Southeast Asia. Replacement further predicts that these lineages will overlap for at least a brief period of time in each region. Like the anatomy, the archaeological record would show abrupt changes in technology and behavior (as modern humans brought their technology with them to new areas), and the genetic record would indicate little overlap between the gene pools of the two lineages.

In contrast, multiregional models predict only a single evolving lineage that displays slightly different anatomical trends in each region. Across regions, we should see anatomical evidence of this evolution in the form of intermediate fossils with characteristics of the ancestors and the descendants. In addition, we should see regional anatomical characters continue from earlier to later populations. The archaeological

ways that optimize their chances of stumbling onto good food patches—primates possess mental maps of the landscape in which they live (Menzel, 1991).

In African forests, many fruit species, such as figs, ripen unpredictably, but a party of chimpanzees usually will be at the tree as soon as ripe fruits appear. This suggests that the apes monitor and remember the fruiting status of trees as they forage (Figure A). Even the small Callitrichid monkeys recall the locations of hundreds of potential food trees in the South American rainforest (Garber, 1989).

A problem with this ecological intelligence model, however, is that many very small-brained animals successfully navigate and forage in the same highly complex environment in which primates were thought to evolve their large brains. There is no evidence that small mammals such as squirrels are less efficient foragers than primates. So was there some additional advantage of those big brains?

The prevailing view is that primate brain size increase is related to **Social Intelligence**. This scenario, also called Machiavellian intelligence, argues that the primary evolutionary benefit of a large brain was that it conferred a reproductive advantage to individuals who were socially clever. In large social groups, each individual must remember the network of alliances, rivalries, debts, and credits that exist among group members. Increases in average group size could have selected for individuals with a larger cerebrum, or neocortex, of the brain which made them better able to handle the additional social information (Dunbar, 1992). Small-brained primates, such as strepsirrhines, typically live alone or in smaller groups than do most monkeys and apes. And large-brained chimpanzees seem to engage in a “service economy” in which they barter alliances and other kinds of support. Thus brain size, social complexity, and group size might form an evolutionary feedback loop.

Since the ability to subtly manipulate others is a fundamental aspect of group life, Richard Byrne and Andrew Whiten studied tactical deception or lying and found Great Apes often deceive one another, but lemurs rarely do (Byrne and Whiten, 1988b). For example, Craig Stanford once watched a low-ranking Gombe male chimpanzee use tactical deception to mate with a female. As a party of chimpanzees sat in a forest clearing, Beethoven (a low ranking male) charged through the middle of the group and into a thicket. Rising to the challenge, the dominant male Wilkie pursued and launched into his own display. With Wilkie suitably absorbed in his dominance display, Beethoven furtively made his way back to the clearing and mated with an awaiting female.

Researchers think that deception is at the heart of understanding the roots of human cognition because in order to lie to someone, you must be able to place yourself in their mind and infer their mental state; that is, you must possess a **theory of mind**. The ability to lie, to imitate, and to teach all rely on the assumption that the object of your actions thinks as you do. To some extent the ability to impute mental states to those around you is a prerequisite to living in a complex social group, but whether nonhuman primates have the ability is a topic of great debate.

One problem with this model is that other animals with more modest relative brain size, such as wolves, exhibit social dynamics as complex as those seen in many nonhuman primates. At the same time, one of the biggest-brained primates, the orangutan, does not live in groups at all, although this might in part be explainable by resource scarcity in their current environment. Some researchers suspect that enhanced cooperation coupled with technological changes in genus *Homo* may have lead to the run away increase in brain size that we see in later *Homo*.

record should show evidence of behavioral continuity, and the genetic evidence should show substantial ancient contributions to the modern gene pool, assuming there has not been a strong genetic bottleneck.

In the next section, we will see how these predictions fare against the fossil, archaeological, and genetic records.

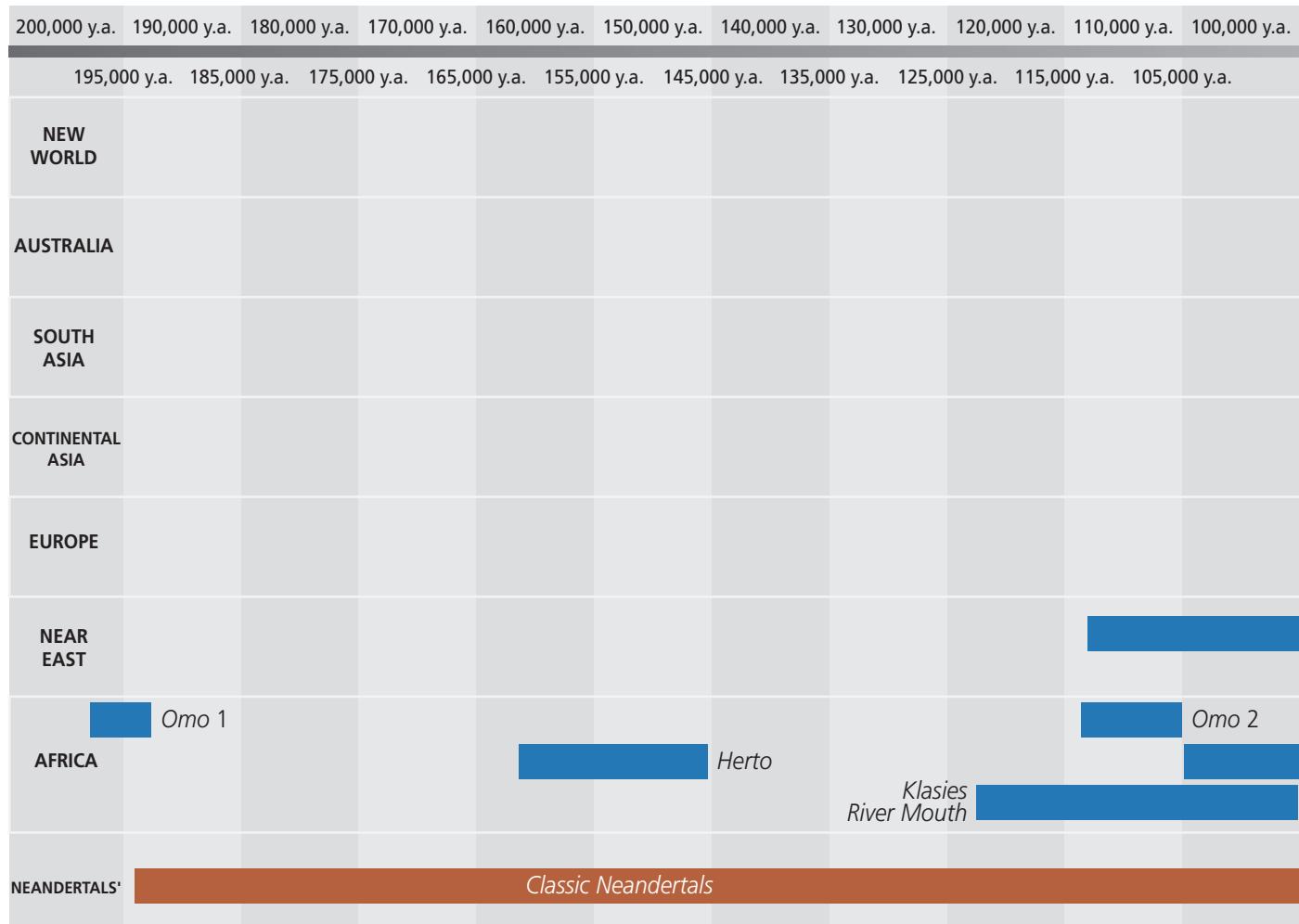
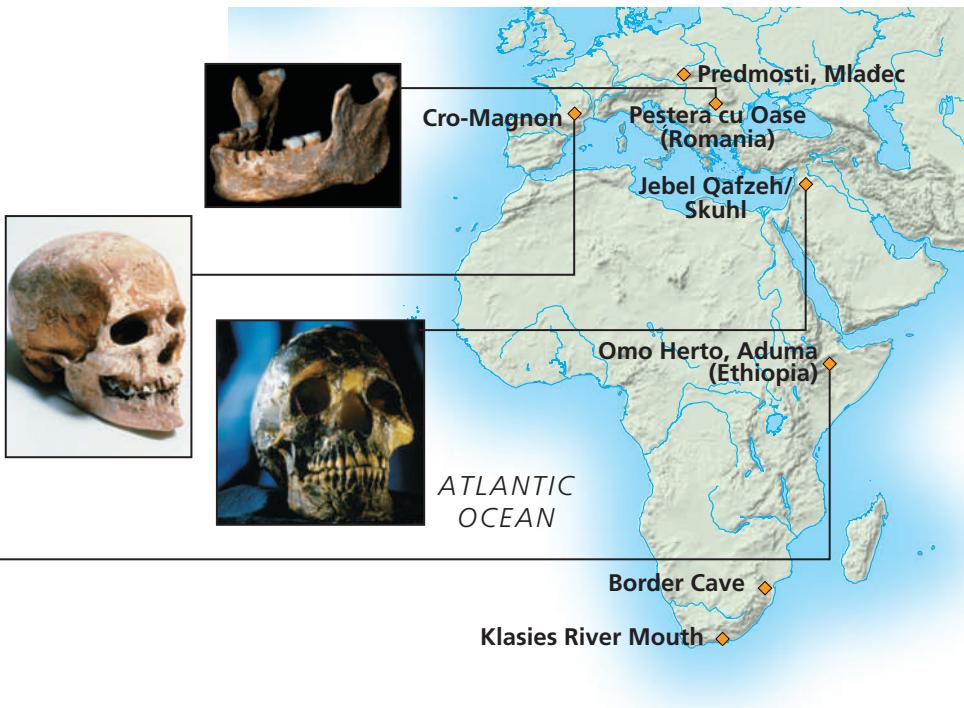
Anatomy and Distribution of Early Humans

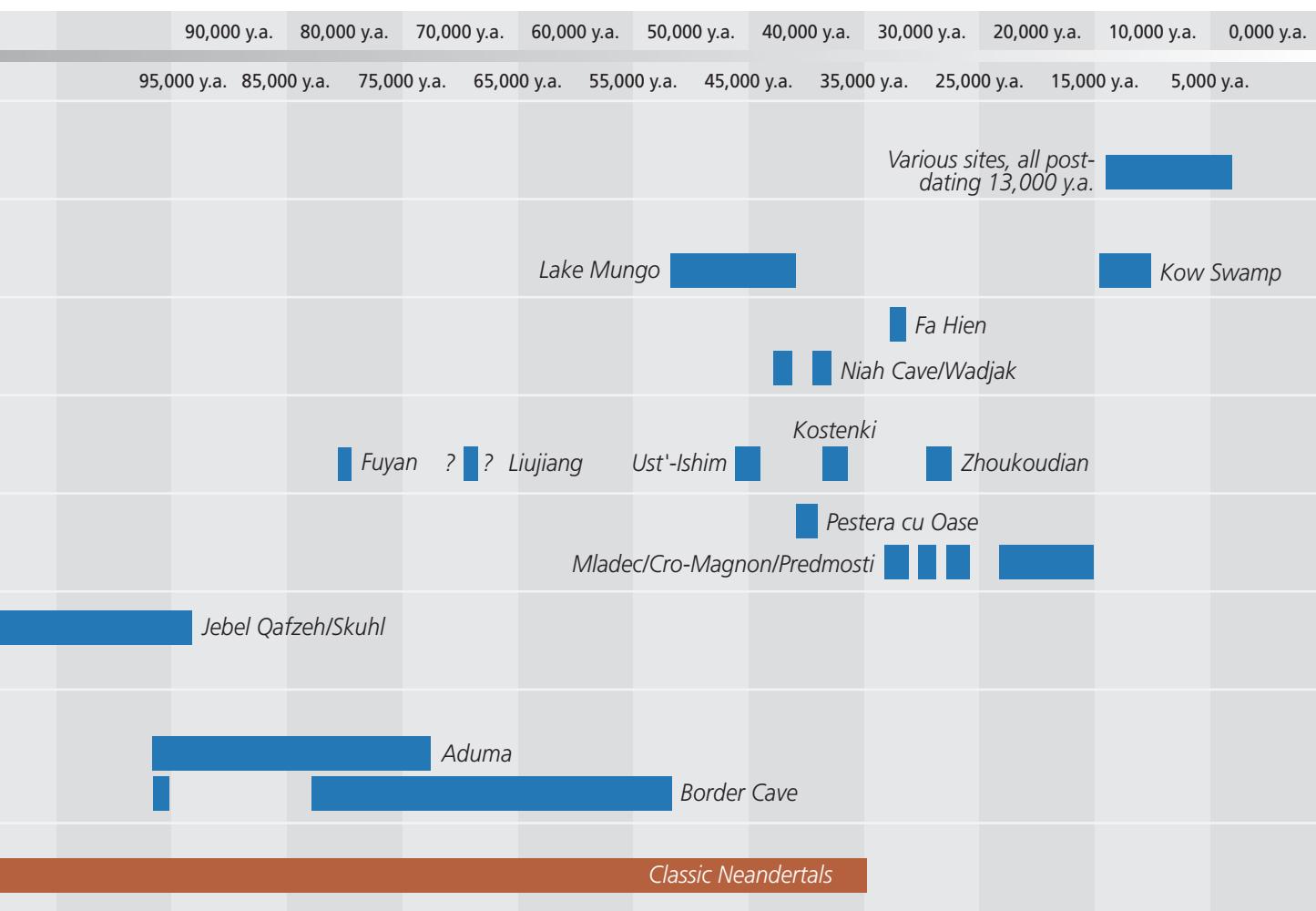
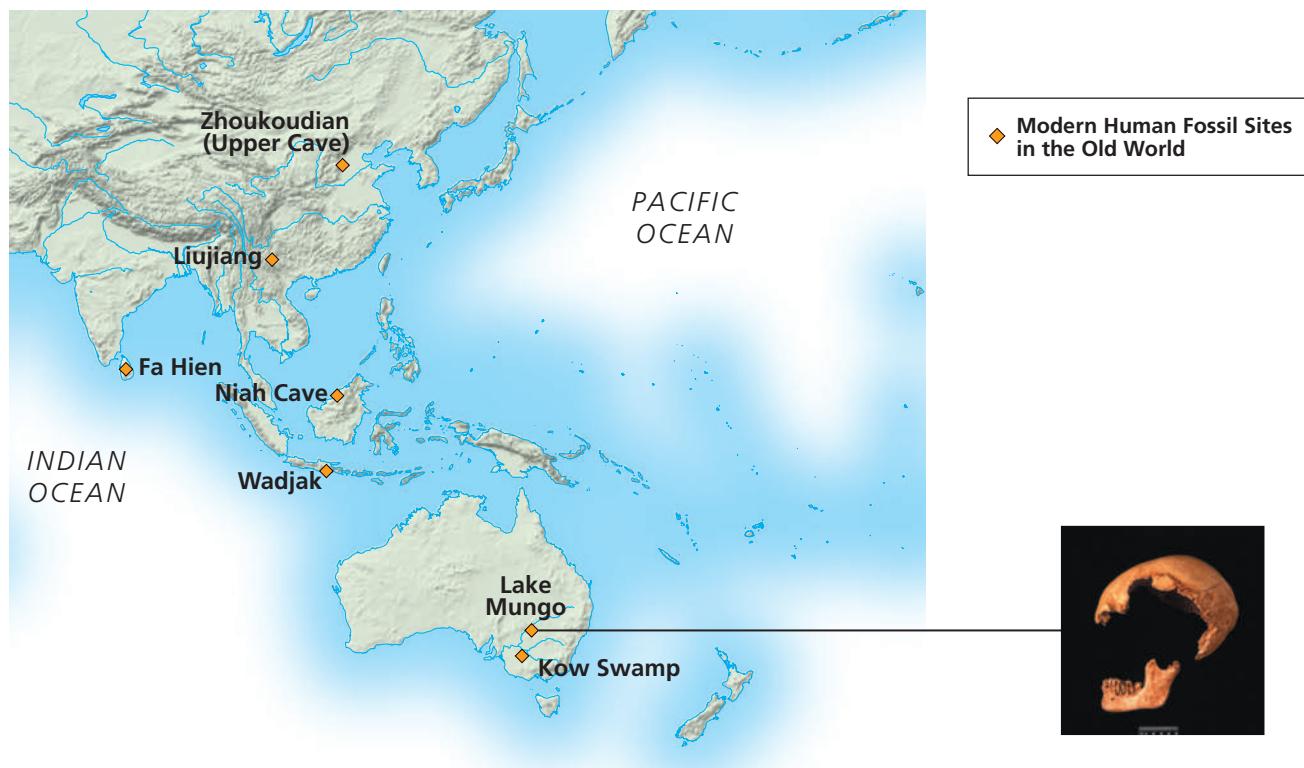
13.3 Discuss the anatomy and distribution of early humans around the world.

Early modern human fossils are rare (Figure 13.2 on pages 412–413). Using archaeological evidence alone to assess the early appearance of modern humans is risky because, as we have seen before, it is unwise to equate a given tool culture only with a specific hominin, especially in periods when significant evolutionary transformations took place. However, where we are certain that earlier hominins did not exist (such as in Australia and the Americas), we can use archaeological sites without human remains to chart the earliest appearance of modern humans.

Modern Human Fossil Sites in the Old World

Figure 13.2 The oldest known fossil *Homo sapiens* are found in Africa. Fossil modern humans are found throughout the Old World starting after 50,000 years ago. In some parts of the Old World, such as the Near East and Europe, modern humans appear to have overlapped with other hominin species, such as Neandertals. But in other areas, such as Asia, they probably did not.





In many cases, early modern human fossils possess both derived features linking them to us and primitive features they may share with archaic *H. sapiens* or Neandertals (Pearson, 2000). For example, several early humans possess a long pubic ramus, a trait also seen in Neandertals. If this trait is unique to Neandertals it would signal Neandertal ancestry for certain modern human populations, supporting a multiregional model. Alternatively, if it is a primitive feature inherited by both Neandertals and modern humans from their common ancestor (we do not know because the postcranial fossil record of archaic *H. sapiens* is so sparse), then it does not necessarily reflect a Neandertal ancestry for some modern human populations and may support replacement models. In each region, we must assess the combinations of traits seen in modern human fossils, and whether the traits they share with earlier hominins of the region are shared-derived characters that suggest a unique relationship between the two or primitive characters that they share from a deeper common ancestor.

Africa

Figure 13.3a Hominin remains from Herto, Ethiopia, are among the oldest anatomically modern humans yet discovered.



Figure 13.3b Early *H. sapiens* from Omo, Ethiopia date to 195,000 years ago.



While Neandertals were evolving in Europe, a different kind of hominin seems to have been evolving in Africa: anatomically modern *H. sapiens*. As we discussed in Chapter 12, archaic *H. sapiens* fossils such as Bodo and Kabwe have been found in Africa during the period from around 600,000 to about 200,000 years ago. Starting at about 200,000 years ago we begin to see fossils that look more, but not entirely modern. They come from sites such as Omo and Herto in Ethiopia, Ngaloba in Tanzania, and Florisbad in South Africa. Their anatomy typically is intermediate in form, and their ages often are imprecisely known. Slightly later, fully anatomically modern humans appear at sites such as Klasies River Mouth and Border Cave in South Africa and Aduma in Ethiopia. Although some scientists like to distinguish these earlier and later groups by calling them different subspecies, most scholars include both in our species and subspecies, *H. sapiens sapiens*.

The oldest of these fossils are those from Omo and Herto in Ethiopia (Figure 13.3). The Omo I partial skeleton is approximately 195,000 years old (Pearson et al., 2008) and remains from other portions of the site date to around 105,000 years old. The Herto locality in the Middle Awash region of Ethiopia yielded the crania of two adults and one juvenile estimated to date to between 160,000 and 154,000 years ago (White et al., 2003). Like other African specimens from this period, the Herto crania “sample a population that is on the verge of anatomical modernity but not yet fully modern” (White et al., 2003, p. 745).

The later group, represented by Aduma in Ethiopia and Border Cave and Klasies River Mouth in South Africa, date to about 120,000 to 50,000 years ago. The cranial remains from Aduma are 105,000 to 70,000 years old (Haile-Selassie et al., 2004). A partial adult cranium from Border Cave in South Africa dates to between 80,000 and 50,000 years ago. Fragmentary cranial and postcranial remains from Klasies River are between 120,000 and 90,000 years old (Rightmire & Deacon, 1991). For the most part, these early *H. sapiens sapiens* are found with typical MSA tool assemblages. But at Border Cave, the Howieson’s Poort industry may be considered an advanced MSA assemblage because it features a tool type more typical of the Upper Paleolithic.

This sequence of African fossils provides evidence that *H. sapiens sapiens* was well established by 100,000 years ago at least on that continent. Furthermore, a series of specimens dating from 200,000 to 100,000 years ago provides strong evidence of the African transformation of archaic *H. sapiens* into anatomically modern humans.

Near East

The Near East is the only region outside Africa to yield reliable evidence of modern humans earlier than 60,000 years ago. As discussed in Chapter 12, anatomically modern *H. sapiens* dating between 110,000 and 90,000 years ago have been found at the sites of Skūhl and Qafzeh, located on Mt. Carmel in Israel. The Near East sits between Africa and Asia, so if modern humans (or modern human morphology) first evolved in Africa some time after 150,000 years ago, then the Skūhl and Qafzeh hominins (Figure 13.4) could be considered the first sign of an expansion out of Africa that would only later (60,000–40,000 years ago) spread into Asia, Australia, and Europe. Neandertals are known to have occupied the Near East for tens of thousands of years, usually during glacial periods. Many scientists have interpreted the correlation of anatomically modern human specimens with warm (interglacial) periods and of later Neandertals with cold (glacial) periods as a sharing of this area by these two groups through time. Both Neandertals and early *H. sapiens sapiens* in the Near East are associated with MSA tool assemblages.

Europe

Scores of classic Neandertal remains have been recovered in Europe that date to between 150,000 and 30,000 years ago. However, modern human skeletal remains do not appear in Eurasia until relatively late, perhaps 45,000 years ago. An Upper Paleolithic assemblage known as the Aurignacian appears in Europe about 40,000 years ago, and when it is found with hominin fossils, starting around 36,000 years ago, they are always *Homo sapiens sapiens*. Recently, the precursor of this technology, the proto-Aurignacian, has also been shown to be associated with modern humans (Benazzi et al., 2015). A mandible from Carpathian region of Romania, at the site of Peștera cu Oase (“cave with bones”), is so far the oldest modern human in Europe, dating from 42,000 to 37,000 years ago. Like other early modern human specimens, the Oase 1 mandible is robust and is argued to exhibit a mix of clearly derived features aligning it with anatomically modern *H. sapiens* (such as development of the chin) and features (such as its robustness and anatomy of the mandibular foramen—a small hole in the mandible through which nerves and blood vessels pass) linking it to Neandertals (Trinkaus et al., 2003; Figure 13.5). The appearance of the mandibular foramen of Oase 1 may be a derived feature shared with Neandertals and not seen in human populations today. Although it is an insignificant biological feature, this is the kind of diagnostic trait that can become quite important in debates about phylogenetic relationships among late Pleistocene hominins. Indeed, recent DNA analyses confirmed that Oase 1 was a male whose lineage showed Neandertal introgression about 200 years before he lived (Fu et al., 2015). The 45,000 year old femur from Ust'-Ishim Siberia showed an even more ancient Neandertal introgression around 58,000 years ago into its lineage (Fu et al., 2014).

The central European sites of Mladeč and Předmostí, both located in the Czech Republic, have yielded numerous fossils of anatomically modern *H. sapiens*, which also display characters that may align them with Neandertals (Smith, 1984; Frayer et al., 2006). These sites date from between 35,000 and 25,000 years ago, with the Předmostí site being somewhat younger than Mladeč. Both were discovered in the late nineteenth century; unfortunately, the Předmostí remains were destroyed during World War II. At these sites several crania, probably representing males, have an occipital bun or hemi-bun, which is not as fully developed as the Neandertal occipital bun. Some anthropologists have argued that this feature, in combination with the development of browridges, suggests a Neandertal ancestry of these early modern humans.

In contrast, early Upper Paleolithic human postcranial skeletons in Europe appear to be tropically adapted, lacking the cold-adapted

Figure 13.4 Anatomically modern humans from the Israeli cave sites of Skūhl and Qafzeh may be the earliest found outside of Africa.

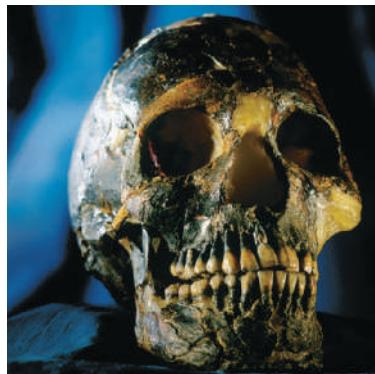


Figure 13.5 The Oase 1 mandible, earliest modern human in Europe.



proportions we saw in Neandertal skeletons. They have narrower, more linear body proportions of the limbs and thorax, associated with humans living in tropical climates who easily dissipate heat (see Chapter 5). Some scholars interpret this as evidence that modern humans migrated from tropical Africa to cold Europe more quickly than their skeleton could adapt to the climatic shift. If true, this would support a replacement model.

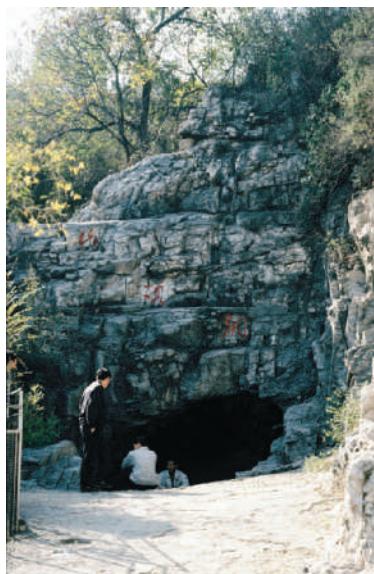
The best-known early anatomically modern humans from Europe come from the Cro-Magnon rock shelter located in the Dordogne region of France, which includes a number of Neandertal sites as well. Discovered in 1868, the Cro-Magnon remains include at least four adults (with partial crania and mandibles), an infant, and an assortment of other cranial and postcranial remains. The site is about 27,000 years old, much younger than the first appearance of modern humans in Europe (Gambier, 1989). The “Old Man” of Cro-Magnon (or Cro-Magnon 1) has a gracile cranium that combines a very small face with a large and bulbous braincase, in striking anatomical contrast to Neandertals from the same region (Figure 13.6). Because of these anatomical differences, archaeologists developed an evolutionary scenario for western Europe in which the Middle Paleolithic Neandertals were replaced quickly by Upper Paleolithic modern humans, sometime between 40,000 and 30,000 years ago. However, critics argue that the Cro-Magnon 1 specimen is not like other early modern humans in Europe (including those from central Europe and even some of the other Cro-Magnon individuals), who show a more mosaic pattern of archaic and modern features.

Given their late appearance, it is not surprising that European anatomically modern humans are found only with Upper Paleolithic technologies. In fact, in western Europe there appears to be a one-to-one correlation between *H. sapiens sapiens* and the Aurignacian technology (and likely also the proto-Aurignacian). As we saw in Chapter 12, a different Upper Paleolithic technology, the Châtelperronian, is contemporaneous with the Aurignacian but is often found with Neandertals.

Figure 13.6 The “Old Man” of Cro-Magnon, from the Dordogne region of France.



Figure 13.7 The Upper Cave at Zhoukoudian yields ages of about 25,000 years for *Homo sapiens*.



Asia and Southeast Asia

In Asia there is a gap in the hominin fossil record between about 100,000 and 40,000 years ago. Archaic or premodern *H. sapiens* are known from a number of sites dating from between 250,000 and 100,000 years ago in China (Etler, 1996), but anatomically modern humans do not appear until perhaps 65,000 years ago or later in China and possibly 40,000 years ago in Indonesia.

Dating is a problem for establishing the earliest human remains in Asia. In China, the site of Liujiang has been dated to at least 18,000 years ago, and perhaps as old as 67,000 years, but there is some question as to the provenience of the human remains recovered from that site (Shen et al., 2002). Recently, a series of modern looking teeth have been described from China. These teeth are argued to be 80,000 years old. (Martinson-Torres et al., 2015). Well-accepted dates of 25,000 years ago have been obtained for the site of Hebei and for the Upper Cave at Zhoukoudian (~42 km southwest of Beijing; Figure 13.7). Stringer and Andrews (1988) think the Upper Cave skulls most closely resemble early modern humans from the European sites of Mladeč and Předmostí (Figure 13.8), which would mean that both European and Asian early modern human populations had a common origin (presumably Africa) and that there is little evidence of regional continuity.

The earliest *H. sapiens sapiens* in Southeast Asia are equally problematic. Specimens such as the “Deep Skull” from the Niah Cave complex in Borneo and Wadjak from Java (one of the first specimens discovered by Eugene Dubois’s team) have been assigned dates of about 40,000 years ago. The complex cave stratigraphy and questions of where precisely the fossils were found led many scientists to consider

Figure 13.8 Fossil remains of anatomically modern humans from the Czech Republic and from China (center crania) are more robust than recent human crania but are otherwise anatomically identical. All four crania are *Homo sapiens sapiens*.



these dates highly provisional. However, recent archaeological and archival work by Graeme Barker and colleagues (2007) lends support to an age of 34,000 to 46,000 years ago for the “Deep Skull” from Niah Cave (Figure 13.9).

The possible evolutionary relationships of these Asian modern humans exemplify contrasting views of the origin of all modern humans. Some researchers argue that fossil *H. sapiens* represent the culmination of an unbroken evolutionary trajectory in China and Indonesia that in Asia began with variants of *H. erectus* in each area and that extends to contemporary East Asian populations (Wolpoff et al., 1994). Other researchers argue that the Upper Cave individuals do not resemble modern Asians in any meaningful way, nor do the early Indonesians represent modern Indonesians, and that both may represent a migration into the region by individuals of an early, geographically undifferentiated modern human group (for example, Stringer & Gamble, 1993). Filling the Asian fossil gap between 100,000 and 40,000 years ago will be essential in resolving some of these issues.



Figure 13.9 The Niah Cave complex in Borneo.

Figure 13.10 Partially cremated skull from Lake Mungo, Australia.



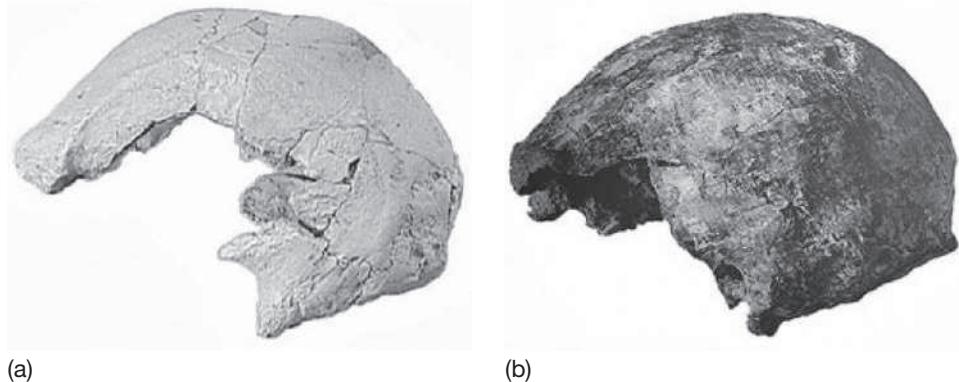
Australia

Although Australia is separated by water from the major Eurasian land mass, evidence suggests that modern humans were in Australia at least as early as if not earlier than they were in Europe. To get to Australia, modern humans almost certainly had to go through island Southeast Asia; so the ages of the earliest Australian occupation are also relevant to the peopling of Southeast Asia. During glacial maxima, when sea levels are lowest, Australia and New Guinea form a single land mass known as Sahul. Sahul is always separated by water from the land mass Sunda, which includes some of the islands of Southeast Asia. Although all kinds of primates, including extinct hominins, occupy or occupied Sunda, only modern humans were able to disperse throughout Sahul. However, as we saw in Chapter 11 a stunning recent discovery from Flores, Indonesia, shows that at least one other hominin was able to make the jump from Sunda. Some scientists argue that the settlement of Australia, New Guinea, and other islands of Melanesia was a fundamental advance in the behavior of modern humans over earlier hominins (Noble & Davidson, 1996), in part because settlement of these islands could have been accomplished only by using a boat or raft of some kind.

The earliest human remains from Australia come from a site in the southeastern part of the continent known as Lake Mungo. Two incomplete skeletons from burials, along with other fragmentary remains and some cremations, have been found and recently dated to 40,000 years ago (Figure 13.10). Flake tools from Lake Mungo date to 50,000 years ago, which matches the earliest archaeological dates in Australia (Bowler et al., 2003). Mungo I, the buried remains of a young female, shows signs of having been cremated; the other burial, Mungo III, is an old male whose body was covered with red ochre. These are the earliest known examples of such mortuary practices. Both specimens are anatomically modern *H. sapiens*, and they both exhibit a gracile build.

Other Australian sites, such as Kow Swamp and Willandra Lakes, have yielded a number of reasonably complete crania that are substantially more robust than those of the Lake Mungo people. They are also substantially younger, dating between 13,000 and 9,500 years ago. The Kow Swamp individuals are interesting, however, because their thick cranial bones and moderate development of browridges have been argued to demonstrate their close affinities with the latest *H. erectus* found at the site of Ngandong in Indonesia (Wolpoff et al., 1984). As we saw in Chapter 12, Ngandong may be a relict population of *H. erectus* that persisted on Java until at least the middle Pleistocene and perhaps as late as 25,000 years ago (Swisher et al., 1996; Indriati et al., 2010; Figure 13.11). However

Figure 13.11 Evidence of regional continuity: (a) The anatomically modern Willandra Lakes Hominid 50 calvaria from Australia and (b) a later *Homo erectus* cranium from Ngandong, Indonesia.



they arose, it seems clear that anatomically modern humans had the ability to cross large bodies of open water and colonize Australia by at least 50,000 if not 60,000 years ago.

Archaeology of Modern Human Origins

13.4 Describe the archaeology of modern human origins including how the upper paleolithic or later stone age differs from middle and early stone age tool technologies and describe the behavioral differences and role of symbolism in the Upper Paleolithic.

The archaeological remains of later modern humans reflect cultural and individual behaviors that are substantially more complex than those of earlier hominins or even of the earliest *H. sapiens sapiens*. But just which of these behaviors allowed us to become the dominant hominin species throughout the world by about 40,000 years ago?

Stone and Other Tools

We can look at the changes in tool cultures and industries associated with the emergence of anatomically modern humans as a tale of two continents: Europe and Africa. For many years, the European archaeological and fossil records formed the basic model for the emergence of modern people. Over the past few decades, however, the archaeology of Africa has provided a new context for understanding human origins.

The very earliest modern humans, those dating to 100,000 years ago or earlier in Africa and the Near East, are found with MSA assemblages that are indistinguishable in most ways from those of earlier hominins (or later Neandertals). Thus modern anatomy appears before the development of modern—Upper Paleolithic—technology.

The European Upper Paleolithic and the African Later Stone Age are distinguished from the MSA by a greater reliance on the standardized production of blades: long flakes that could be used as blanks to produce a variety of different flaked tools. A number of blades could be taken off a prepared stone core in a systematic manner (see Figure 12.23 on page 394). Refinements in tool flaking techniques also distinguish Upper Paleolithic and Later Stone Age tool industries from the MSA. For example, long, exquisitely flaked blades from the Solutrean industry of Europe demonstrate the extraordinary level of skill of Upper Paleolithic toolmakers (Figure 13.12).

Microliths are another common feature of Upper Paleolithic and Later Stone Age tool industries, which appeared after 25,000 years ago in most regions. **Microliths** are small, shaped flakes that probably were once attached to wood or bone to make composite tools. Arrowheads are a late-version microlith that appear for the first time around 13,000 to 10,000 years ago. Unlike the MSA, in which a basic set of tools and techniques emerged early and persisted for the next 250,000 years, tool types change frequently and continuously throughout the Upper Paleolithic and Later Stone Age.

Another striking feature of the Upper Paleolithic and Later Stone Age is the vastly greater use of tools made from bone, ivory, antler, and shell. These were ground, polished, and drilled to form objects such as harpoons, fishhooks, spear-throwers, awls, needles, and buttons. (Such materials were used but at a much cruder level and very rarely in earlier industries.) Upper Paleolithic peoples also produced well-known examples of representational cave art and other artistic or ritual objects.

Figure 13.12 Upper Paleolithic refinement in stone tool production, a Solutrean blade.



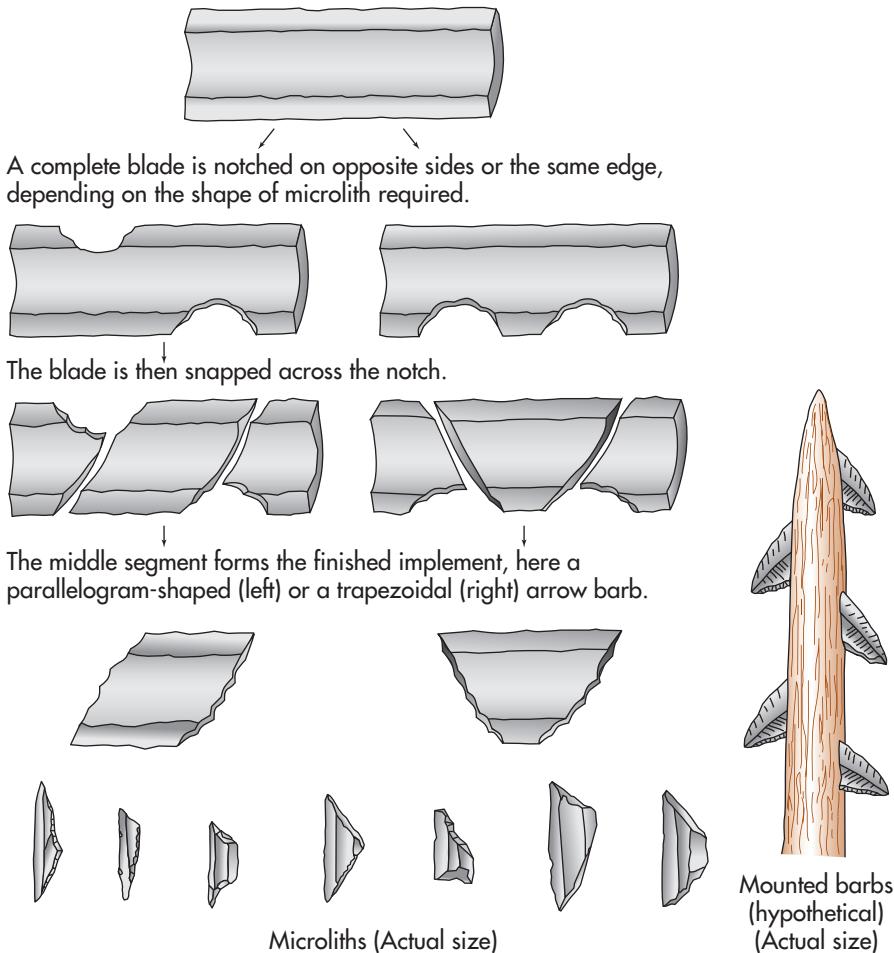
microliths

Small, flaked stone tools probably designed to be hafted to wood or bone; common feature of Upper Paleolithic and Later Stone Age tool industries.

With one or two exceptions, the appearance of Upper Paleolithic tool industries in Europe coincided with the appearance of anatomically modern humans. In the nineteenth century, the shift from the Mousterian to the Upper Paleolithic was considered to represent a behavioral or cultural revolution that occurred when modern humans replaced Neandertals in Europe. For decades many scientists thought that similar replacements had occurred in other parts of the world as well. However, given the relatively late appearance of modern humans in Europe, it seems unlikely that Europe should be a good model for the original appearance of modern humans.

Indeed, many archaeological elements thought to be uniquely associated with the Upper Paleolithic and Later Stone Age actually made their first appearance in the Middle Stone Age of Africa (McBrearty & Brooks, 2000). These innovations did not appear suddenly in a single locality but in different sites at different times. For example, blades are known from several sites, dating from 75,000 years ago to perhaps as early as 280,000 years ago in East Africa. Flake technologies based on the production of points rather than scrapers (a hallmark of the Mousterian in Europe) are also abundant in African MSA sites, some dating to 235,000 years ago. More surprisingly, microliths (Figure 13.13), which are typically associated with the late Upper Paleolithic, were being made in the African MSA 65,000 years ago. The site of Mumba in

Figure 13.13 Microlith production. Although microliths are typically considered an Upper Paleolithic technology, their origins can be traced to the Middle Stone Age of Africa.



Tanzania shows a continuous sequence of the development of microlith technology, starting from larger flake tools. In South Africa, the Howieson's Poort industry (dating to 70,000–60,000 years ago) is also characterized by an abundance of microliths. At Border Cave, the Howieson's Poort industry is found in association with anatomically modern human remains. Tools made from bone have also been found at a variety of African MSA sites.

Based on these data, Sally McBrearty and Alison Brooks (2000) suggest that the transition to the kind of cultural assemblage we associate with modern humans developed through the gradual accumulation of different techniques and tool types and that it was more evolutionary than revolutionary. Thus, the rapid replacement of the Middle Paleolithic by the Upper Paleolithic in Europe may not be representative of what happened in Africa, the region where modern humans first evolved. The pattern of change in the Australian archaeological record appears similarly gradual (Habgood & Franklin, 2008).

We should pause at this point to reflect on what *modernity* really means. The appearance of such tools as blades often has been the basis for inferring the appearance of modern behavior. However, it is not clear that these archaeological signals are good proxies for modernity. Can modern behavior, like modern anatomy, be signaled by the appearance of a single derived character or the presence of a single tool type, however briefly it appears in the record? Or is it indicated only by the presence of a comprehensive package of behaviors that signifies a different set of interactions with the world?

Subsistence

Much evidence supports the idea that modern humans exploited a wider variety of foodstuffs than did Neandertals or archaic *H. sapiens*. Ultimately, this ability to exploit natural resources led to the development of agriculture, starting about 12,000 years ago, which allowed a sustained increase in population growth. However, by expanding their subsistence base in other ways, early anatomically modern humans may have established a pattern of increased population growth relative to other hominins even at the very origins of our species, long before the introduction of agriculture.

One example is the use of aquatic resources, such as fish and shellfish. Earlier hominins, including some Neandertal populations, made limited use of marine resources. And some African MSA coastal sites show exploitation of marine mammals, fish, shellfish, and tortoises earlier than 40,000 years ago, perhaps signaling an earlier shift to modern behavior on that continent. However, only in the Upper Paleolithic and Later Stone Age do aquatic resources become a widespread and systematic part of human subsistence.

Besides archaeological remains, other information points to the expansion of subsistence patterns in modern humans. Dental microwear analyses reveal wear patterns on Neandertal teeth that are more similar to those seen in recent human populations (Inuit and Fuegians) who have highly carnivorous diets (Lalueza et al., 1996). In contrast, Upper Paleolithic wear patterns indicate a diet incorporating a greater amount of vegetable matter. Similarly, stable isotope analyses of Neandertals across their time span and early Upper Paleolithic burials (aged 26,000–20,000 years) indicate that Neandertals ate mostly terrestrial herbivores, like deer, but that the Upper Paleolithic people ate a more varied diet that included fish, mollusks, or possibly shorebirds (Richards et al., 2001; see Chapter 8 for a review of the stable isotope methods).

Late in the Upper Paleolithic, changes in subsistence allowed humans to finally occupy high latitudes. Colonization beyond 55° latitude north or south seems to have

been biologically limited until perhaps 45,000 years ago or so, when new behavioral adaptations overcame the problem. Living humans show a skin color cline that is related to the availability and intensity of UV radiation (see Chapter 5). Darker skin color is prevalent in the tropics, and lighter skin color toward the poles. The cline seems to be selected for by two opposing forces—the tendency of melanin in darker skin to protect against folate degradation in UV-intense environments, such as those near the equator, and for lighter skin to allow sufficient vitamin D synthesis in UV-deprived environments nearer the poles. Given that they lived in the tropics, earliest *Homo* populations were probably dark-skinned. Subsequent migrations to higher latitudes eventually led to the evolution of the skin color cline; ancient DNA (aDNA) evidence suggests that some skin depigmentation occurred in the Neandertal lineage (see Innovations: Neandertal Genes in Chapter 12 on pages 392–393). However, even this skin color cline reaches its biological limit at about 50° latitude north or south. At about this latitude even light-colored skin does not receive enough UV radiation during any part of the year to adequately synthesize vitamin D (Jablonski, 2004). It is not until human populations are able to routinely acquire vitamin D through their diets, as opposed to synthesizing it from sunlight, that we see permanent archaeological sites beyond this latitude. Dietary sources of vitamin D include marine mammals, fish, lichen, or meat from animals that eat lichen, such as reindeer. Neandertal populations make it to just past 50 degrees north latitude at Okladnikov and Mezmaiskaya, but early *H. sapiens* from Ust'-Ishim is the first known at greater than 55 degrees north.

Symbolism

Perhaps the most striking difference between later modern humans and earlier hominins is the extent to which modern human archaeological assemblages incorporate clear evidence of symbolic behavior. Remember the scant and debatable evidence of Neandertal symbolism reviewed in the last chapter. In contrast, by 50,000 to 40,000

years ago modern humans apparently dedicated large percentages of their time to symbolic acts such as creating and presumably wearing ornamentation, making cave and portable art, and burying their dead. All this suggests that symbolic behavior had a survival value for modern humans and that their relationship to the world and to other hominins may have been ordered by symbols (see Innovations: Symbolism and Human Evolution on pages 424–425).

BURIALS The significance and even the existence of Neandertal burials are debated, and their symbolic implications are questioned as well. By about 40,000 years ago these questions became moot because evidence of new mortuary practices, including cremation at Lake Mungo in Australia, appears at modern human sites at this time. In Europe, Upper Paleolithic burials (the earliest of which date to about 28,000 years ago) differ from Mousterian burials in several ways.

Whether found in caves or open air sites, Upper Paleolithic burials are composed of burial pits. More important perhaps, a number of Upper Paleolithic burials contain an elaborate array of grave goods and multiple, carefully arranged bodies (Figure 13.14). Upper Paleolithic European burials often are covered in beads and bear other indications that the dead were buried in decorated garments that represented hundreds or thousands of hours of time in their preparation (Stringer &

Figure 13.14 Anatomically modern humans left archaeological clues, including evidence of burials, which indicate that ritual and symbolic behavior were important parts of their culture.



Gamble, 1993). Obviously, not every Upper Paleolithic burial is an elaborate affair complete with an abundance of finely made grave goods. However, such burials are completely absent in the earlier archaeological records. Interestingly, evidence of deliberate burial of any kind in the later MSA is quite scanty, and Aurignacian burials are also scarce.

ART AND ORNAMENTAL OBJECTS Unlike the equivocal engravings of Neandertals, the artistic expression of Upper Paleolithic humans is astounding (Figure 13.15). Cave art and *petroglyphs* (rock carvings) occur not only in Europe but also in Africa and Australia. Ornamental objects like statues, beads, and pendants are also prevalent in the Upper Paleolithic (see Innovations: Symbolism and Human Evolution on pages 424–425). These elaborate displays of human symbolic behavior occur late in the archaeological record of modern humans, usually 40,000 years ago or later, not with the earliest moderns. However, several examples of perforated shell, bone, and stone have been found at African MSA sites earlier in time, and perforated shell beads have been argued to be present at 73,000 years ago at Blombos Cave in South Africa (Henshilwood et al., 2004). If these prove on further inspection to be worked beads, they would represent the earliest known ornamentation and important support for a gradual accumulation of modern human behaviors.

The extensive evidence of artistic abilities of late Pleistocene modern humans, expressed in a wide range of media over a large number of populations, stands in stark contrast to the paucity of evidence for such activities in Neandertals and other hominins. Of course, this does not mean that earlier hominins were incapable of symbolic or artistic expression. Indeed, two examples of putative anthropomorphic carvings have been found in Acheulean deposits from Morocco and Israel dated to between about 400,000 and 250,000 years ago (Bednarik, 2003), which may give us a hint of the artistic abilities of archaic *H. sapiens*. Nonetheless, even though modern humans may not have been the only hominin capable of making art, it is clear that symbolic behavior took on a whole new significance with the evolution of our species.

Figure 13.15 Abundant cave art from about 30,000 years ago is evidence of the importance of symbolic behavior for modern human cultures.



Innovations

Symbolism and Human Evolution

Symbols are things that, by accepted practice, represent other things—like the red and white stripes and white stars of the flag of the United States represent the country itself. Symbols are powerful things because they convey often complex meaning to others, but understanding their meaning requires knowledge of the conventions and norms of the group using the symbol. So, for some groups the U.S. flag may imply positive American sentiments, such as baseball and apple pie, but for others it might have negative associations, such as imperialism or capitalism. While we can never know what the precise meanings were of the symbols used by our fossil ancestors, we can see when in human evolution symbolic behavior, possibly group identity, and perhaps extended kin networks started to be important for survival.

By the end of the Pleistocene, say 40,000 to 50,000 years ago, the archaeological record is replete with evidence of symbolic behavior. *Homo sapiens* were burying their dead with elaborate displays of grave goods, making

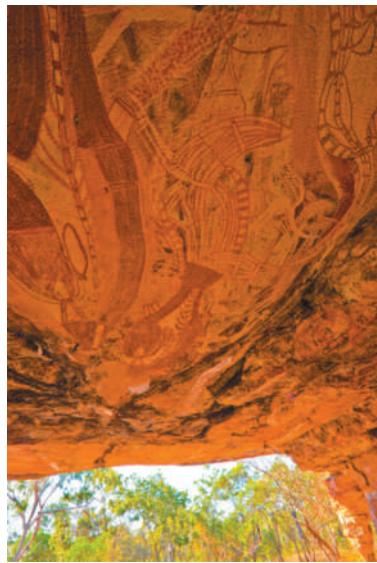


art, and using personal ornaments. All of these activities took time, time that could otherwise have been used to gather food or hunt or on some other survival practice. Archaeologists are using new experimental methods and theory to understand the meaning of these practices.

Perhaps the most stunning evidence of symbolic behavior is the the practice of cave painting. Many paintings are found deep in caves, often in nearly inaccessible places. Imagine being an early modern human, with no flashlight to light your way and no climbing gear to ease your passage, moving into the dark, damp chambers of a cave, with a small flame throwing shadows around you, barely lighting your way. What inspired you to voyage into this space? What were you seeking to convey?

The earliest cave art known in Europe appeared about 32,000 years ago at Chauvet, France, and is complex in its technique and representation. Rock art appeared in Africa about 26,000 years ago at Apollo 11 cave in Namibia, and somewhat earlier than that in Australia, at places such as Carpenter's Gap, which may be 40,000 years old. Recent spectacular claims suggest that rock art just as old may also be found in Indonesia. The ages of all of these sites are hard to establish though, because of the difficulty of dating when the art was applied to the walls. Typically, uranium series techniques are used—but it is unclear whether the carbonates on rock walls really form the closed systems required by the technique (see Chapter 8). The rock art of Australia, which spans thousands of years,





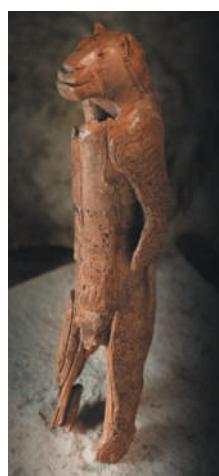
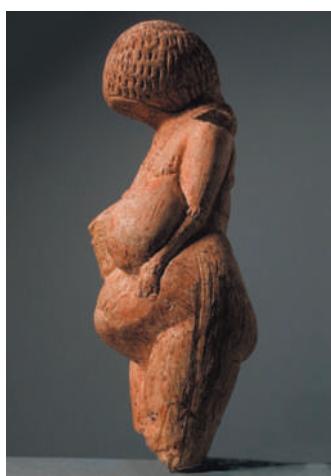
provides a particularly rich record of human artistic expression. The animals represented on cave walls in Chauvet, France were once interpreted as sympathetic magic to assist in hunting success. But when compared with animal bones from archaeological sites of the same period, it seems the cave paintings mostly depict animals that early humans did not hunt. Perhaps the animals had some other symbolic or ritual importance for them.

Red ochre (iron oxide) and the color red were of great significance to modern humans. Evidence from one of the Lake Mungo burials in Australia indicates that the body may have been covered with red ochre. At the Qafzeh site, dating to about 92,000 years ago, seventy-one red ochre pieces, including some that were flaked or marked in some way, were associated with remains of anatomically modern humans, and several stone artifacts were stained with red ochre, although there was no evidence that the bodies themselves were covered

in ochre (Hovers et al., 2003). Erella Hovers and her colleagues suggest that the form and distribution of the red ochre pieces indicate they were deliberately mined from a variety of local sources.

Portable art and ornaments are also prevalent in modern human archaeological sites. The most famous are the so-called Venus figurines that represent various female figures, often interpreted as fertility totems. However, other figurines also exist, including many zoomorphic (animal) statuettes. All are small enough to be carried around in a pocket, although we do not know if they were. Pendants made from ivory and even from animal teeth, often from animals that Upper Paleolithic people did not eat, such as fox, are also found. There are even examples of pendants made from human molars. And thousands of beads have been found at Upper Paleolithic sites. Some beads were found isolated or in batches, and others were found laying on bodies within burials suggesting the individuals were decorated before burial. Experimental work by Randall White suggests that most beads were attached to garments and took a few hours per bead to make. Thus, the Upper Paleolithic peoples invested a huge amount of time into making these grave items and personal ornaments, indicating that they had important symbolic meaning and probably were in some way important for survival.

It is important to remember that symbols are not edible, and unlike stone tools they do not even help you break open bones, cut meat off a carcass, or access a nut or fruit that you might eat. But symbols may help in survival in other ways. Perhaps they help to identify you as part of a particular group, one that lives over an extended range and with whom you might exchange food resources during difficult times. Or perhaps this group will recognize you as part of an extended group of “friends” not “foes” when they recognize your symbols, even if you do not know one another personally. We can’t know for sure, but what is clear is that organizing the world in symbolic ways was of great importance to modern humans after about 40,000 years ago.



Molecular Genetics and Human Origins

13.5 Explain the role of molecular genetics and human origins, including the role of mitochondrial, Y-chromosome, nuclear and ancient DNA in testing models for human origins.

most recent common ancestor (MRCA)

In a phylogenetic tree, the MRCA is indicated by the deepest node from which all contemporary variants can be shown to have evolved.

In looking at modern human origins, geneticists have used two types of data. The first considers living human genetic variation with the goal of identifying the **most recent common ancestor (MRCA)** of all people living today. The second set of data attempts to isolate DNA sequences from fossil hominins. These ancient DNA analyses then consider the difference between the ancient groups and the extent of relatedness between them (see Innovations: Neandertal Genes in Chapter 12).

In a phylogenetic tree, the MRCA is indicated by the deepest node from which all contemporary variants can be shown to have evolved. Because all living people are genetically related to each other, the deepest node in a phylogenetic tree corresponds to a basic biological reality: All the variation we observe today evolved from a common ancestor. However, identifying the deepest node poses some problems. First, in large, complex datasets we can construct a huge number of possible phylogenetic trees. Thus, any particular tree represents a statistical model, which incorporates our assumptions about population size, the effects of natural selection, and other factors. Second, after identifying the deepest node in a tree, researchers want to know the date of the node. Putting a date to the node representing the MRCA entails calibration and an accurate determination of rates of genetic change (that is, setting the molecular clock; see Chapter 9). Finally, genetic data provide no insights into what the bodies carrying the genes looked like. In the case of human origins, for example, the MRCA need not have been an anatomically modern human.

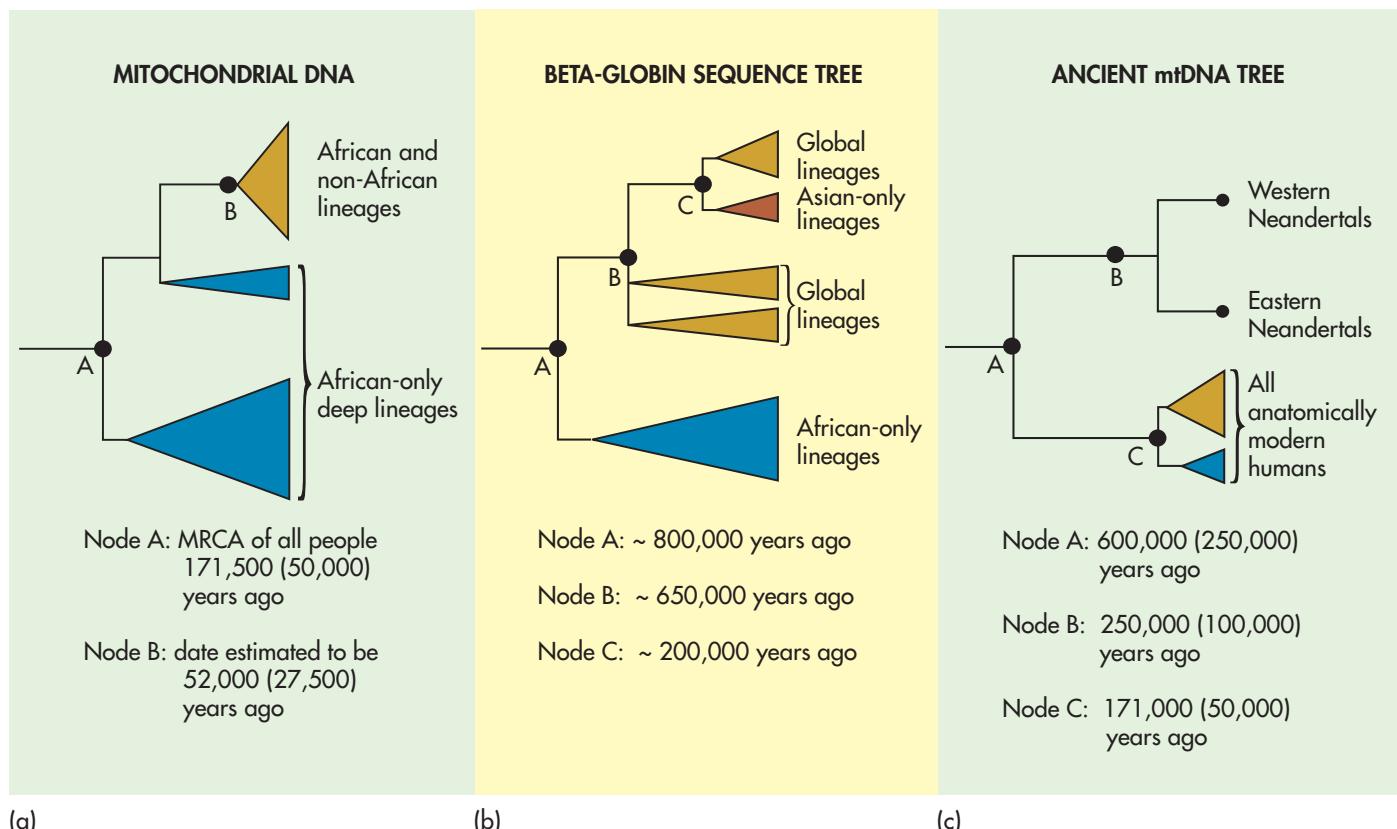
At a fundamental level, the biological issue of modern human origins can be addressed only by both genetic and anatomical (paleontological) data. The molecular identification of the MRCA does not give us any idea about the physical or behavioral changes that led to the establishment of our species; the fossil record has no direct information about whether any past species or populations had any descendants.

Mitochondrial DNA

Mitochondrial DNA is transmitted maternally (only through the mother), has a relatively rapid rate of evolution, and does not undergo recombination. In the 1980s, researchers began using mtDNA to investigate modern human origins. In a landmark study, Rebecca Cann and her colleagues (1987) constructed a phylogenetic tree based on sequence differences distributed throughout the human mtDNA genome. To do this they used mtDNA from a large group of people representing several populations. The tree was quite complex, and there was much overlap between individuals from different populations. There was one exception: At the deepest node (representing the MRCA), on one side of the tree there was a cluster of mtDNA lineages represented exclusively in Africa. Although African mtDNA lineages were also found on the other side of the tree, the exclusive African cluster indicated that the MRCA lived in Africa. Cann and her colleagues suggested a tentative date for the MRCA between 90,000 and 180,000 years ago. Although an mtDNA phylogeny traces the lineages down to a single mtDNA source, it is important to remember that there was more than one female in the population at the time; we should not think of the mtDNA studies as identifying an African “Eve.”

Subsequently, Max Ingman and his colleagues (2000) confirmed that the three deepest branches of the tree were exclusively African, with the next deepest being a mixture of Africans and non-Africans (Figure 13.16). All non-African mtDNA branches are of a very similar depth. Ingman and colleagues argued that such a pattern would arise if mtDNA lineages evolved initially for some time in Africa, followed by a migration of a small number of individuals out of Africa. This resulted in

Figure 13.16 Three phylogenetic representations of modern human origins: (a) mtDNA, (b) beta-globin gene, and (c) ancient mtDNA.



a population bottleneck, followed by a population expansion, with all later Eurasian mtDNA lineages derived from this initial small population that left Africa. Ingman and colleagues put the date of the MRCA for the whole tree at 171,500 ($\pm 50,000$) years ago, somewhat earlier than that found in Cann's study. The date of the earliest clade that included African and non-African mtDNA was 52,000 ($\pm 27,500$) years ago.

By 2012, more than 18,000 complete mitochondrial genomes had been published (Disotell, 2012). Phylogenetic analyses show that they all derive from a common ancestor who lived less than 200,000 years ago. In other words, the mtDNA of modern humans shows no evidence of having a contribution from a lineage that split off more than 200,000 years ago.

The Y Chromosome

The Y chromosome is in some ways the male equivalent of mtDNA. Like mtDNA, it is transmitted across generations in only one sex, in this case, males. Although parts of the Y chromosome undergo recombination, a large portion does not, and studies of this portion have been widely used in evolutionary research (Mitchell & Hammer, 1996; Stumpf & Goldstein, 2001; Jobling & Tyler-Smith, 2003). Phylogenetic analyses of the Y chromosome are based on both sequence and haplotype data. Haplotypes are combinations of mutations found together on a single chromosome; we can analyze them phylogenetically or calculate population frequencies for different haplotypes (see Chapter 5). There are at least eighteen major haplotype groups for the Y chromosome, which are themselves composed of dozens of different haplotypes. Haplotypes are useful for tracing population movements and demographic events that have occurred across human history (see Chapter 17, Innovations: Ancestry and Identity Genetics).

The Y-chromosome data seem to support the mtDNA story (Underhill and Kivisild, 2007). Several estimates of a date for the Y chromosome MRCA have been suggested; most researchers accept an estimate of 100,000–180,000 years ago. Thus, the variation we observe in the Y chromosome and mtDNA of living humans appears to have evolved within similar time frames. For both, the MRCA is dated with some confidence to less than 200,000 years ago. The Y-chromosome and mtDNA data also both place the location of the MRCA in Africa. As was the case for the mtDNA, the deepest Y-chromosome lineages are found exclusively in Africa, indicating evolution there first, followed by a population expansion into other parts of the world. Both kinds of genetic information provide evidence of founder effects in more isolated populations. Some differences between Y-chromosome and mtDNA phylogenies can be found in Europe, where the mtDNA suggest a more unified population, but the Y chromosome indicates a split between Eastern and Western European populations. The Y chromosome also shows that there was a late Pleistocene migration out of Africa into Europe that is not represented in mtDNA data.

MRCAs for Nuclear Genes

Although the Y-chromosome is part of the nuclear genome, it is a special case because such a large proportion of it is nonrecombining and it has only a small number of genes that are subject to natural selection. The remainder of the nuclear genome affords countless opportunities for reconstructing the evolutionary histories of human populations.

Large-scale compilations of protein allele data (see Chapter 5) are generally consistent with the evolutionary picture provided by mtDNA and the Y chromosome (Cavalli-Sforza et al., 1994; Cavalli-Sforza & Feldman, 2003), especially in locating the MRCA in Africa. In a phylogenetic tree derived from an analysis of allelic variation in 120 protein genes distributed in 1,915 populations, Luca Cavalli-Sforza and his colleagues show that the deepest node in the tree represents a split between African populations and all other populations.

In contrast to mtDNA and Y-chromosome analyses, phylogenetic analyses of some nuclear genes (or portions of genes) and noncoding regions of chromosomes indicate MRCAs that are substantially older than 200,000 years. In the case of genes that code for proteins, this is not necessarily surprising because variation in their structures could be strongly constrained or influenced by natural selection (of course, this is also true of the coding regions of mtDNA and the Y-chromosome). However, even if natural selection is involved in shaping the patterns of variability we see, the geographic origins of different alleles can provide insights into human evolutionary history.

Rosalind Harding and her colleagues (1997) analyzed a 3,000-base pair region of the beta-globin gene (one of the chains of the hemoglobin protein). They calculated an MRCA for the gene as existing 800,000 years ago, with the oldest sequence coming from Africa (Figure 13.16b on page 427). This finding does not contradict the mtDNA and Y-chromosome results because the variation in this gene could have arisen and evolved in Africa before a population expansion out of Africa less than 200,000 years ago. However, Harding and her colleagues also found Asia-specific beta-globin sequences that had MRCAs more than 200,000 years ago. This would indicate that Asian populations that existed before 200,000 years ago made unique genetic contributions to the contemporary human genome, a finding that is difficult to reconcile with the mtDNA and Y-chromosome results, although one that may be consistent with the data from the Denisovan DNA (see Insights and Advances: The Denisovans in Chapter 12 on pages 400–401). Harding and her colleagues also found evidence of gene flow between Asian and African populations during the last several hundred thousand years.

Results broadly similar to those for the beta-globin gene have been obtained in other studies of the nuclear genome (Zhao et al., 2000). These findings support the

beta-globin results in that an ancient MRCA (>400,000 years old) is identified, with the deepest root of the tree indicating an African origin, and the MRCA for regional variation outside Africa is found to be more than 200,000 years old. A more recent study by Michael Hammer and colleagues (2011) demonstrates the complex nature of gene flow in ancestral human populations. Hammer's group sequenced 61 noncoding autosomal DNA regions derived from modern Africans. They found strong evidence that a small proportion of the genetic material was derived from an archaic population that had split off from the main human lineage 700,000 years ago, but which had been reintroduced via admixture about 35,000 years ago. Such reintroduction by admixture is called *introgression*. Again, these kinds of results indicate a more complex picture of the genetic origins of our species than those suggested by mtDNA and Y-chromosome analyses.

The mapping of the entire human genome has provided even more information from nuclear DNA that can be used by geneticists to chart population history. For example, individual human genomes contain large numbers of base pair substitutions, many of which occur in non-coding regions. Like any other kind of genetic variation, these *single nucleotide polymorphisms* (SNPs) can be used to construct phylogenetic trees. As might be expected, people from the same family or same population share more SNPs than those who are less closely related. This fact is sometimes used in forensic analyses (see Chapter 17). Brian McEvoy and colleagues (2011) looked at 242,000 SNPs found in 17 populations from throughout the world. Again, Africa was found to be the source for modern humans. However, their analysis also indicated that there have been multiple "Out of Africa" events in the last 50,000 years or so, and a major division between Europeans and East Asians at around 22,000 years ago.

Ancient DNA

Ancient DNA (aDNA) recovered from fossils can provide a direct window into the genetics of past populations. Ancient mtDNA has been isolated from more than a dozen Neandertals and fossil *H. sapiens*. Nuclear DNA has now been isolated as well (see Chapter 12, Innovations: Neandertal Genes on pages 392–393). These studies agree that the Neandertal mtDNA samples generally fall outside the range of variation that has been observed in modern humans (Figure 13.16c on page 427). And, Neandertal samples cluster together as a clade separate from living humans on a phylogenetic tree. Sequence variation in the Neandertal clade is approximately equivalent to that observed in living modern human groups. More importantly, ancient mtDNA from Neandertals also falls outside the range of variation found in ancient DNA from fossil modern humans.

The ancient nuclear and mitochondrial DNA results suggest a broadly similar picture for when the MRCA for modern humans and Neandertals lived. Estimates from ancient mtDNA indicate the MRCA lived between 365,000 and 853,000 years ago. The inferred population split is between 270,000 and 440,000 years ago based on nuclear DNA. When these results were first published in the early 2000s, many researchers saw the ancient DNA data as strong support for the replacement model of modern human origins. However, some genetic analysts (for example, Nordborg, 1998; Relethford, 2001) had long argued that a small number of divergent mtDNA sequences from Neandertals did not rule out the possibility that they may have interbred with anatomically modern humans; it is not that difficult to construct mathematical population models that can account for the mtDNA data in the context of modern human–Neandertal admixture. Indeed, subsequent research has proven these analysts correct.

The initial Neandertal genome nuclear DNA results suggested a small genetic contribution from Neandertals of about 1–4% to the modern human genome (Green et al. 2010). Two recent studies based on early Eurasian modern human fossils from Siberia provide a clearer picture of the timing of this contribution (Fu et al. 2014, 2015).

A genome recovered from a 45,000 year old anatomically modern human femur from western Siberia contains about the same amount of Neandertal-derived segments as would be seen in present-day Eurasians. However, these segments are longer than those in modern genomes. The Neandertal gene flow into the ancestors of this individual from Ust'-Ishim is thought to have occurred 7–13,000 years before he lived (i.e., between 52–58,000 years ago). The genome of the 37–42,000 year old modern human from Peștera cu Oase, Romania, shows an even more profound and “recent,” in terms of the individual’s ancestry, Neandertal genetic introgression. Approximately 6–9% of the Oase 1 genome is Neandertal-derived, and chromosomal analyses indicate that this contribution occurred only four to six generations before Oase 1 had lived. Interestingly, the researchers also found that the Oase individual was not more closely related to modern Europeans than modern East Asians, suggesting that his population was not a source for later humans in Europe.

Interpreting Models of Human Origins

13.6 Use the data in this chapter to help in interpreting models of human origins.

We have looked at three sets of data—paleontology, archaeology, and genetics—that are the basis for understanding the origin of modern human origins. Remember that the two main models for human origins, the Out of Africa and Multiregional models, differ in whom they see as the immediate ancestors of modern humans. The Out of Africa model suggests that modern humans evolved in Africa and subsequently replaced more archaic hominins elsewhere in the Old World. Alternatively, the Multiregional model suggests that the appearance of anatomically modern humans throughout the Old World resulted not from replacement of many populations by one but from the transmission of alleles underlying the modern human phenotype between archaic populations that were in genetic contact. We now consider how our three datasets are interpreted in light of these models.

Paleontology and Archaeology

As originally developed by Milford Wolpoff, Wu Xin Zhi, and Alan Thorne (1984), the Multiregional model proposed that *local regional anatomical continuity* provides strong evidence of the multiregional origins of modern humans (see also Wolpoff et al., 1994; Wolpoff & Caspari, 1997). *Local regional continuity* means we can trace a particular evolutionary trajectory through a suite of anatomical features shared by fossil hominins in a particular region. For example, widely dispersed populations of *H. erectus* exhibited regional anatomical variation (see Chapter 11) and that regional variation may have been retained in later hominin populations living in the same area.

In contrast to the Multiregional model, the Out of Africa model suggests that the earliest modern humans should look very different from the local populations they replaced and should exhibit regional continuity in only one source region, Africa (Bräuer, 1984; Stringer & Andrews, 1988). Fossil lineages from archaic *H. sapiens* at Bodo to Herto, Aduma, and Klasies River Mouth provide evidence of an African origin of *H. sapiens sapiens* that predates such a lineage elsewhere in the world. At the same time as anatomically modern humans appear in Africa, archaic *H. sapiens* populations in Europe seem to be evolving into classic Neandertals. For a short period from about 45,000–39,000 years ago, Neandertals and anatomically modern humans appear to overlap in time and space in Europe, although they are physically and culturally distinct. After about 39,000 years ago Neandertal sites are unknown in Europe.

Multiregional model proponents argue that the occasional appearance of occipital buns in modern human crania, the appearance of a retro-molar gap in some early

human fossils, and the general robustness of early European modern human fossils, especially those from central Europe, are all evidence of regional continuity in Europe (Smith, 1984). However, some of these transitional populations, such as Vindija and Mladeč, reveal no sign of genetic admixture in their ancient mtDNA (Vindija is entirely Neandertal-like, Mladeč entirely modern human-like) does not support the multiregional position. However, nuclear DNA does suggest a small genetic contribution from Neandertals.

Asia and Australia may provide the best evidence of multiregional evolution, although the gap in the fossil record between about 100,000 and 40,000 years ago poses an interpretive challenge. Multiregional proponents argue that regional characters seen in *H. erectus* in China and Indonesia are mirrored in modern humans in China and Australia. For example, the high vertical frontal bone of Chinese *H. erectus* is considered continuous with that seen in Chinese modern humans. The sagittal keel, occipital torus, and supraorbital tori of Indonesian *H. erectus* are suggested to continue through, in lesser degrees, to modern human Australians. Likewise, the Ngandong hominins are thought to represent morphological and temporal intermediates between *H. erectus* and some modern Australians (Frayer et al., 1993). Alternatively, replacement proponents counter that Ngandong is not anatomically intermediate but morphologically aligned with *H. erectus* and potentially overlaps in time and space with modern humans of the region (Swisher et al., 1996; Antón, 2003). Replacement proponents also suggest that early modern human fossils from Asia more closely resemble modern humans from other regions of the world than they do earlier Asian *H. erectus* (Stringer & Andrews, 1988).

It is probably safe to say that within the paleoanthropological community, there is more support for some version of the replacement model than for the multiregional version of evolution. However, it is equally safe to say that the field is far from consensus on the issue and that many paleoanthropologists think that the fossil record provides at least some support in some regions for multiregional evolution.

Molecular Genetics

Genetic data from both living humans and fossil remains provide some clear support for a replacement model of human origins. Although the molecular data can say nothing about the anatomy of the MRCA, the picture presented by mtDNA and the Y-chromosome is easy to reconcile with the paleontological replacement model, which places the origins of anatomically modern humans in Africa during roughly the same time period of the MRCA for these molecular phylogenies. The divergent mtDNA sequences of the Neandertals provide further support for a replacement event in Europe, especially in light of the fact that early modern humans in Europe have mtDNA that is well within the range of variation seen in contemporary humans. According to estimates from several genetic systems, modern humans may have evolved from a population of about 10,000 breeding individuals that existed about 100,000 years ago (Harpending et al., 1998). However, newer ancient nuclear DNA analyses as well as the ancient DNA from Denisova (see Chapter 12) point to some level of gene flow between archaic hominins and modern humans as well as evidence of introgression from Neandertals to modern humans genomes. This means that a strict replacement model without any interbreeding cannot be supported.

There is no simple answer to the question, Where did modern humans come from? (Table 13.1 on page 432). Genetic, paleontological, and archaeological data can be woven together to produce several different scenarios to explain our complex origins. Some of the controversy surrounding the issue derives from scientific success as new dating methods, new archaeological and fossil discoveries, and innovative genetic approaches provide an unprecedented amount of information devoted to a single evolutionary

Table 13.1 Comparing Replacement and Multiregional Models of Human Origins

| | Fact | Replacement Interpretation | Multiregional Interpretation |
|---|---|---|---|
| Paleontological Record, Middle Pleistocene | Between about 200,000 and 500,000 years ago, archaic <i>H. sapiens</i> lived in Africa, Europe, and Asia. Fully modern humans and classic Neandertals appeared by 125,000 years ago. | Archaic <i>H. sapiens</i> in Europe evolved into Neandertals. African archaic populations evolved into anatomically modern <i>Homo sapiens</i> . | Neandertals and modern humans are not separate evolutionary lineages. Neandertals are transitional to European modern humans. |
| Paleontological Record, Late Pleistocene | The anatomically modern human phenotype first appeared outside Africa 90,000–100,000 years ago in the Middle East. | Anatomically modern humans replaced preexisting hominins throughout the Old World without (or with little) genetic mixing. Similarities between early anatomically modern humans from widely dispersed populations are best explained by evolution from a common source population in Africa. | Anatomically modern humans arose from extensive gene flow between Middle and Late Pleistocene hominin populations throughout the Old World. Some fossils show transitional anatomy. |
| Recent DNA Studies | mtDNA and the Y-chromosome phylogenies indicate greatest variability in Africa, suggesting that the most recent common ancestor (MRCA) of modern humans lived in Africa 150,000–200,000 years ago. Nuclear gene sequences indicate MRCAAs that significantly predate 200,000 years ago. Furthermore, deep lineages of these trees have been traced to variants that appear to have originated outside Africa. | mtDNA and the Y-chromosome support an African origin for modern humans and indicate a population expansion out of Africa starting about 100,000 years ago. Nuclear gene sequences reflect the age of the first dispersal (<i>H. erectus</i>) from Africa and do not preclude another dispersal by modern <i>H. sapiens</i> about 100,000 years ago. They are inconsistent with a complete replacement event. | Nuclear gene sequences indicate extensive gene flow between Old World populations over the last 500,000 years and perhaps longer. Diverse ancient Old World populations contributed to the modern human gene pool. |
| Ancient DNA | Ancient DNA from Neandertal and modern human fossils of the same age differ more from one another than does the DNA of living human groups. Differences between Neandertal and modern human DNA are not as great as those between chimp species. Even some fossils considered transitional in anatomy do not have transitional DNA. But Neandertal nuclear DNA may indicate a 1–4% contribution to recent populations. And there is evidence from some early human fossils of late introgression from Neandertals into the modern human genome. | Neandertals are a separate species that did not make a substantial genetic contribution to modern humans. Neandertals were replaced across their entire range by about 39,000 years ago. Neandertals were replaced across their range but a small amount of interbreeding occurred. The majority of the gene pool is of African origin. | Differences between Neandertals and humans are less than those between chimp species and do not support a separate species for Neandertals. Any interbreeding implies a single species and continuity rather than replacement. |

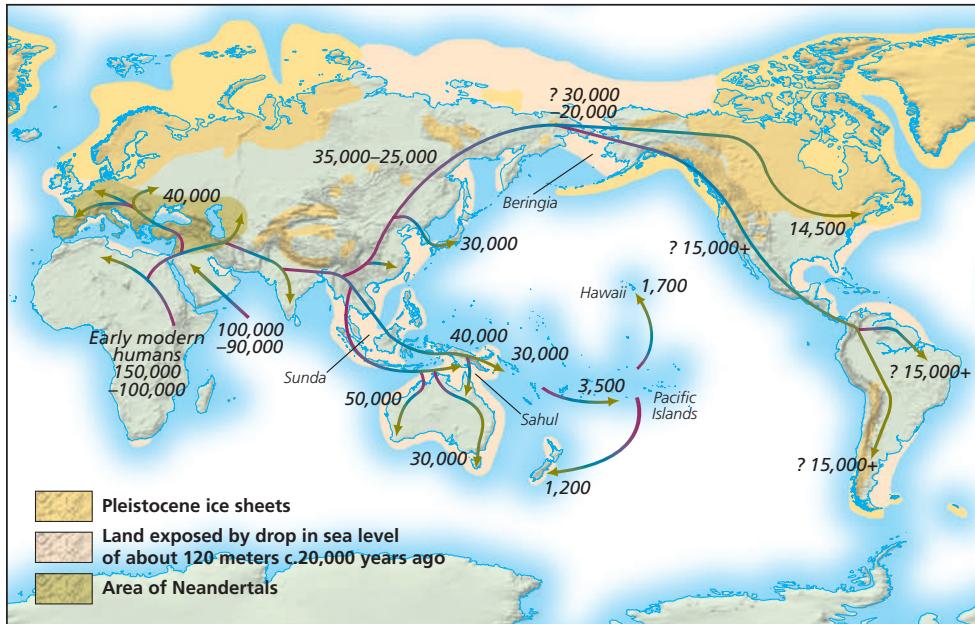
event. The evolution of modern humans may have been far more complicated than either of the original models proposed. However, the controversy over which particular model of human origins is correct should not blind us to the fact that we know far more about the biological and cultural evolution of our own species than ever before.

Settlement of the New World and Pacific Islands

13.7 Discuss the settlement of the New World and the Pacific Islands.

Using behavioral rather than physical adaptations and perhaps ordering their world symbolically, modern humans also had the ability to dominate environments that were already occupied by other hominins and to settle regions that

Figure 13.17 Routes for the human colonization of the New World and Pacific islands.



earlier hominins could not. As we have seen, modern humans were the first to colonize Australia, perhaps 50,000 years ago. And, they would also settle high-latitude areas at least by 30,000 years ago, and later the Americas, and the remote islands of the Pacific.

The Americas

During ice ages, when sea levels are at their lowest, the Old and New Worlds are connected via the Bering land bridge, a broad swath of land (more than 2,000 km wide at its maximum) linking eastern Siberia with western Alaska (Figure 13.17). This bridge was open and ice free only periodically. Most recently it was closed between about 24,000 and 15,000 years ago (Goebel et al., 2007). Crossing the land bridge, even when it was ice free, was no walk in the park. The effort seems to have entailed a level of technological or subsistence development not reached by earlier hominins. Alternatively, we know that at least some modern human populations had watercraft by about 40,000 years ago, as demonstrated by the successful over-water colonization of Australia. Thus, colonization of the New World via the coast of Siberia and Alaska or along the Pacific Rim may have been possible (Dixon, 2001).

Archaeological and ancient DNA evidence favor colonization of the Americas from Siberia/Beringia. Archaeological sites are present in Beringia by about 32,000 years ago, providing a potential source population for the colonization. However, Paleo-Indian skeletal remains are rare in the Americas. The earliest remains such as those from Wizard's Beach, Nevada, Anzick, Montana and the Hoyo Negro girl from Yucatan, Mexico, date between 10,000 and 13,000 years ago, but many are too young or incomplete to assess ancestry from their remains. But the Hoyo Negro girl (11,750–12,900 years old), and somewhat younger remains such as Kennewick Man from Washington State (8,400–9,200 years old; see Figure 13.18), the Browns Valley skull from Minnesota (8,700 years old), and the Warm Mineral Springs crania from Florida (perhaps 10,000 years old; see Figure 13.19 on page 434), exhibit anatomical features that differ from recent Native American populations. These skulls show a great degree

Figure 13.18 Paleo-Indian skeletal remains are rare. Kennewick man was discovered eroding from a riverbed and is about 9,000 years old.

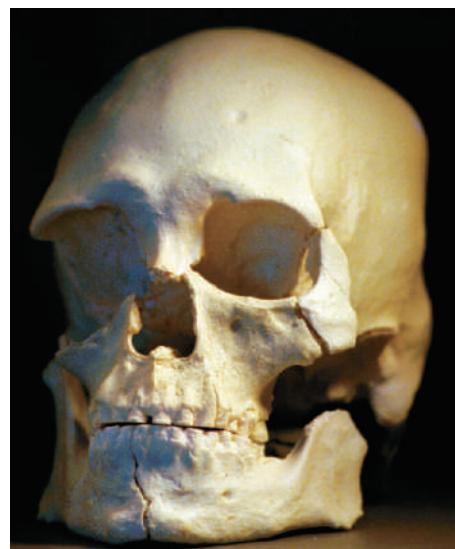


Figure 13.19 The Warm Mineral Springs individual from Florida may be among the earliest Paleo-Indian skeletal remains.



of variation and often show a greater resemblance to crania from the Pacific, including Polynesians or Ainu (Jantz & Owsley, 2001; Chatters et al., 2014; Rasmussen et al., 2015). This has led some to speculate further about the possibility of multiple migrations from different source populations. However, new DNA results from a few of these ancient Americans including Kennewick and Hoyo Negro share DNA affinity with recent Native Americans. Indeed, the Hoyo Negro girl's mtDNA is from the mtDNA haplogroup "D1", which is exclusive to groups in Beringia and recent Native Americans, apparently sealing the case for a Siberian origin of native groups.

By around 13,000 years ago, Paleo-Indian sites of the Clovis culture, which is distinguished by a characteristic finely flaked point, appeared all over North America. Additional Paleo-Indian sites appear not much later at sites in Central and South America. For many years the Clovis people were considered the first colonizers of the New World. However, scholars continue to argue over whether a pre-Clovis settlement existed, and new evidence suggests it may have (see Insights and Advances: Peopling of the New World on page 435). The settlement history of the Americas is clearly complex and is being addressed by genetic, linguistic, archaeological, and paleontological researchers.

The Pacific Islands

The last regions of the world to be colonized by humans are the Pacific Islands. Although people crossed the ocean between Sunda and Sahul about 50,000 years ago and inhabited islands such as New Britain off the east coast of Papua New Guinea as early as 28,000 years ago, most of the Pacific was not colonized until 3,500 years ago or later. Only the invention of long-distance voyaging technology allowed such crossings, which settlers undertook over vast areas of ocean (Irwin, 1992).

Genetic, archaeological, and linguistic data seem to indicate that the peopling of the Pacific started with populations somewhere in East Asia or the islands of Southeast Asia who moved into New Guinea, fusing with peoples and cultures there, and then moved into Polynesia (Kirch, 2001). The earliest expansion of these peoples in the Pacific often is traced by their archeological sites, characterized by a pottery style called Lapita. The Lapita peoples appeared earliest in Near Oceania (the Bismarck Archipelago) around 3,500 years ago and from there spread to Fiji (around 3,000 years ago)

and then further out to Tonga, Samoa, and Far Oceania. Presumably in outrigger canoes, they brought with them pigs, dogs, rats, agricultural crops, and enough food and water to survive their journey. Once on these remote islands, humans did what we do best. They modified the landscape, took advantage of new natural resources, and interacted with the environment in symbolic ways (Figure 13.20). The archaeological records of most islands reveal strong, not necessarily positive, human influences on these island ecosystems, including the extinction of land birds and evidence of deforestation.

These settlements mark the end of the initial colonization of the globe by humans. Although the rest of human history on Earth will be marked by both dispersal and migration, no longer is it into ecosystems never before occupied by humans.

Figure 13.20 Far Oceania was the last of the regions of the world to be colonized by humans. Pictured here is an example of the importance of symbolism as shown by an ancient rock carving in the Cook Islands.



Insights and Advances

Peopling of the New World: Was Clovis First?

When and how did people enter the New World? They could have come through an ice-free corridor in the middle of the Bering land bridge. Or, perhaps they travelled a coastal route. Was it a quick dispersal around 13,000 years ago, or a more leisurely one that started earlier? Did they carry the Clovis toolkit, or were they a pre-Clovis people? Recent genetic and archaeological evidence are providing new insights to these longstanding questions.

Nuclear, mitochondrial, and Y-chromosome DNA suggest that all Native Americans came from a common genetic source population in Asia and likely travelled from Beringia into the New World (Goebel et al., 2007). The DNA of these groups suggests that Native Americans diverged from their Asian ancestors sometime between 15,000 and 25,000 years ago. Additionally, a particular mtDNA haplogroup known as D1 is unique to native peoples of Beringia and the Americas and is shared by some ancient early Americans and ultimately derives from a Eurasian ancestor (Chatters et al., 2014). As we've seen, Siberia yielded important early modern human fossils and has a fairly continuous archaeological record starting by about 32,000 years ago. Beringia, the area across which migrants from Siberia are likely to have travelled to the New World, has an archaeological presence as early as 32,000 years ago and a more continuous set of archaeological sites starting at about 15,000 years ago. It has been inferred from these and other data that the colonization of the Americas began in Beringia and proceeded into the Americas between 16,000 and 11,000 years ago. Although much of the Bering land bridge and coast were locked in glacial ice over parts of the late Pleistocene, the coastal corridor was probably ice free by about 15,000 years ago, and

the interior corridor somewhat later—perhaps 14,000 or 13,000 years ago.

Clovis sites with their signature fluted lanceolate projectile points are well documented and well dated to about 13,000 years old (12,800–13,200; Waters and Stafford, 2007). These sites appear nearly simultaneously across North America, perhaps in a span of as little as 200 to 300 years, although the direction of this speedy dispersal is hard to ascertain. The assemblages are bifacial, upper Paleolithic stone, bone and antler tools that seem to signify a highly mobile hunter-gatherer population. As the best documented and dated sites, many scholars infer that the Clovis people were the first to enter the New World and that they dispersed quickly into new, unoccupied territories. Such a suggestion is not incompatible with the timing indicated by the genetic data, although some would argue that aspects of the genetic patterning suggest that the differences among Native Americans could not have arisen over such a quick dispersal time. But even if an earlier, perhaps slower dispersal had occurred, finding earlier sites has proved challenging. Pre-Clovis sites in the Americas are few, far between, and highly contentious.

However, new evidence of pre-Clovis assemblages has been surfacing. Monte Verde is a site in Chile that is widely accepted as indicating an old age (13,900–14,200 years ago) for a pre-Clovis industry. This site, with evidence of the use of coastal resources such as seaweed, would seem to support an early coastal migration (Dillehay et al., 2008). The Paisley 5 Mile Point Caves in Oregon yielded mtDNA from human coprolites that date to about 14,000 years ago, but few tools were found making the relationship to Clovis or pre-Clovis industries difficult to establish (Gilbert et al., 2008). Recently, a pre-Clovis industry known as the Buttermilk Creek Complex has been discovered in the Friedkin Site along the Buttermilk Creek in Texas (Figure A; Waters



Figure A The Friedkin Site in Texas yielded a long sequence of artifacts from the Late Archaic through the pre-Clovis (Buttermilk Creek Complex). The site is dated using the OSL method.



Figure B Pre-Clovis artifacts of the Buttermilk Creek Complex are small in size and use a different mode of production than Clovis artifacts.

et al., 2011). The site has a fairly long sequence that includes tool assemblages from youngest to oldest that are typical of the Late Archaic, Early Archaic, Paleo-Indian, Folsom, Clovis, and Pre-Clovis. Most importantly for this discussion, the site includes both a younger (stratigraphically higher) Clovis component and below that an older pre-Clovis component.

The site was dated using the optically stimulated luminescence (OSL) technique described in Chapter 8. The thick pre-Clovis unit is dated to between 15,500 and 13,200 years ago, and the tool assemblage is reasonably large with more than 15,000 pieces, fifty-six of which are formal tools. The tools (Figure B) are mostly small in size, and they are made in a different way than is the Clovis material. So recent evidence, including the presence of these and other pre-Clovis sites, has begun to suggest that it was a pre-Clovis people, perhaps taking initially a coastal and then an inland route, who initially colonized the Americas. The quick spread of Clovis may not have been the initial peopling of the continent, but a secondary dispersal or the diffusion of a toolkit itself.

Summary

THE EMERGENCE OF MODERN HUMANS

13.1 Discuss the anatomical characteristics that identify the emergence of modern humans compared to earlier hominins.

- Modern humans have large, globular crania and small faces.
- Modern humans have more gracile postcrania than Neandertals and archaic *Homo sapiens*

MODELS OF MODERN HUMAN ORIGINS

13.2 Compare and contrast the Replacement and Multiregional models of modern human origins; review the archaeological and molecular genetic evidence for modern human origins; and review how paleontology, archaeology, and genetics are interpreted.

- The Out of Africa or Replacement model hypothesizes a single, probably African, origin of modern humans, with subsequent dispersal into the Old World and replacement of archaic hominins by *H. sapiens*.
- Indicates little or no gene flow between modern humans and earlier hominins in the various regions of the Old World.
- Predicts anatomically distinct, temporally overlapping lineages of hominins in each region of the world.
- Predicts possible disjunction in the archeological and genetic records.
- The multiregional model hypothesizes that the origin of modern humans is the result of the diffusion of the genetic underpinnings of the modern human phenotype among multiple archaic hominins from multiple regions via gene flow.
- Predicts the presence of intermediate fossil forms in each region.
- Predicts continuity of behavior (as inferred from the tool types).
- Predicts genetic contribution from archaic to modern populations in a region

ANATOMY AND DISTRIBUTION OF EARLY HUMANS

13.3 Discuss the anatomy and distribution of early humans around the world.

- Earliest modern humans appear in Africa about 195,000 years ago.
- The earliest modern humans outside Africa are in the Near East around 100,000 years ago. They may appear as early as 80,000 years ago in China.
- Modern humans disperse into Island Southeast Asia and Australasia by 50,000 years ago.
- Early modern humans are recognized by: a chin, reduced facial size, reduced brow size, and presence of a canine fossa large globular brain case with parallel sides and the greatest breadth high on the parietals, and a distinct mastoid process and a relatively gracile postcranial skeleton compared to Neandertals or archaic *H. sapiens*.

ARCHAEOLOGY OF MODERN HUMAN ORIGINS

13.4 Describe the archaeology of modern human origins including how the upper paleolithic or later stone age differs from middle and early stone age tool technologies and describe the behavioral differences and role of symbolism in the Upper Paleolithic.

- Earliest AMH are found with Middle Stone Age technologies.
- Upper Paleolithic technologies are more typical of most AMH-associated finds.
- Symbolic behavior, as represented by personal ornaments, portable art, cave art, and burials, seems an increasingly important part of how *H. sapiens* organized the world, suggesting that symbolism had important survival value.

MOLECULAR GENETICS AND HUMAN ORIGINS

13.5 Explain the role of molecular genetics and human origins, including the role of mitochondrial, Y-chromosome, nuclear, and ancient DNA in testing models for human origins.

- Ancient DNA suggests that fossil *H. sapiens* of Europe are more similar to living humans than they are to fossil Neandertals from Europe of the same geologic age.
- The last common ancestor for all *H. sapiens* is reconstructed to be approximately 200,000 to 800,000 years ago based on various kinds of DNA comparisons.

INTERPRETING MODELS OF HUMAN ORIGINS

13.6 Use these data to help in interpreting models of human origins.

- Two models for the origins of modern humans have been proposed: replacement and multiregional models.
- Genetic, archaeological and anatomical data are combined to address each model
- Anatomical and archaeological evidence of overlapping lineages support replacement.
- Small amounts of genetic introgression from Neandertals to AMH rules out complete replacement.

SETTLEMENT OF THE NEW WORLD AND PACIFIC ISLANDS

13.7 Discuss the settlement of the New World and the Pacific Islands.

- *H. sapiens* disperses into the New World by at least 13,000 and probably by 15,000–16,000 years ago.
- Genetic evidence suggests a single Asian origin of the dispersing peoples and ancient DNA shows ties to Beringia.
- Early dispersal may have been along both coastal and inland routes.
- *H. sapiens* disperses into the Pacific by 3,500 years ago.
- These are the last of the initial dispersals by humans into “hominin-free” ecosystems.

Review Questions

- 13.1 What behavioral and anatomical characters signal the origin of *Homo sapiens*?
 - 13.2 How do the predictions of the replacement model for modern human origins differ from those of the multiregional model?
 - 13.3 Where and when do we first see early humans and how do these worldwide populations compare?
 - 13.4 How does *Homo sapiens* behavior and tools differ from earlier hominins?
 - 13.5 What does ancient DNA evidence contribute to the debate over the origin of humans?
 - 13.6 What do the three main lines of evidence suggest about models for modern human origins?
 - 13.7 When do humans first reach the New World and the Pacific Islands and what happens when they arrive there?
-

Key Term

microliths, p. 419

most recent common ancestor
(MRCA), p. 426

multiregional models, p. 409

replacement models, p. 409

Chapter 14

Evolution of the Brain and Language



Learning Objectives

- 14.1** Define and discuss the concept of encephalization and its relevance to understanding human brain evolution; compare and contrast the importance of brain size increase and brain functional reorganization in brain evolution.
- 14.2** Describe the biological basis of human language in the brain and the throat; explain different approaches to understanding how and when language evolved, including four scenarios for the origins of language.
- 14.3** Recognize the complex interaction between brain and language in the evolution of intelligence.

On the morning of April 12, 1861, Professor Paul Broca walked through the surgical ward of the Bicêtre Hospital in Paris. An eminent scientist and surgeon and later a member of the French Senate, Broca walked like a man who was used to people getting out of his way. He was there that morning to meet a patient, named Leborgne, who was gravely ill with a gangrenous infection of his entire right leg. Broca was not particularly concerned with Leborgne's infection. Rather, he was interested in Leborgne as a neurological patient with a long history of abnormal behavior.

At the time of Broca's meeting with Leborgne, scientists interested in the human brain were embroiled in a fundamental debate about the nature of brain function. Some argued that the functions of the brain were evenly distributed throughout the brain; they believed that there were no regions of the brain that were specialized for any particular behavior or function. Others, such as Broca, believed that at least some of the functions of the brain were based in, or localized to, certain specific areas. Unfortunately for the advocates of localization, the pseudoscience of phrenology held a similar viewpoint, although the phrenologists believed they could define localized, functional areas of the brain based on the external morphology—of the skull. That the phrenologists' claims were not based on empirical studies did not prevent phrenology from becoming a popular fad, famous throughout the world.

When Broca examined Leborgne, he found a 50-year-old man who was very weak and could no longer walk. His vision was poor, but his hearing was still good. He clearly understood what was being said to him, but he had only one response to any question asked of him: "Tan." As Broca talked to his caregivers (Leborgne had been under care for more than 20 years), his parents, and other patients on the ward, he learned that Leborgne had suffered from seizures as a child but had recovered from them. At age 30, however, Leborgne lost the ability to speak, at which time he was first admitted to the Bicêtre hospital. Starting 10 years after losing his speech, Leborgne had slowly developed a paralysis in his right arm and then his right leg, which eventually confined him to his bed.

Leborgne was not senile or insane, although the other patients generally considered him to be egotistical and rude. Because almost the only word he could say was *tan*, he became known as Tan to the rest of the hospital. The other word he could say was an expletive that he uttered when agitated or angry. Broca inadvertently elicited this expletive while repeating a test that Leborgne found tiresome.

Leborgne died only 5 days after meeting Broca, on the morning of April 17. Within 24 hours, Broca had performed an autopsy on the patient, and on that same day, obviously with some sense of urgency, he discussed Leborgne's case at a meeting of the Society of Anthropology, an organization he had founded in 1859, which was the first anthropological organization in the world. Broca described in careful detail the damage he had found on the outer (lateral) surface of the left hemisphere of Leborgne's brain, a region that he concluded must have a specialized function involving the articulation of speech.

Broca had identified a language area of the brain. Later neuroscientists called this part of the brain "Broca's area" in honor of his demonstration of the localization of function in the human brain.

language

The unique system of communication used by members of the human species.

Although the human species possesses many features that help to make us unique, it is our complex behavior and extraordinary traditional and material cultures that set us apart from all other animals. Our behavior is ultimately the product of an anatomical feature: the human brain. Complex cultural behavior is made possible by a specific behavioral adaptation—**language**—which has evolved since the hominin lineage split from the great apes. The study of the evolution of the brain and language highlights the relationship between our behavior and our biology.

In this chapter, we will review the evolution of the human brain and language. The human brain is a structure of great complexity, and it produces behaviors that are of unparalleled sophistication in the animal world. At some point in hominin evolution, changes in the brain led to the appearance of a species that behaved more like us and less like our ape cousins. Compared with the brains of our closest relatives, the human brain is larger, and it exhibits important differences in its functional organization.

Some of these organizational differences in the human brain reflect the evolution of language. When we consider the fundamental importance of language to human social existence, it is not surprising that it is a behavior that is well represented in the organization of the brain. Language has also helped shape the anatomy of the throat, leading to the development of an organ of speech capable of producing an extraordinary range of sounds. Language, and the soft tissues that produce it, do not fossilize. But with a greater understanding of brain function and of the natural history of language, anthropologists, linguists, psychologists, and other scientists in recent years have turned to the problem of language origins with increasing enthusiasm.

Issues in Hominin Brain Evolution

14.1 Define and discuss the concept of encephalization and its relevance to understanding human brain evolution; compare and contrast the importance of brain size increase and brain functional reorganization in brain evolution.

The anatomy of the brain is rather complex. At the microscopic level, the brain is composed of a 80–90 billion specialized cells called **neurons** (nerve cells), which communicate with one another to form functional networks (see Appendix A). In addition to the neurons, there are an equal number of supporting nonneuronal cells (Azevedo et al., 2009). At the visible level, the **cerebral cortex**, the surface of the brain composed of neuron cell bodies, is divided into a complex pattern of grooves and ridges called *sulci* (sing., *sulcus*) and *gyri* (sing., *gyrus*), some of which can be used as landmarks to divide the brain into functional regions. Two of the major parts of the brain are the **cerebellum** and the **cerebrum**. The cerebellum, or “little brain,” sits tucked under the cerebrum, and is important in the control of balance, posture, and voluntary movements. It also plays an important role in “higher” cognitive functions that were once thought to be solely under the control of the cerebrum. The cerebrum itself, which is where most complex cognitive functions are located, is the part of the brain that most people recognize as being “the brain.” In humans and other primates, the cerebrum forms most of the brain’s volume, and it is generally thought that the expansion of the cerebrum in human evolution has occurred as a direct result of selection for more complex forms of behavior. Interestingly, the cerebellum, which represents only about 10% of the total brain mass, contains about 80% of all the neurons in the brain, which are smaller and more densely packed than the neurons of the cerebrum (Azevedo et al., 2009).

Recent technological advances have provided us with some extraordinary tools for examining the brain, but the study of the evolution of brain structure and function, or **paleoneurology**, remains for the most part dependent on the study of endocasts. Endocasts are impressions of the interior part of the cranium, from which we can make inferences about the size and structure of the brain (Tobias, 1971) (Figure 14.1 on page 442). Scientists make endocasts from fossil skulls (as a latex mold), or in rare cases endocasts form naturally during fossilization. The use of computed tomography (CT) scanning has made it possible for scientists to study virtual endocasts. Micro-CT scanning has even been used to study the endocasts of tiny plesiadapids, revealing the very primitive nature of the brains of these possible earliest primates (Orliac et al., 2014).

neurons

The basic cellular units of the nervous system. A neuron consists of a cell body and specialized processes called dendrites (which receive inputs from other neurons) and axons (outgrowths through which neurons send impulses to other neurons).

cerebral cortex

The layer of gray matter that covers the surface of the cerebral hemispheres, divided into functional regions that correspond to local patterns of neuronal organization.

cerebellum

The “little brain” tucked under the cerebrum, and important in the control of balance, posture, and voluntary movement.

cerebrum

The largest part of the human brain, which is split into left and right hemispheres. Seat of all “higher” brain functions.

paleoneurology

The study of the evolution of brain structure and function.

Figure 14.1 Endocasts from South African australopithecines.



Unfortunately, the brain is separated from the inside of the cranium by several protective tissue layers and cerebrospinal fluid, so endocasts, whether physical or virtual, are inevitably a poor reflection of the brain's anatomy. Nonetheless, they provide us with the only source of direct information we have about the brain structure of extinct species.

Most of the important questions concerning hominin brain evolution address ways in which the human brain is different from the brains of other primates and mammals. But there are many ways in which our brains are similar to those of other mammals. We use the same neurochemicals, share a basic microscopic and macroscopic architecture, and have some basic sulci and gyri around which functional regions are organized.

Brain Size and Encephalization

One of the defining features of the genus *Homo*, and especially of our own species, is large brain size (Allen, 2009). But what do we mean by large? In absolute terms, the human brain weighs in at about 1,300 g, and human cranial capacities usually are reported to be in the region of 1,300 to 1,400 cc. These are average figures, and there is much variation in brain size. However, for purposes of cross-species comparisons, the 1,350-cc estimate for the volume of the typical human brain is good enough.

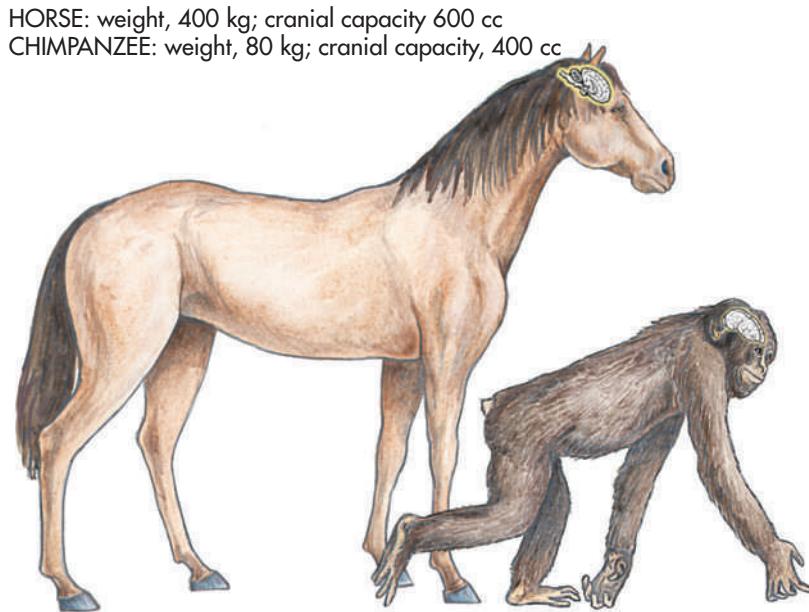
Look at the cranial capacities of various primates listed in Table 14.1. As you can see, humans have the largest brains among primates. The second largest brains belong to the gorillas. Among the Old World monkeys, baboons appear to have relatively large brains. As discussed in Chapter 6, among the New World monkeys, spider monkeys have substantially larger brains

Table 14.1 Cranial Capacities, Body Weights, and EQs of Several Primate Species

| Species | Cranial Capacity (cc) | Body Weight (kg) | EQ |
|--|-----------------------|------------------|------|
| APES | | | |
| <i>Homo sapiens</i> , male | 1,424.5 | 71.9 | 4.32 |
| <i>Homo sapiens</i> , female | 1,285.2 | 57.2 | 4.64 |
| <i>Gorilla gorilla</i> (gorilla), male | 537.4 | 169.5 | 0.85 |
| <i>Gorilla gorilla</i> (gorilla), female | 441.4 | 71.5 | 1.34 |
| <i>Pan troglodytes</i> (chimpanzee) | 388.6 | 83.7 | 1.48 |
| <i>Pongo pygmaeus</i> (orangutan), male | 393.1 | 87.7 | 1.08 |
| <i>Pongo pygmaeus</i> (orangutan), female | 341.2 | 37.8 | 1.69 |
| <i>Hylobates lar</i> (gibbon) | 98.3 | 5.5 | 2.10 |
| OLD WORLD MONKEYS | | | |
| <i>Papio anubis</i> (baboon), male | 166.4 | 23.5 | 1.18 |
| <i>Papio anubis</i> (baboon), female | 141.4 | 11.9 | 1.69 |
| <i>Cercocebus albigena</i> (gray-cheeked mangabey) | 97.3 | 7.69 | 1.63 |
| <i>Colobus guerza</i> (black and white colobus) | 75.4 | 9.05 | 1.11 |
| NEW WORLD MONKEYS | | | |
| <i>Ateles geoffroyi</i> (spider monkey) | 126.4 | 6.00 | 2.55 |
| <i>Alouatta palliata</i> (howler monkey) | 62.8 | 6.55 | 1.18 |
| <i>Saimiri sciureus</i> (squirrel monkey) | 24.4 | 0.68 | 2.58 |

NOTE: Values from Kappelman (1996), using Martin's (1983) formula for EQ. New World monkey values calculated from Harvey et al. (1987). If male and female values are not shown, midpoint values between male and female averages are shown.

Figure 14.2 Chimpanzees and horses have brains that are similar in size.



than their close relatives, howler monkeys. To put these data in a broader zoological context, cattle have brains of about 486 cc and horses of about 609 cc—somewhat larger than that seen in a great ape (Figure 14.2). The bottle-nosed dolphin has a brain volume of about 1,118 cc, which is nearly human-sized (Hofman, 1988).

ENCEPHALIZATION QUOTIENTS Many scientists find absolute brain size values to be of limited usefulness in understanding brain evolution or the relationship between brain size and behavior. After all, it comes as no surprise that bigger animals have bigger brains than smaller animals, but just because a big animal has a big brain does not mean that the animal is more intelligent. For many years, scientists have tried to determine ways to measure brain size relative to body size. Researchers such as Harry Jerison (1991) and Robert Martin (1983) have shown that the relationship between brain size and body size is somewhat more complicated than a simple linear relationship. By looking at large numbers of mammal species, they derived equations that allow us to calculate the expected brain size for a mammal of any size. The **encephalization quotient (EQ)** is a ratio of the actual brain size to the expected size. Thus mammals that have EQs greater than 1.00 have brains that are larger than expected for a mammal of their size; an EQ less than 1.00 means that it is smaller than expected.

Returning to Table 14.1, we see that humans have the largest brains not only in absolute but also in relative terms, as measured by the EQ. In general, anthropoid primates have EQs greater than 1.00, indicating that their brains are larger than would be expected for mammals of their size. So even though cattle and horses have brains that are ape-sized in absolute terms, their EQs are smaller than those of apes because of their larger body sizes. It is generally assumed that the larger brain size in anthropoid primates has evolved in conjunction with the evolution of complex social behavior and adaptation to the arboreal environment.

Can we say that mammals with higher EQs are in some sense smarter than those with lower EQs? Yes and no. Terrence Deacon (1997) points out that the encephalization quotient is derived from both brain size *and* body size and that there is a tendency to overlook the fact that animals face strong selection pressures that shape body size as well as brain size. In fact, body size is probably more malleable than brain size in the

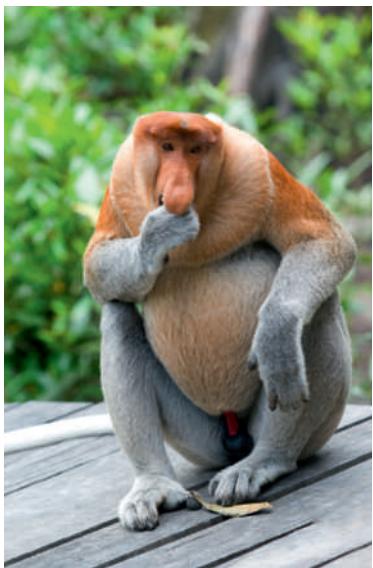
encephalization quotient (EQ)

The ratio of the actual brain size of a species to its expected brain size based on a statistical regression of brain-to-body size based on a large number of species.

Figure 14.3 Encephalization is a function of both brain size and body size.



Figure 14.4 The proboscis monkey demonstrates that large gut size contributes to a lower EQ.



face of evolutionary pressures. Among dog breeds, for example, chihuahuas are more encephalized than German shepherds; artificial selection on chihuahuas has driven body size down at a faster rate than brain size (Figure 14.3). But no one (except chihuahua fanciers) would argue that a chihuahua is smarter than a German shepherd. In anthropoids, small or even dwarfed species, such as the squirrel monkey in the New World or the talapoin monkey in the Old World, have high EQs. Again, rather than interpreting this as a sign of large brain size, we could also see it as an example of selection for small body size, which is probably more correct.

Colobine monkeys tend to have lower EQs than cercopithecine monkeys (see the mangabey versus the colobus in Table 14.1 on page 442). There is no evidence that colobine behavior is in some sense less sophisticated than cercopithecine behavior (Figure 14.4). As discussed earlier colobine monkeys are adapted to a leafy diet; this digestive requirement has driven selec-

tion for greater gut and body size, resulting in lower EQs. Colobines are still more encephalized than a typical mammal. Gorillas, who have large brains in absolute size, also have low EQs. Again, their low-quality, leafy diet (as well as other factors, such as protection from predation) may have driven selection for larger body size, leaving them with EQs lower than their closest relatives, the other apes. However, in a comparison of two closely related species sharing a particular environment, such as the spider and howler monkeys, it is reasonable to hypothesize that larger brain size in the spider monkey may have evolved as a result of the greater cognitive demands of a fruit-based diet. In summary, the EQ is a potentially valuable indicator of cognitive ability but we need to remember that it is a function of both brain and body size.

SEX DIFFERENCES IN PRIMATE BRAIN SIZE In almost all primate species, males have larger brains than do females. In the three highly sexually dimorphic species listed in Table 14.1 on page 442 (orangutans, gorillas, and baboons), the absolute brain size differences are large, as are the body size differences. In each case, EQs for the females are substantially larger than for males. The EQ for male gorillas is below 1.0, indicating that their brains are smaller than we would expect for a mammal their size. There is strong selection for increased male body size in highly sexually dimorphic primate species, but there is no reason to suppose that there are profound differences in behavioral sophistication between the sexes.

Even in less sexually dimorphic primate species, such as rhesus macaques and humans, males have larger brains than females. This is true after we correct for body size (Holloway, 1980; Falk et al., 1999). Although we could speculate on the selection forces on behavior or other biological processes that might drive such a sex difference, one conclusion is that the sex difference in brain size observed in humans is not a function of recent evolution for higher cognitive function in hominins but seems to reflect a general primate trend (Falk et al., 1999).

Brain Size and the Fossil Record

In previous chapters, you read that increasing brain size is a characteristic of genus *Homo*. A compilation of average cranial capacities of different hominin fossil taxa is presented in Table 14.2. (Please note that the *Homo sapiens* values in Tables 14.1 and 14.2 differ because they are based on different samples.) As you can see, the different

Table 14.2 Average Cranial Capacities for Fossil Hominins (Adult Specimens Only)

| TAXON | NUMBER OF SPECIMENS | AVERAGE CRANIAL CAPACITY (CC) | RANGE (CC) | ESTIMATED EQ |
|---|---------------------|-------------------------------|-------------|--------------|
| <i>A. afarensis</i> | 2 | 450 | 400–500 | 1.87 |
| <i>A. africanus</i> | 7 | 445 | 405–500 | 2.16 |
| <i>A. robustus</i> and <i>A. boisei</i> | 7 | 507 | 475–530 | 2.50 |
| <i>H. habilis</i> | 7 | 631 | 509–775 | 2.73–3.38 |
| <i>H. erectus</i> | 22 | 1,003 | 650–1,251 | 3.27 |
| Archaic <i>H. sapiens</i> | 18 | 1,330 | 1,100–1,586 | 3.52 |
| <i>H. neanderthalensis</i> | 19 | 1,445 | 1,200–1,750 | 4.04 |
| Modern <i>H. sapiens</i> (older than 8,000 years) | 11 | 1,490 | 1,290–1,600 | 5.27 |

SOURCES: Aiello and Dean (1990), Kappelman (1996), and Holloway (1999).

NOTE: Estimated EQs are not derived using all the specimens included in the second column.

groups can be sorted to some extent according to their cranial capacities and EQs. Of course, this comes as no surprise because cranial capacity is one of the morphological features we use to classify specimens into different taxonomic groups. Brain evolution in hominins can be divided into three phases (Holloway et al., 2004).

PHASE 1: EARLY HOMININS AND ROBUST AUSTRALOPITHECUS Brain size increases from the early australopithecines (*Australopithecus afarensis* and *Australopithecus africanus*) to the robust australopithecines, or *Paranthropus*. The early australopithecines have cranial capacities in the range of 400 to 500 cc, whereas the later *Australopithecus robustus* and *Australopithecus boisei* are in the 475 to 530 cc range. The early australopithecines have cranial capacities similar in size to those seen in chimpanzees, orangutans, and female gorillas, whereas the cranial capacities of the paranthropines are more similar to those seen in male gorillas.

Are the robust australopithecines species more encephalized than the earlier australopithecines? Are graciles and robusts more encephalized than the contemporary great apes? Answers to these questions depend on estimates of body mass and brain size. As we have already seen, gorillas have large brains, but they also have large bodies, especially male gorillas, so they are not impressively encephalized. (They *are* impressively big.) Estimating body mass of fossilized individuals is very difficult and depends on how well sizes of available parts of the skeleton correlate to overall body size. EQs calculated for any individual fossil specimen therefore should be taken with a grain of salt. Henry McHenry (1992; see also Kappelman, 1996) estimates that *A. afarensis*, *A. africanus*, and *A. robustus* had male body sizes of 40 to 45 kg and female sizes of 30 to 32 kg; *A. boisei* was about 10% larger. These estimates indicate that these hominins were smaller than contemporary great apes; given that their cranial capacities were at least as large, we can conclude that gracile and robust australopithecines were indeed more encephalized than the great apes. In addition, the brain size increase seen in the robust forms relative to the earlier forms may reflect a further increase in encephalization. However, the reworking of the robust australopithecine skull in response to the biomechanical demands of hard object chewing could have increased cranial capacity without changing brain size. The relationship between cranial capacity and brain size varies somewhat across species, and the relatively small increase in cranial capacity we see in going from gracile to robust australopithecines may or may not have resulted in (or been the result of) more brain tissue (Allen, 2009).

PHASE 2: EARLY HOMO AND HOMO ERECTUS Hominin fossils assigned to *Homo habilis* or early *Homo* have cranial capacities substantially larger on average (by 25–30%) than those seen in *Australopithecus* or the great apes. Although the smallest

early *Homo* specimens (for example, KNM-ER 1813, which has a cranial capacity of 509 cc) and the largest gorillas may overlap in cranial size, the relatively small habiline body size, estimated by McHenry (1992) to be 52 kg for males and 32 kg for females, combined with the larger brain size, represents an increase in encephalization over earlier hominins. As you read earlier, the appearance of *H. habilis* roughly coincides with the widespread appearance of stone tools in the archaeological record, providing evidence of at least one kind of cognitive evolution.

The average cranial capacity of fossils assigned to *Homo erectus* shows an even more profound jump than *H. habilis* in both relative and absolute size compared with earlier hominin taxa. Although both brain and body size increased in *H. erectus*, brain size may have increased relatively more quickly leading to an increase in encephalization (Kappelman, 1996). As discussed earlier, *H. erectus* was widely distributed geographically and exhibited gradual change over its more than 1 million years in existence. On average, the earliest *H. erectus* specimens (such as KNM-ER 3883 and KNM-ER 3733) have smaller cranial capacities than do later specimens. Thus the range of cranial capacities seen in *H. erectus* specimens is quite large (from 650 to 1,250 cc), which is one reason that some investigators have justified splitting the taxon into two or more species. The Dmanisi crania from Georgia, dating to 1.75 million years ago, have cranial capacities of between 600 and 780 cc; the smallest of these is a subadult (Vekua et al., 2002). Their cranial capacities are well within the range of *H. habilis* and *H. erectus*, but their cranial anatomy links them with *H. erectus*.

PHASE 3: ARCHAIC *HOMO SAPIENS*, NEANDERTALS, AND MODERN *HOMO SAPIENS* Cranial capacities in the modern range are found in both archaic *H. sapiens* and Neandertal specimens. Indeed, one of the apparent paradoxes of the later hominin fossil record is that Neandertal cranial capacities often exceed the average cranial capacity of modern humans (see Table 14.1 on page 442 and Table 14.2 on page 445).

Figure 14.5 Although Neandertal brain sizes fall well within (or exceed) the modern human range, their EQ is lower than modern humans because they had larger bodies.

Even the archaic *H. sapiens* mean is within the range of modern *H. sapiens*. The increase in average cranial capacity from *H. erectus* to the later *Homo* species is quite profound and undoubtedly exceeds any increase in body size. Thus the hominin trend for increasing brain size and encephalization continues—and even accelerates—through the appearance of archaic *H. sapiens* and Neandertals.

What about the apparent decline in brain size in modern humans compared with Neandertals and even with earlier modern humans? We should keep in mind that there may be some kind of sampling bias (for example, toward larger males); after all, we have only small numbers of fossils available to compare with large numbers of modern humans. More critically, John Kappelman (1996) points out that the larger body size of archaic *H. sapiens* and Neandertals, relative to modern humans, often is overlooked or under-emphasized. Thus modern humans are more encephalized than Neandertals because their bodies are much smaller but their brains are almost as large as Neandertal brains (Figure 14.5).

Although Neandertal and modern human brains are similar in size, their overall shapes are quite different. Modern humans have brains that are much more globe-shaped than Neandertal archaic *Homo sapiens* brains (Lieberman et al., 2002; Bruner, 2004). This “globularization” may reflect in particular changes in the parietal lobes and the region around the border of the temporal and parietal lobes. Studies of endocasts of very young Neandertal and human children suggest that this difference in shape emerges very early, within the first year of life (Gunz et al., 2010). The globularization of the human brain thus appears to reflect a unique pattern

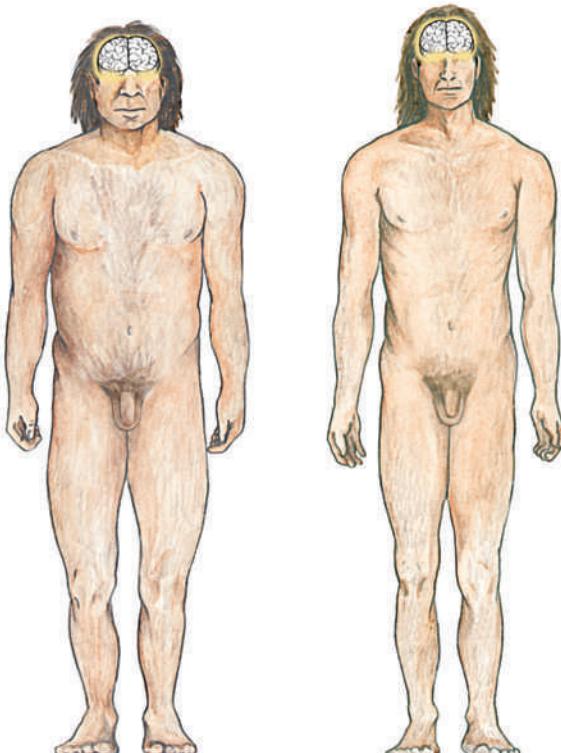
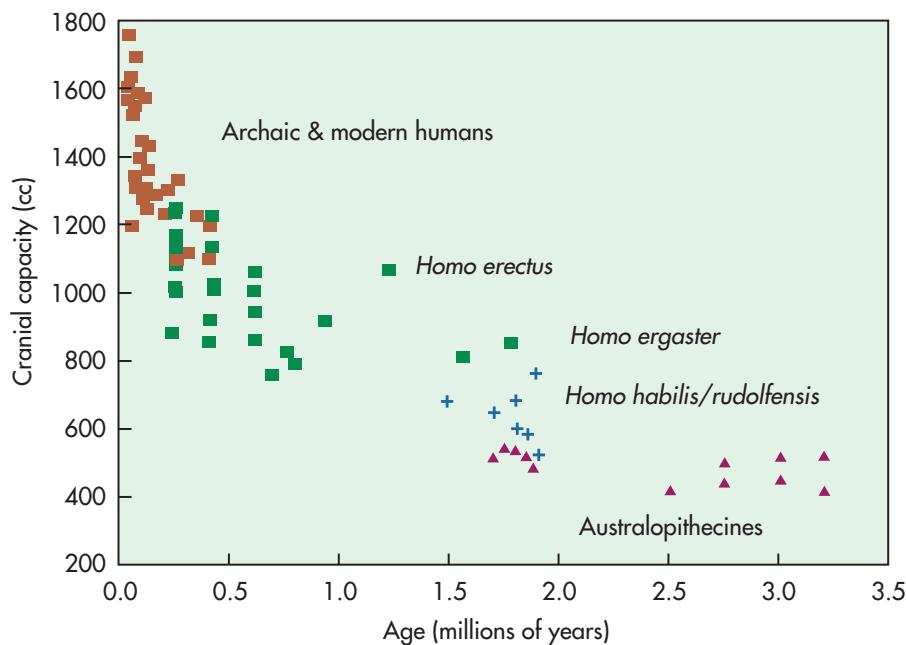


Figure 14.6 Cranial capacity has increased approximately fourfold over the last 3.5 million years of hominin evolution.



of brain growth and development within primates, which may be distinct from changes in size.

Brain size increase and increased encephalization have characterized hominin evolution over the past 3 to 4 million years (Figure 14.6). These trends have become more marked over the past 2 million years, as absolute brain size has nearly tripled. During the past 2 million years, increases in brain size have outpaced increases in body size, thus leading to increasingly encephalized hominins. Although brain size and encephalization are not everything, expanding brain size in the hominin lineage clearly reflects an adaptation, given how “expensive” brain tissue is.

Brain Reorganization

As the brain has expanded, its functional organization has also changed. We know this by comparing our brains with those of our closest relatives, such as the chimpanzee, or the rhesus macaque, an animal often used as the primate standard in experimental neurological research. For example, there are parts of the brain that are essential for normal language production. Because other primates do not have language, obviously some functional reorganization of the brain has accompanied the evolution of language ability. Although scientists debate the relative importance of reorganization and expansion in hominin brain evolution, it is quite reasonable to assume that both processes have been crucial.

Investigators have tried to trace the evolution of other aspects of brain organization via both comparative anatomy and the examination of fossil endocasts. Reorganization can occur in three ways: An anatomical region of the brain associated with a specific function can become larger or smaller compared with the rest of the brain or functional regions of the brain can shift or change position, independently of regional expansion or contraction. Alternately, new behaviors may lead to the evolution of new functional fields, which would supplant or enhance previously existing functional associations in those areas.

We will discuss examples illustrating the first two kinds of reorganization in this section but will save the third for the section on language later in this chapter. Several

Insights and Advances

The Ten-Percent Myth: Evolution and Energy

We have all heard the myth that we humans use only 10% of our brains. Indeed, it is apparent that not only have many people heard it, they believe it. Psychologist Barry Beyerstein (1999) has spent many years researching the origins of this mistaken idea. One of the first groups that latched onto and spread the myth was the early self-improvement (positive thinking) industry. For example, a 1929 advertisement states that “scientists and psychologists tell us that we use only about TEN PERCENT of our brain power” and that by enrolling in the course being advertised, a person might tap some of that brain that is not being used. The advertisement uses the 10% figure as though it were common knowledge. This indicates that the origins of the myth must date to significantly earlier than 1929. Although Beyerstein has tried to identify the “scientists and psychologists” who may have said something like this, he has so far failed to find any specific reference to it in the literature.

Even if the 10% figure came from a scientist working in the early twentieth century, neuroscience was not particularly advanced at that time. Such a sweeping scientific pronouncement, based on little empirical research, is probably due for some reconsideration. Indeed, there is plenty of evidence from neurology and psychology that the 10% figure is wholly untenable. Research methods that directly measure the activity of the brain show that even at rest, a large proportion of the brain may be showing metabolic activity. In addition, although certain functions of the brain are localized to small areas of the brain, these regions are connected to other regions via networks of neurons that draw on multiple brain regions.

One of the most compelling arguments against the 10% myth comes from the perspective of energy and evolution. The brain uses a lot of energy. In humans, it accounts for about 2% of the body mass but uses about 16–20% of the total energy and oxygen consumed by the body. It is an “expensive tissue” (Aiello & Wheeler, 1995). The brain cannot store significant energy reserves and is extremely vulnerable if the oxygen supply is cut off.

From an evolutionary standpoint, maintaining such an expensive organ only to use 10% of it does not make any sense. When you consider that there are other costs associated with large brain size (such as birth difficulties), if we used only 10% of the brain, there would have been substantial fitness benefits in reducing the brain to a more efficient and less costly size. This did not happen, of course, as brain expansion has characterized evolution in genus *Homo*.

Leslie Aiello and Peter Wheeler point out that the brain is not the only “expensive” tissue in the body. The heart, kidneys, liver, and gastrointestinal tract consume at least as much energy as the brain. Human bodies use energy at about the rate that would be expected for a mammal our size. Given that our brains are much larger than would be expected for a mammal our size, how do we maintain the expected energy consumption rate? Aiello and Wheeler argue that a tradeoff with one of the other expensive tissues has occurred. Specifically, at the same time as the brain has increased in size in human evolution, it appears that the stomach and intestines have decreased in size. These size reductions presumably have been accompanied by a reduction in energy use.

The smaller gastrointestinal tract also indicates a reliance on higher-quality, easier-to-digest foods, such as meat. Richard Wrangham (2009) has noted that cooking meat and high quality plant foods (such as tubers) makes them easier to eat and digest. Thus he suggests that cooking may have been essential for providing the high-quality diet necessary to support a larger brain. Other researchers argue that early *Homo* started to exploit marine resources as a way to improve the quality of their diets (Broadhurst et al., 2002; Langdon, 2006).

The complex relationship between behavior, brain size, diet, and gut size is one of the most fascinating problems in the study of human evolution. Although it is tempting to see brain size and gut size as engaged in a neat tradeoff, the situation probably was a bit more complex than that. Nonetheless, Aiello and Wheeler make clear that we have to pay for what we have: a large, energy-hungry brain. And a brain that wastes 90% of its volume would never have evolved.

studies have shown that when we look at large numbers of mammal species, the anatomical organizations of their brains are remarkably uniform in terms of the relative size of one structure compared with another or with the whole brain (Jerison, 1991; Finlay & Darlington, 1995). These *scaling* relationships hold whether the brains are big or little. In terms of cell numbers, including both neurons and nonneurons, the human brain looks to be a scaled-up version of a primate brain (Herculano-Houzel, 2012). The cerebral cortex is relatively enlarged but has about the number of neurons that would be expected for an extra-large primate brain. However, since body size and brain size change independently, the metabolic requirements of the larger human brain has increased disproportionately compared to overall body size (see Insights and Advances: The Ten-Percent Myth: Evolution and Energy).

Although there are scaling patterns in the relative size of brain regions that can be derived by looking at large groups of species, these are statistical generalizations for which there are always exceptions or outliers. The human brain overall is a scaled-up primate brain, but there are certainly specific regions within the brain that have changed in size relative to other regions (Rilling, 2006). What are some of these regions and how do these reorganizational changes contribute to, or reflect, human cognition?

OLFACTORY BULBS In the human brain, the **olfactory bulbs**, which control our sense of smell, are small, knoblike structures found on the bottom of the frontal lobes in each hemisphere (Figure 14.7). Compared with other mammals, anthropoids have olfactory bulbs that are small for their overall brain size (Jerison, 1991), measuring only about 0.1 cc in volume (Stephan et al., 1981). In contrast, wolves have olfactory bulbs that are about 6 cc in volume, a 60-fold advantage over the human-sized olfactory bulb. Humans have olfactory bulbs that are about the same size as those found in strepsirrhine species whose brains are only 1–2% the size of human brains.

Humans reflect (in more extreme form) a basic trend in olfactory bulb reduction that we can see in all living anthropoids. We presume that this reduction occurred as other sensory domains (such as vision) and higher-level cognition became more important, reducing reliance on the sense of smell. Studies of endocasts of the Oligocene primate *Aegyptopithecus* may indicate that olfactory bulb reduction was already present in this early anthropoid (Radinsky, 1979). The *Plesiadapis* endocast mentioned earlier may show a shift in position of the olfactory bulbs similar to that seen in the earliest definitive primates (Orliac et al., 2014).

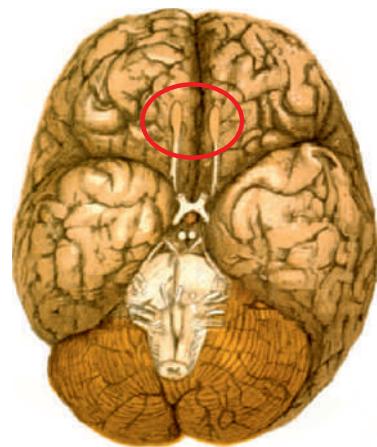
FRONTAL LOBES Olfactory bulbs are a good example of reorganization by size reduction in the human brain. At the other end of the spectrum, many brain investigators (such as Deacon, 1997, but see also Holloway, 1968) have argued that one of the largest regions of the brain, the frontal lobe, has expanded over the course of hominin evolution, relative to the rest of the brain (see Appendix A). Scientists believe that the **prefrontal region**—the parts of the frontal lobe that do not include the primary motor regions—has shown a marked relative expansion. In other words, we may have a larger prefrontal region (and frontal lobe) than we would expect given the size of the human brain.

Why should we expect that humans have evolved a larger frontal lobe relative to overall brain size? The functions of the frontal lobe seem to coincide with many of the higher functions that we associate with intelligence, specifically with the kind of intelligence that we seem to have more of than any other animal, such as forming goals and devising plans to attain them. It is not unreasonable to predict that given our apparent reliance on these functions, our prefrontal region should be large.

However, MRI studies of human, ape, and monkey brains conducted by Katerina Semendeferi and her colleagues (2000, 2002) indicate that the frontal lobe is not proportionally larger in human brains (Figure 14.8 on page 450), and in fact, there is a trend in this dataset to suggest that the frontal proportion is slightly lower in humans (Rilling, 2006). They found that the frontal lobe makes up about 36–37% of the hemisphere in humans, orangutans, chimpanzees, and gorillas. It is proportionally larger in humans and great apes than in gibbons (29%) and in a combined sample of rhesus macaque and cebus monkeys (31%). These results indicate that we and the great apes may share a small increase in relative frontal lobe size. Note that even if the frontal lobe in humans is not larger overall, the prefrontal region could occupy a greater proportion of the lobe, as some evidence suggests (Deacon, 1997; Schoenemann et al., 2005).

The high forehead of modern humans compared with the sloping foreheads of close relatives such as Neandertals and archaic *H. sapiens* might seem to be an obvious indication of frontal lobe expansion. As you recall in Chapter 13 Neandertals and archaic *H. sapiens* differ substantially from modern humans in the anatomy of the forehead and eye orbits: In general, their foreheads slope backward from large browridges.

Figure 14.7 View of the bottom surface of the human brain. The olfactory bulbs are small structures located on the underside of the frontal lobes.



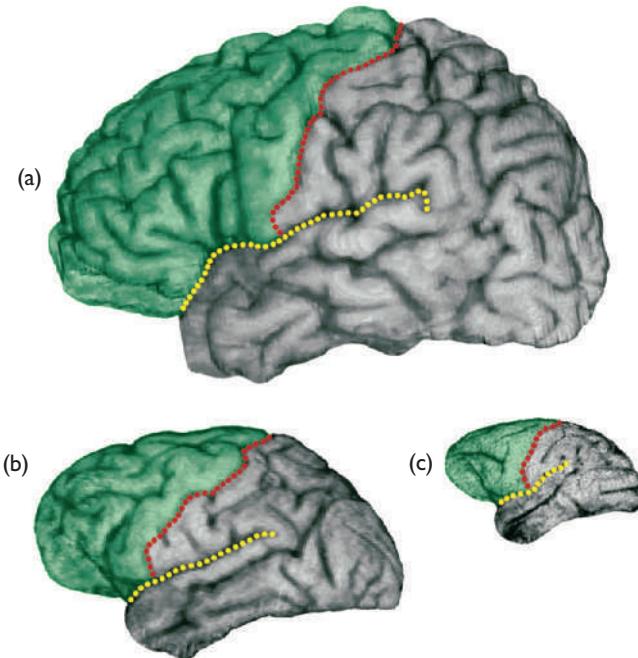
olfactory bulbs

Knoblike structures, located on the underside of the frontal lobes, that form the termination of olfactory nerves running from the nasal region to the brain.

prefrontal region

The association cortex of the frontal lobes, located forward of the primary motor region of the precentral gyrus and the supplemental motor areas.

Figure 14.8 The frontal lobe (green) bounded by the Sylvian fissure (yellow line) and central sulcus (red line), in a (a) human, (b) chimpanzee, and (c) gibbon.



Looking at profiles of frontal bones in cross section, Fred Bookstein and his colleagues (1999) found that despite differences in external morphology of the frontal region, the internal morphology was remarkably similar, indicating that the shape of the frontal lobe probably was also similar in these groups, despite the increased “globularization” of the human brain (see aforementioned).

PRIMARY VISUAL REGIONS The *primary visual region* is the part of the brain where visual information from the eyes is initially processed. Although it is present in the occipital lobes (at the rear of the cerebrum) in both humans and other primates, in humans the primary visual region is located in a sulcus on the inner surface of the lobe, whereas in primates the primary visual cortex encompasses most of the lobe’s outer surface.

Furthermore, the visual cortex is smaller than we would expect for a primate brain its size: It is only about 1.5 times larger than the visual cortex of a chimpanzee or gorilla, whereas the brain as a whole is about 3 times larger (Stephan et al., 1981). The reduction and shift of the visual region in primates presumably has allowed the expansion of the association areas of the parietal and occipital cortices. The parietal cortex is a region where sensory information from different sources is processed and synthesized; it is also important in tool usage.

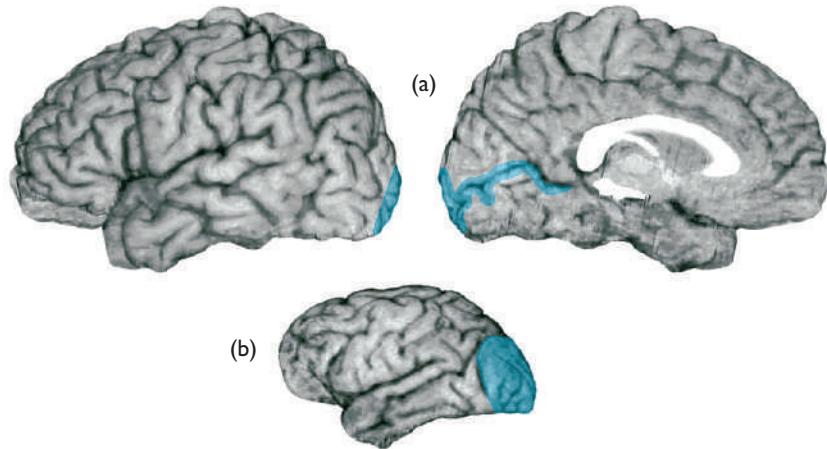
Controversy about reorganization of the visual region in hominin brain evolution has been not about whether but about when it occurred. The beginnings of the controversy go back to when Raymond Dart (1925) published his initial description of the Taung child (*A. africanus*) skull and endocast. In nonhuman primates, the primary visual region of the occipital lobe is reliably separated from the rest of the brain by the **lunate sulcus**, a well-defined sulcus that is almost always present. In contrast, in humans the lunate sulcus often is absent or very poorly developed and it does not mark the primary visual region, which is marked by the calcarine sulcus located on the interior surface of the occipital lobe (Figure 14.9).

When Dart analyzed the Taung endocast, he confidently marked the lunate sulcus in a posterior, human-like position. He interpreted this to mean that despite the ape-like

lunate sulcus

A prominent sulcus on the lateral side of the hemisphere of most nonhuman primates, which divides the primary visual cortex of the occipital lobe from the rest of the cerebrum.

Figure 14.9 Primary visual processing areas (blue) in (a) a human (lateral and mesial views) and (b) a chimpanzee. In humans, the primary visual areas surround the calcarine sulcus. In chimpanzees, the lunate sulcus forms the anterior boundary.



size of the Taung brain, it showed evidence of human-like brain reorganization. This conclusion was accepted for many years, but in the 1980s a vigorous debate about the location of the lunate sulcus in Taung and other australopithecines broke out between Ralph Holloway and Dean Falk, two of the most experienced paleoneurologists working in the field (Falk, 1980, 1983b, 1985a, 1985b, 1989, 1991; Holloway, 1981, 1984, 1988, 1991; Holloway & Kimbel, 1986). Falk argued that Dart's positioning of the lunate was incorrect and that it was in a more ape-like position. Holloway, who initially accepted Dart's placement, argued that Falk's positioning of the lunate on the endocast was also anatomically untenable. Currently, the weight of evidence, including new discoveries and further reassessments of older specimens, indicates that the lunate sulcus was located more posteriorly in australopithecines compared to its location in the great apes (Holloway et al., 2004). This change in position marked the beginning of the extensive reorganization of the visual regions of the human brain, compared to great apes and other primates (Allen et al., 2006).

TEMPORAL LOBE As James Rilling (2006) points out, if the primary visual areas of the occipital lobe and the frontal lobe in general (possibly) are proportionally smaller in humans compared to the great apes, then some part of the human brain should be relatively larger. His research has indicated that the temporal lobe (the “thumb” of the brain, see Appendix A) may have increased in proportional size in humans (Rilling and Seligman, 2002). This increase is mostly in the white matter (not the gray matter containing neurons), reflecting greater connectivity, especially between the temporal and frontal lobes. As we will see later, the production of spoken language in the brain depends on pathways connecting the temporal and frontal lobes (especially the pre-frontal region). Rilling suggests that enhanced and expanded connectivity between these two regions in particular may reflect the unique cognitive demands of language.

Language: Biology and Evolution

14.2 Describe the biological basis of human language in the brain and the throat; explain different approaches to understanding how and when language evolved, including four scenarios for the origins of language.

Spoken language is a critical factor in making human behavior more complex and sophisticated than the behavior of other animals. Humans have a range of unmatched

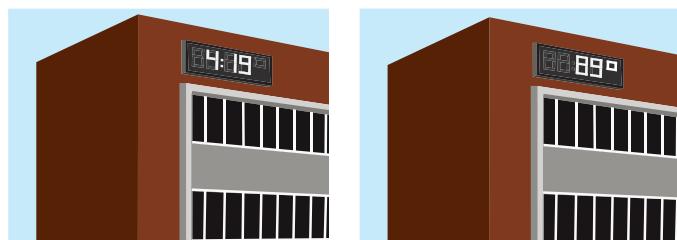
cognitive abilities—to make plans; to draw complex cause-and-effect relationships between the things you see in the environment; and to think in terms of the past, present, and future. Without the ability to convey these thoughts to other members of the social group, their usefulness for enhancing survival and reproductive success would be limited.

Language is an adaptation: Modern humans are designed by natural selection—in the anatomy of the throat and respiratory system and in various aspects of the structure and function of the brain—to produce language. But what is language? Language is the unique form of animal communication used by members of the human species. Language is *spoken*, and we are anatomically specialized to produce language and to process language-oriented sounds. Language is *semantic*: The words we use when speaking have meanings that represent real-world objects, events, or actions. Language is *phonemic*. Words are made from small sound elements called phonemes; there is no biological limit to the number of words that can be formed from phonemes and there is no intrinsic association between a word and the object or concept it represents. Finally, language is *grammatical*. All languages have a grammar, an implicit set of rules that governs the way word classes are defined and used. Although there may be a limit on the number of words a person can know, there is no limit on the ways they may be grammatically linked together. Grammar allows *recursion*, the ability to string together clauses in a sentence or to embed clauses one within another. Some cognitive scientists believe that recursion in language reflects the unique ability of the human mind to keep track of multiple ideas, objects, and processes all at the same time. As a child acquires its first language, he or she assimilates the grammatical rules of language subconsciously.

The Evolution of Grammar

The place of grammar in defining language and studying its evolution has been a point of controversy over the years. One school of linguistic thought, led by Noam Chomsky (1967), placed grammar at the center of the linguistic universe. Chomsky and his followers (such as Jackendoff, 1994) argued that by studying the general grammatical rules of language, we can find a “deep structure,” which in turn reflects a “mental grammar” found in the brains of all people. Evidence of the existence of mental grammar comes from language acquisition in children. With little effort, children master the rules of grammar of any language to which they are exposed, despite their complexity. Linguist Steven Pinker (1994) has called this ability the *language instinct*: Children appear to be genetically specialized to learn language.

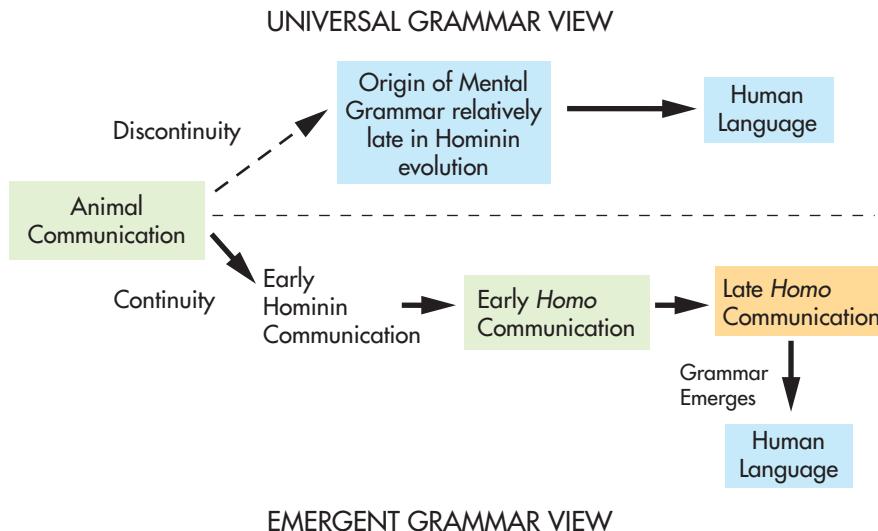
Figure 14.10 A comparison of (a) pidgin and (b) Hawaiian creole.



| Pidgin | Hawaiian Creole English |
|---|---|
| Building – high place – wall part – time – now-time – and then – now temperature every time give you. | Get one (There is an) electric sign high up on da wall of da building show you what time an' temperature get (it is) right now. |

An interesting piece of evidence of the relationship between children and a possible deep structure of language comes from the study of *pidgins* and *creoles*. Pidgins are simplified, nongrammatical communication systems that have arisen in areas where speakers of different languages need to communicate with one another but do not spend enough time around each other to learn each other’s languages (new colonial situations, fishers from different countries meeting on the seas). In contrast, creoles are grammatical languages that have arisen and developed, typically in colonial situations (such as in Hawaii or New Guinea), in the context of an ongoing situation of linguistic change or instability (Figure 14.10). It has long been noticed that creole languages around the world converge on a similar grammatical structure. Linguist Derek Bickerton (1983, 1990) suggests that the source of this convergence is not a common language of origin but the fact

Figure 14.11 The universal grammar and emergent grammar viewpoints lead to very different scenarios of the evolution of language.



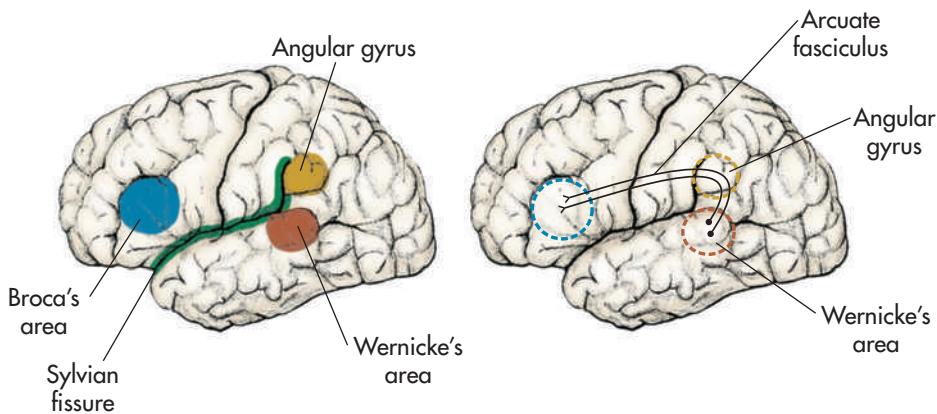
that creoles are invented by children who share a common, biologically based, deep structure for language. The first generation of children growing up in these disrupted linguistic environments will not tolerate a nongrammatical system of communication, and they impose a linguistic structure on the language around them, thus leading to the development of creoles.

Many advocates of the deep grammar point of view believe that language represents a cognitive process that is fundamentally different from that underlying any other form of animal communication. However, several evolutionary theorists of language have argued against the existence of a universal mental grammar (Savage-Rumbaugh & Rumbaugh, 1993; Schoenemann, 1999; Christiansen & Chater, 2008). Savage-Rumbaugh and Rumbaugh believe that syntax and grammar must develop once anyone tries to go beyond a two-word utterance; rules have to exist to let the listener know what the speaker is talking about. They write, "Whatever commonalities there are among grammars may well exist because only a limited number of solutions to the same problem are workable, given the constraints placed on the problem itself" (1993, pp. 106–107). Thus grammars inevitably emerge, but there is no universal grammar. Such a position is consistent with the view that human language exhibits evolutionary continuity with other forms of animal communication, because it does not posit a zoologically unique cognitive mechanism, such as a deep mental grammar, for the evolution of language (Figure 14.11).

Language in the Brain

We can define a *language area* of the brain as any part of the brain that is activated during the production or comprehension of speech. The classical language regions are found around the left Sylvian fissure, or *perisylvian language area* (Figure 14.12 on page 454). In the frontal lobe, there is *Broca's area*. As we saw in the chapter opening, a lesion in Broca's area causes a disruption in speech production (an *aphasia*), yet comprehension remains intact. At the posterior end of the Sylvian fissure, spanning the top of the temporal lobe and the bottom of the parietal lobe, is another language area, which was identified by German physician Carl Wernicke in 1874. *Wernicke's area* lesions cause a person to have difficulties in speech comprehension. People with Wernicke's area aphasia produce fluent but nonsensical speech, substituting one word

Figure 14.12 The major language areas of the left hemisphere of the brain. The connection between Wernicke's and Broca's areas passes through the angular gyrus.



for another or producing incomprehensible strings of words. Wernicke predicted that because it is likely that his area and Broca's area are in communication, different lesions in the white matter joining the two should produce aphasias with different symptoms. These *conduction aphasias* have been observed; for example, a lesion in the projection from Wernicke's area to Broca's area causes someone to produce fluent, nonsensical speech while retaining comprehension (Damasio & Damasio, 1989).

Wernicke's insights about conduction aphasias taught us to think about language as the product of interactive networks in the brain rather than of just one or two areas. In addition to Broca's and Wernicke's areas, the perisylvian language areas include several other regions important for speech. In the frontal lobe, Broca's area sits just in front of the motor strip controlling the tongue and mouth, which are obviously involved in speech production. Along the top of the temporal lobe lies the primary auditory cortex, where sound signals from the ear are initially processed, which is essential for speech perception. The angular gyrus in the parietal lobe is important for the comprehension of written language. This is not surprising because projections from the primary visual cortex in the occipital lobe pass through the angular gyrus on the way to Wernicke's area.

LANGUAGE LATERALIZATION When a function of the brain typically and consistently occurs in only one of the hemispheres, we say that function is *lateralized*. In 95% of people, the perisylvian language area is in the left hemisphere.

Most people are also right-handed, and because motor control of one side of the body is housed in the opposite side of the brain, it is very likely that right-handedness and language ability evolved in tandem. The classical view that both language and right-handedness are associated with the left hemisphere has led to the notion of left hemisphere dominance over the right hemisphere (except in about half of the left-handers—who make up about 10% of the population—who have right hemisphere dominance).

Although it is easy to focus on the classical left perisylvian regions as the seat of language, keep in mind that lesions in other parts of the brain also disrupt normal speech. Lesions in the right hemisphere (of people with left hemisphere language dominance) disrupt the musical or *prosodic* elements of speech. Prosody is essential for speech to sound normal; otherwise, it would have the flat sound of computer-synthesized speech. Lesions in the right inferior frontal lobe (opposite Broca's area) lead to deficits in the production of normal prosody in speech, and lesions in the right hemisphere opposite Wernicke's area lead to deficits in the comprehension of prosody in speech (see Innovations: Music, the Brain, and Evolution on pages 456–457). Neuroimaging studies have shown that the numerous parts of the brain dedicated

to the control of the lips, tongue, larynx, and voluntary control of the diaphragm are active during speech production (Wise et al., 1999).

Language in the Throat

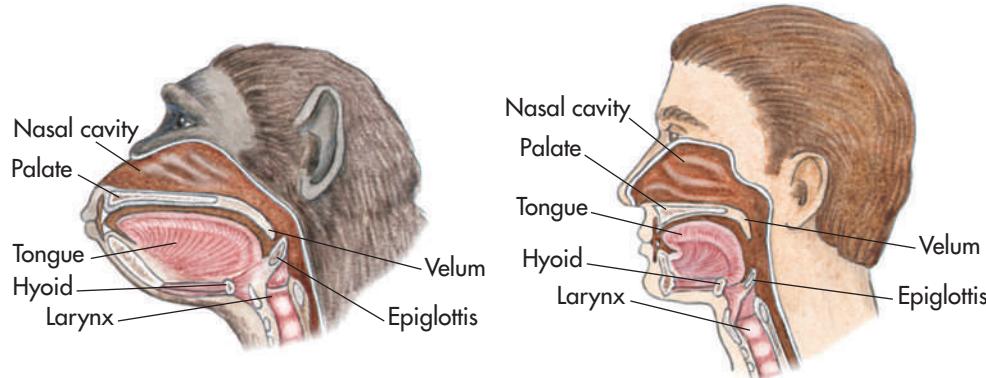
The evolution of language has not “cost” humans anything in terms of brain function. In fact, just the opposite is likely true—language has opened up new domains for cognitive evolution, especially in relation to social behavior. The same thing cannot be said for the rearrangement of the anatomy of our throats for language purposes; it is clear that this has introduced new risks in everyday life that our ancestors did not have to worry about (Laitman, 1984; Lieberman, 1991). To offset these risks, there must have been a strong selective advantage for the development of language abilities over the course of hominin evolution.

The *supralaryngeal airway* is a more precise way to describe the parts of the throat and head that have undergone changes during hominin evolution (Figure 14.13). As the name suggests, it is that part of the airway that is above the *larynx*, or voice box. The larynx sits at the top of the *trachea* and has vocal folds (vocal cords), which can modulate the passage of air through the trachea to produce different sounds. The cavity above the larynx, at the back of the mouth, is known as the *pharynx*. The posterior part of the tongue, the epiglottis, and the soft palate form the boundaries of the pharynx.

When we compare the supralaryngeal airway of a human with that of a more typical mammal, such as a chimpanzee, we can see several differences that have profound functional implications (Figure 14.13). First, the larynx in humans is much lower than in other mammals. The new position of the larynx leads to an expansion of the pharynx. This expanded pharynx's anterior wall is formed uniquely in humans by a shortened and rounded tongue, and is much more efficient for modifying the stream of air passing through the larynx to generate a greater variety of sounds, leading to fully articulate speech. In other mammals, the small pharynx has very little capacity for modifying the sounds produced by the larynx; supralaryngeal modification of sound can be done only by alteration of the shape of the oral cavity and lips (Laitman, 1984) (see Insights and Advances: Ape Language Studies on pages 460–461).

These changes in anatomy have a profound cost; however, they greatly increase the risk of choking on food or liquid. There is too much distance between the human larynx and nasal cavity for a sealed connection to form between the two, as it does in the typical mammal. The epiglottis and soft palate are separated by the rear part of the tongue. Everything we swallow must pass over the incompletely sealed opening of

Figure 14.13 The supralaryngeal airway in a chimpanzee and a human. Note the relatively low position of the larynx in the human and how the back of the thickened and shortened tongue forms the front part of the pharynx.



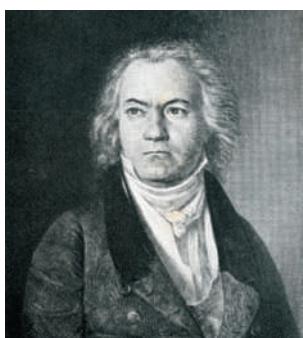
Innovations

Music, the Brain, and Evolution

Music is cross-cultural and universal. If we survey the world's cultures, we will find that people engage in vocal behaviors that use standardized tones (notes) and rhythmic patterns; these elements form the basis of musical production. The notes and rhythms are not the same in all cultures, just as the phonemes employed in different languages are not all the same, but it is possible to recognize musical behavior as distinct from other kinds of behaviors (for example, talking versus singing; walking versus dancing). In some cultures, a sharp line can be drawn between musicians and nonmusicians, reflecting differences in formal or informal training or professional status. It is important to remember, however, that almost everyone can sing or dance at some level, even if there are great individual differences in competence (Peretz, 2006).



Over the past two decades, neuroscientists with their growing arsenal of imaging tools have become increasingly interested in music and the brain. What evidence is there for the biological basis of music? First, there is the existence of people who have great difficulty producing or recognizing music, even with extensive training; this is a condition known as *amusia*, or tone deafness, and it affects about 4% of the population. The congenital absence of this ability suggests that the more typical human brain has structures



or networks dedicated to the recognition of tones. Imaging studies indicate that part of the right frontal lobe (the inferior frontal gyrus) is important for processing tone, and that people with amusia may have reduced neuronal connections in this area (Hyde et al., 2006).

At the other extreme, there are people who have *perfect pitch*, an ability to identify musical notes without a reference tone. Only a small proportion of all trained musicians have perfect pitch. Many famous musicians and composers had it (among them Mozart, Beethoven, and Jimi Hendrix), but many others did not. The existence of people with perfect pitch suggests an elaboration of the structures in the more typical brain dedicated to musical ability. Anatomical studies suggest that there are differences between musicians, those with and those without perfect pitch, in the regions of the temporal lobe associated with processing sound (Schlaug et al., 1995). In addition, Robert Zatorre has used functional brain imaging to show that when identifying tones, people with perfect pitch use their working memory differently than those without it (Zatorre, 2003).

Both amusia and perfect pitch likely reflect the individual differences in musical ability with which people are born, however, neuroscientists are also interested in looking at the effects of formal musical training on brain structure. Producing music requires integrating mental and physical operations—such as memory, reading, and complicated hand and arm movements—into the production of sound that must be simultaneously self-monitored by listening (Gaser & Schlaug, 2003). One area of the brain that appears to reflect intensive musical training is the anterior part of the corpus callosum. This part of the *corpus callosum* includes the connections between the motor regions of the frontal lobes of the two hemispheres. Gottfried Schlaug (2001) has found that this region is bigger in musicians who began musical training before the age of 7 years as compared to those who started training at a later age. He suggests that the development of the fibers of the corpus callosum reflects the plasticity of the brain during childhood, and that greater connections between these two regions may be a result of the coordinated bimanual action required in keyboard and string playing.

What about the evolution of musical ability? We have seen that there is individual variation in musical ability that is both biologically and genetically based. Such variability is the possible raw material for selection to have acted on, if musical ability was a kind of adaptation. Some researchers, such as the cognitive scientist Steven Pinker, see music as the evolutionary equivalent of cheesecake—we like it, but



it simply takes advantage of senses and abilities that are in place for other reasons. For example, spoken language also employs rhythm and tone, so it is possible that musical ability arises from those abilities without being specifically selected for. In terms of selection, many researchers have pointed out that vocal calling, as seen in gibbons, is usually the result of sexual selection (Geissman, 2000). Could singing be a product of sexual selection? It's possible; but if so, it would be competing with sexual selection that is operating in several other potential domains (for example, body size and shape, provisioning ability, even language ability itself). It has also been suggested that the rhythmic qualities of music work to enhance group solidarity and it may have been selected for in that context (Mithen, 2006).

There is still much to be learned about the biological basis and origins of music. People sing, dance, and chant for many reasons and in many contexts, ranging from the ridiculous to the sublime. Whatever the evolutionary history of music, it remains a quintessentially human activity.



the larynx, which greatly increases the risk of choking and suffocation. Interestingly, human babies less than 1 year old have a supralaryngeal anatomy that more closely resembles the mammalian norm. This allows them to drink, swallow, and breathe at the same time, which greatly enhances their suckling ability. During the second year, the larynx begins the shift to the adult position, which increases their risk of choking while increasing their ability to produce articulate speech. Darwin noted in *On the Origin of Species* that the position of the trachea in the human throat was an example of natural selection working with what history makes available to it.

Language Ability and the Fossil Record

The brain and supralaryngeal tract—anatomical structures that demonstrate most clearly our adaptations associated with the production of spoken language—are composed primarily of soft tissues that do not fossilize. However, we do have endocasts, which might preserve information about gross changes in the brain that might be associated with the development of language. In addition the supralaryngeal tract is connected by muscles and ligaments to bony structures at the base of the cranium and in the neck. It is possible some insights into the evolution of the soft tissues of the throat may be gained by examining these bony structures.

ENDOCASTS, DENTITION, AND THE EVOLUTION OF BRAIN ASYMMETRIES Because language in the brain is associated with a leftward lateralization of function, it is possible that asymmetries in gross brain structure may be pronounced enough that they could be seen in endocasts. In most modern humans, the left occipital lobe protrudes further back than the right occipital, and the right frontal lobe protrudes more forward than the left. Other primates also show this pattern, but Holloway and de Lacoste-Lareymondie (1982) found that the left occipital and right frontal pattern is found most often in contemporary humans and in hominins, including australopithecines and the KNM-ER 1470 *H. habilis* specimen. Although this asymmetry may not be directly related to language or handedness, it does reflect an asymmetric pattern that may be unique to hominins.

Another region of the brain that might also show evidence of asymmetry in an endocast is Broca's area. The endocast of 1470 has a well-preserved left inferior frontal region (the location of Broca's area). Anthropologists interested in hominin endocasts tend to agree that 1470 resembles humans more than pongids in the anatomical complexity of the region corresponding to Broca's area (Holloway, 1976, 1999; Falk, 1983b; Tobias, 1987). A similar claim has been made for an Indonesian *H. erectus* specimen, Sambungmacan 3 (Broadfield et al., 2001). Although this specimen has protrusions in the inferior frontal lobe on both the left and right hemispheres, the total size of the protrusion is larger in the left hemisphere, indicating the possible presence of a Broca's area in that hemisphere. Protrusions on the lateral surfaces of the frontal lobes corresponding to Broca's area have also been found on a Chinese *erectus* specimen (Nanjing 1) dating to 600,000 years ago (Wu et al., 2011).

Habitual right-handedness is accompanied by an asymmetry of function in the brain; therefore, evidence of right-handedness in the fossil or archaeological record could provide evidence of the evolution of lateralization that is possibly related to language. Nicholas Toth (1985) has argued that flake patterns in the production of stone tools associated with early *Homo* are consistent with right-handed construction. More recently, an analysis of wear patterns on the anterior teeth of archaic *Homo sapiens* (*Homo heidelbergensis*) from the Spanish site of Sima de los Huesos (500,000 years old) suggests that this population was also predominantly right-handed. Marina Lozano and her colleagues (2008) looked at the distribution of cut marks made by stone tools on the anterior teeth (incisors) of individuals from this site. They believe that this group used the "stuff and cut" method, whereby an item being cut with a stone tool

was held with the front teeth and one hand, while the other hand wielded the stone tool for cutting. It was inevitable that on occasion, the front teeth would get nicked by the stone tool when cutting in this fashion. In almost all cases, the scratch marks on the teeth were consistent with the cutting tool being held in the right hand, leaving the left hand to serve as the anchor. If language lateralization is associated with right-handedness, then the origins of language may extend quite far back in the *Homo* lineage.

BASE OF THE CRANIUM AND HYOID BONE

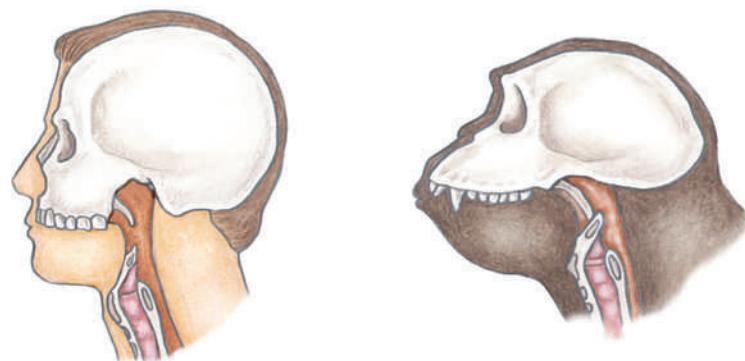
According to some investigators, the bony remains of fossil hominins yield real clues to the form and position of the supralaryngeal tract, offering insights into the vocal abilities of these earlier hominins. However, most of these claims are somewhat controversial and reflect the inherent difficulty of reconstructing soft tissues from fossil remains.

Jeffrey Laitman (1984; Laitman & Heimbuch, 1982; Laitman & Reidenberg, 1988) has argued that the degree of *flexion* of the *basicranium* is an anatomical marker of larynx position (Figure 14.14). His studies show that among living mammals, human adults are unique in that they have a pronounced degree of basicranial flexion; the more flexed the base of the cranium, the lower the larynx and the wider range of sounds that can be produced. Laitman and Reidenberg suggest that the degree of flexion seen in the base of *H. erectus* crania is greater than that seen in pongids and australopithecines and may signal the beginning of the lowering of the larynx to a more human-like position. These claims are controversial, and other investigators (Arensburg et al., 1990) believe that the basic premise of a correlation between variation in the cranial base and vocal abilities has yet to be proven.

Reconstructions of the Neandertal vocal tract have been equally controversial. Philip Lieberman (1984, 1991) claims that because of their long palate and other factors, the shape of the Neandertal tongue would be different from a modern human's, the pharynx would not be as large, and the larynx would be higher up in the throat. In fact, Lieberman argues that it would be impossible to put a human supralaryngeal tract into a Neandertal because the larynx would have to be placed in the chest cavity. Lieberman suggests that Neandertals would be missing phonetic elements present in human spoken language. Like claims about the basicranium and language ability, these assertions have also been the subject of much criticism (such as Falk, 1975).

A potentially more direct source of evidence about the speech abilities of Neandertals has come with the discovery of a Neandertal **hyoid bone** from Kebara Cave, Israel, dating to about 60,000 years ago (Arensburg et al., 1990). The hyoid is a small, free-floating bone (that is, it does not articulate with any other bones) that sits in the throat in front of the larynx and in close association (via muscles and ligaments) with the mandible, larynx, and other structures. Arensburg and colleagues argue that the Kebara hyoid is essentially human-like in its size and shape and very distinct from that of a chimpanzee, for example (Figure 14.15). The hyoids of chimpanzees and other apes have a boxlike body with two narrow, flaring horns, whereas the human hyoid has a much more regular horseshoe shape. The structure of the chimpanzee hyoid reflects its relationship with an air sac in the larynx, which is no longer present in modern humans (Steele et al., 2013). Presumably the presence of

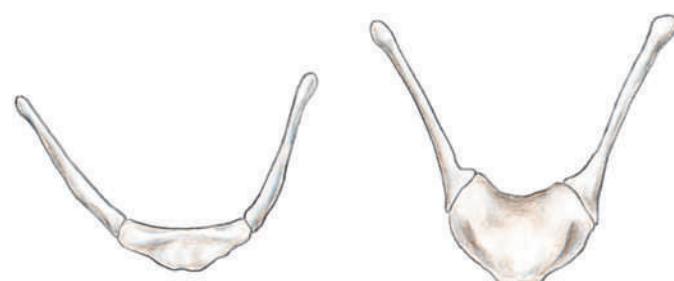
Figure 14.14 The base of the human cranium is more flexed than the base of the chimpanzee cranium.



hyoid bone

A small “floating bone” in the front part of the throat, which is held in place by muscles and ligaments.

Figure 14.15 The hyoid bone from a Neandertal and a chimpanzee. The Neandertal hyoid is much more similar to those found in modern humans.



Insights and Advances

Ape Language Studies

Few scientific developments in the twentieth century captured the public's imagination as much as the extraordinary spectacle of great apes communicating with their handlers and others via sign language (see Lieberman [1984] and Ristau [1999] for historical overviews). Although there had been several attempts to teach apes raised in close contact with humans to talk, these all failed miserably. Humans are adapted to produce the sounds of spoken language, and apes are not. In 1965, a husband-and-wife team of psychologists named Allen and Beatrix Gardner had the idea to train a 10-month-old chimpanzee named Washoe to communicate using American Sign Language, thereby bypassing the inherent vocal limitations of chimpanzees. Although Washoe was disadvantaged in starting her language training at an advanced age and her handlers were not expert ASL signers, she still managed to obtain a substantial number of signs (at least 132) in her initial 4 years of training, used them appropriately, and even coined novel two-word combinations, such as *water bird* for swan and *metal hot* for cigarette lighter. Washoe was also observed signing to herself and to other chimpanzees. In overall language skill, Washoe reached the level of a 2- or 3-year-old human child. Using ALS, she had no trouble making her wishes known to her handlers: "You go car gimme orange. Hurry" (quoted from Lieberman, 1984, p. 248). Washoe died in 2007 at the age of about 42 years.

Other investigators taught sign language to other apes, such as a gorilla and an orangutan. In some "ape language" studies, hand sign language was not used; rather, chimpanzees were taught to communicate via symbols they could point to or via a kind of keyboard. But even as some

investigators were initiating and expanding research into the language skills of great apes, a backlash against such research started to grow. Many scientists were critical of the idea that the word *language* could be used in association with the communication skills displayed by Washoe and the other signing apes. Critics claimed that the signing apes were exhibiting nothing more than a Clever Hans phenomenon. Clever Hans was a horse who amazed people in Europe around the turn of the twentieth century with his counting and adding abilities until it was discovered that his numerical skills (which he expressed by stomping with one hoof) were actually unintentionally cued by his trainer. Although it was easy to refute the Clever Hans claims about signing apes (by using substitute handlers, setting up situations where cuing would have been impossible, and so on), the critics made it difficult to obtain funding for ape language studies (Gibbons, 1991).

However, despite the critics, research on signing apes continued throughout the 1970s and 1980s. Roger Fouts and colleagues took over the Washoe project, which had grown to include several other signing chimpanzees, from the Gardners. Among these were Loulis, a young male whom Washoe adopted as a 10-month-old. Loulis was not exposed to signing by humans, and Fouts and his colleagues did a series of careful studies to chart the cultural transmission of sign language from Washoe to her adopted son. They observed Loulis making his first sign 7 days after Washoe adopted him; by age 15 months, Loulis was able to combine signs, and by 73 months of age, he had a vocabulary of 51 signs, all learned without human intervention (Fouts & Waters, 2001). Fouts also initiated a project of remotely video taping the activities of the signing

this air sac system limits the production of speech sounds. Because the Kebara hyoid was found with a mandible and neck vertebrae, its location in the living individual could be reconstructed because these are the bony structures with which the hyoid makes soft tissue connections. According to Arensburg and colleagues, its position was human-like within a neck that was similar in length to human necks. Thus they conclude that the larynx was also in a human-like position and that Neandertals were fully capable of producing speech.

Hyoid bones from the pre-Neandertal/archaic *Homo sapiens* site of Sima de los Huesos in Spain, dating to 530,000 years ago, have also been recovered and analyzed (Martinez et al., 2008). Like the Kebara hyoid, these appear to be fully human-like in form. In contrast to the later *Homo* hyoids, the *A. afarensis* juvenile from Dikika, Ethiopia (dated to 3.3 MYA) possesses a hyoid bone that is much more similar to those of the great apes than to modern humans (Alemseged et al., 2006). If the hyoid is indeed a marker of speech ability, then this hyoid suggests that *A. afarensis* did not possess human-like speech. However, this is a hypothesis that still remains to be fully tested; at this point, it is reasonable to say that *A. afarensis* retained the primitive condition of the hyoid as seen in the great apes and that the derived modern human form appeared at least half a million years ago, predating the appearance of modern *Homo sapiens*.

chimpanzee group; this work showed definitively that they used signing during interactions among themselves in the absence of human cuing. Fouts and Waters (2001, p. 790) describe one incident: ". . . chimpanzees often signed emphatically during high-arousal interaction such as fights and active play. For example, after separating Dar and Loulis during a fight and with all the chimpanzees still screaming, Washoe signed *come hug* to Loulis. He signed *no* and continued to move away from her."

In the 1980s Sue Savage-Rumbaugh and Duane Rumbaugh initiated a sign language research project with bonobos, using symbols (lexigrams) that could be pointed to in sequence to generate phrases. One of their subjects, a young male named Kanzi, similarly to Loulis, picked up the language by simply observing his mother as she was being taught by humans (Figure A). He has since become the most proficient sign language ape yet studied, mastering hundreds of symbols and generating thousands of novel combinations of symbols, often referring to objects and situations not in his immediate vicinity (Savage-Rumbaugh & Rumbaugh, 1993). His ability to comprehend simple and complex sentences in spoken English, even though he had never been explicitly taught to do so, is also striking. At 5 years of age, his grasp of spoken English exceeded that of a 2-year-old child. For a fascinating account of Kanzi's life, training, and personality, see Savage-Rumbaugh, Shanker, and Taylor (1998).

No one would argue that Kanzi and the other signing apes have *human language*, but they do provide us with several insights into the evolution of human language. First, a certain level of linguistic competence is present as part of the general cognitive abilities of great apes and presumably of the common ancestor we shared with them. Second,



Figure A Kanzi talks using his keyboard language.

the research with Kanzi indicates that comprehension exceeds production in the apes. This means that the speaker-receiver issue probably was not a problem in the evolution of language: The evolution of speech production skills would not have been limited by the ability of listeners to understand that speech. Third, the learning situation (exposure at a young age to a rich linguistic environment) is critical for language acquisition. We did not know about the language abilities of apes until they were placed in an environment where they could be expressed. Critics of the studies have argued, why would they have such capacity and never use it? But, all reasonably complex, behaviorally sophisticated animals have new skills they can develop given the proper environmental stimuli. Language abilities in hominins did not evolve from nothing, but reflect an enhancement and elaboration of abilities found in their pongid ancestors and cousins.

Scenarios of Language Evolution

In 1866, the Société de Linguistique de Paris famously banned discussion of the origins or evolution of language. Speculation was far outpacing the available evidence. Even today, some researchers still believe that we are far from unraveling the mystery of language evolution (Hauser et al., 2014). The absence of direct evidence concerning the evolution of language ability allows for many theories or models for how it might have occurred (Hewes, 1999). Most of these models or scenarios are untestable, although it is possible to assess their plausibility based on contemporary data. Since the 1980s, scenarios about the evolution of language have proliferated as new kinds of information have become available to researchers. We will discuss and assess four of these speculative models, keeping in mind that the ratio of speculation to evidence is always going to be a bit higher than we might like.

THROWING AND LANGUAGE EVOLUTION In the 1980s, neuroscientist William Calvin (1982, 1983) suggested that there was an intimate connection between the evolution of one-armed throwing ability, handedness, and language. Calvin pointed out that language and throwing are both lateralized activities (left hemisphere dominance). The throwing of projectiles is clearly important in hunting by humans, and it is reasonable to assume that expert throwing ability could have been an important adaptation in hominin evolution. Calvin argued that because the motor strip controlling

the hands and arms is close to important centers for speech control, the evolution of language could have “piggybacked” on the evolution of throwing ability.

Calvin’s hypothesis is fascinating, and it attempts to tie together several different kinds of information. Some problems with it include the fact that regions in the brain controlling throwing and speech are not really that close to each other, and there is no way to determine whether language piggybacked on throwing or vice versa. Nonetheless, the model is useful in that it highlights the potentially profound importance of the evolution of throwing ability, which is indeed a lateralized behavior just like language.

LANGUAGE AS A REPLACEMENT FOR GROOMING As you learned earlier, one of the main ways in which primate social groups maintain group cohesion is by social grooming (Figure 14.16). Primatologist Robin Dunbar (1993, 1997) points out that although humans may gain comfort from touch, they do not actually engage in very much social grooming. Looking at a wide range of primate species, Dunbar found that there was a positive statistical relationship between time spent grooming, brain size, and social group size. In other words, primates with larger brains lived in larger social groups, which required them to spend more time grooming in order to maintain social cohesiveness.

Humans are an exception to this pattern. Dunbar hypothesized that at some point in human evolution, with selection pressures to increase group size, hominins replaced social grooming with social language. Based on empirical studies, Dunbar argues that most of what people talk about is other people and their relationships (that is, gossip). Through such discussions, language maintains its primary role as a social reinforcer.

Dunbar’s model has the basic chicken-and-egg problem: Did we evolve language in order to have larger group sizes, or did larger group sizes (and brain size) evolve because we evolved language? Furthermore, the grooming hypothesis does not say much about language *per se* but simply about one of the many ways language can be used (although gossip obviously is one of the more important ways). Dunbar’s hypothesis brings home a fundamental point, however. At some point during our evolution, hominins stopped living in primate-like social groups of small size and started living in larger, ethnicity- or culture-based societies. Without language, such a transition would have been impossible.

SYMBOLS AND SEX In his model of language origins, anthropologist Terrence Deacon (1997) emphasizes symbols as the key feature of human language. Language puts us in a world fully shaped by symbols. Early hominins would have had a verbal and nonverbal communication system similar to those seen in other primates.

Figure 14.16 Language facilitates social interaction among humans. In apes, grooming one another is an essential part of social interaction, while gossiping may have a similar function in human communication.



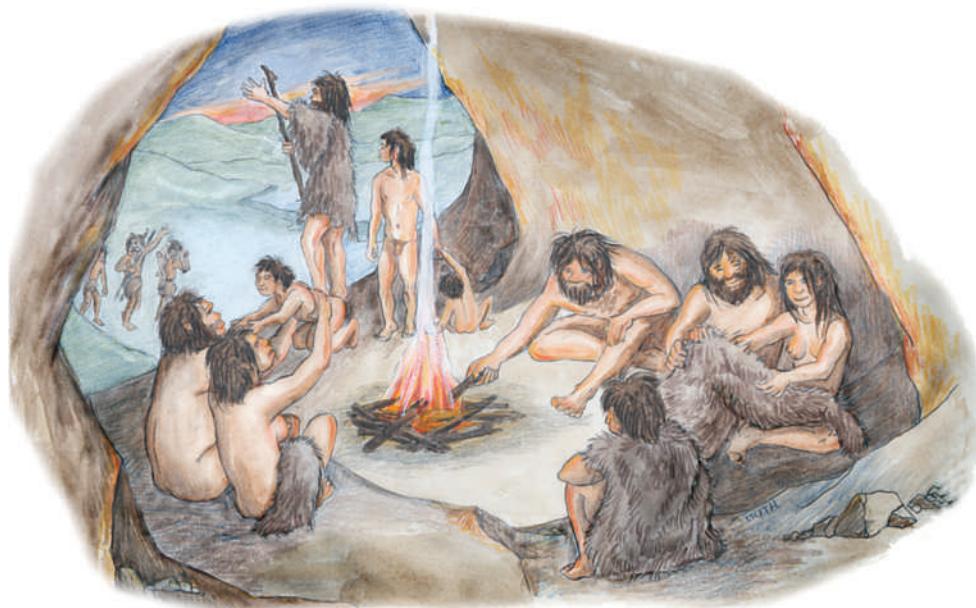
They would have adopted symbolic communication slowly, in the context of the preexisting communication system. As the use of symbols increased, however, the costs of learning and mastering them would also increase. But because humans have clearly evolved a symbolic system of communication, the benefits must have outweighed the costs.

Deacon suggests that symbolic communication may have first arisen in the context of the maintenance of exclusive sexual and provisioning relationships. His scenario posits that around 2 million years ago, at the onset of genus *Homo*, male hominins began provisioning sexual partners and their offspring in the context of an exclusive relationship. Deacon argues that these hominins were living in multimale, multifemale groups—as you would find with chimpanzees today—in which paternity would be difficult to establish. Because cooperative hunting increases the chances for success, there would be a conflict between selection for paternity certainty and for a social lifestyle. Deacon suggests that hominins evolved symbolic language to reinforce the pair bond between a male and a female within a social group, ensuring sexual exclusivity for the male and provisioning for the female. Symbols would also be useful in communicating to others in the social group that such an exclusive relationship exists (Figure 14.17).

A weakness of Deacon's model is its emphasis on pair bonds, which is a controversial issue in hominin evolution. However, it does not really require that pair bonds exist, only that exclusive and identifiable sexual and provisioning relationships are present within a larger social group. For example, establishing an exclusive relationship between one male and two females would also benefit from symbolic communication. Deacon's theory asserts that the reproductive advantages conferred by a component of language—symbolic communication—at a specific moment in hominin evolution may have initiated the journey down the path to full-blown human language.

GESTURE AND SPOKEN LANGUAGE In addition to spoken language, human communication relies on an ability to read nonverbal cues as well. Nonverbal forms of communication, such as making gestures, using body language or reading faces, can be a critical aspect of how people interact with one another.

Figure 14.17 Symbolic language may have helped reinforce exclusive sexual relationships within social groups in later hominin evolution.



Obviously, we can communicate fully using spoken language alone, but there is clearly another dimension to communication that is present when nonverbal cues can be taken into account.

Michael Corballis (2002) has been the strongest advocate for the idea that gesture preceded talking in the evolution of language. He points out that among primates, vocal communication is almost always emotive, tied to specific contexts, and largely involuntary. In contrast, gestures and other actions of the hands are under precise cortical control. It is not an accident that scientists have had much better success at teaching apes sign language rather than vocal language. Corballis argues that forms of protolanguage would have been present across millions of years of hominin evolution. However, it was only relatively recently, perhaps during the last few hundred thousand years, that the vocal tract for spoken language developed, allowing a transfer from gestural to vocal language. In a sense, this would have been a “discovery” on the part of the first speakers, that they could use language vocally as well as gesturally. It was a discovery that was ultimately highly adaptive.

Like so many of language evolution scenarios, the gestural model is difficult to test. Direct or indirect evidence for the existence of a transitional gestural form of language will be difficult to come by. It highlights, however, just how unique spoken language is as a form of primate vocalization.

Brain Size, Language, and Intelligence

14.3 Recognize the complex interaction between brain and language in the evolution of intelligence.

If there is a fundamental issue in understanding the evolution of human behavior, it is interpreting the relationships of brain size, language, and intelligence. We have not been too concerned with defining what intelligence is. People interested in material culture, such as archaeologists, have tended to look for clues of intelligence in stone tool remains, attempting to define the level of technical intelligence our ancestors may have had (Wynn, 1999) while acknowledging that these tools may represent only a biased sample of the total material culture repertoire of past hominins. But if language ability is closely tied to level of intelligence, tools give us little to go on. As Thomas Wynn (1999, p. 284) has said, “Tools tell us little about language . . . [They] are not windows to symbolic behavior.” This does not mean that no insights into human cognition are to be gained from the archaeological record but that stone tools must be considered in a broader investigatory context (Mithen, 1996).

In contrast to archaeologists, scientists more interested in the behavior of living animals and humans have emphasized the importance of social behavior in the lives of past hominins as the driving force behind the increase in intelligence (Byrne & Whiten, 1988a; see Dunbar’s grooming model of language evolution described earlier). They argue that technical aspects of intelligence have been emphasized over the social aspects. That may be true, but a reasonable view is that both technical and social intelligences were critical in human evolution. Theorists of intelligence have emphasized the multifaceted nature of intelligence in the real world (Gardner, 1993; Sternberg, 1990), which goes beyond things such as IQ test scores. As we discussed earlier, increases in brain size tend to be distributed throughout the structure rather than localized to specific regions (with some exceptions, of course). Thus selection for one aspect of intelligence that is localized to one part of the brain will lead to size increases in other parts of the brain. This might in turn lead to the appearances of new capabilities that may themselves be selected for (Allen, 2009).

Although we lack direct information about the evolution of brain functional organization, intelligence, and language, we are developing a clearer and more

sophisticated understanding of what happened in human evolution over the past several million years. Increases in knowledge about brain structure and function, the nature of language as an evolving system, the communicatory behavior of humans and other animals, and the hominin fossil and archaeological record means that our speculations are both informed and constrained by a growing scientific database.

Summary

ISSUES IN HOMININ BRAIN EVOLUTION

14.1 Define and discuss the concept of encephalization and its relevance to understanding human brain evolution; compare and contrast the importance of brain size increase and brain functional reorganization in brain evolution.

- The increase in complexity of human behavior and cognition has been made possible by changes in the size and functional organization of the brain.
- Compared to other primates, human brains are larger in both absolute and relative size, although some brain structures are relatively smaller in humans.
- The fossil record provides a reasonably good record of changes in brain size over evolution, but only a small amount of information about changes in organization.
- Early hominins had cranial capacities that are similar to those seen in the living great apes (400–600 cc).
- Brain volume expansion begins around 2 million years ago with the appearance of various early *Homo* species.
- A second period of brain expansion occurred with the advent of archaic *Homo sapiens* and Neandertals.
- Neandertals may have slightly larger average cranial capacities than modern humans, but their larger body sizes mean that they were less encephalized.
- Compared to the great apes, humans have brain regions that have become reorganized during human evolution.
- The relative reduction in size of the olfactory bulbs in humans compared to other primates is an example of reorganization by a change in relative size.
- The primary visual area in the human brain is not only relatively smaller compared to what is seen in other primates, but it has also shifted position within the occipital lobe.
- The “lunate sulcus controversy” involved the interpretation of the position of a sulcus in fossil endocasts, which potentially could yield insights into the timing of visual cortex reorganization during hominin evolution.

LANGUAGE: BIOLOGY AND EVOLUTION

14.2 Describe the biological basis of human language in the brain and the throat; explain different approaches to understanding how and when language evolved, including four scenarios for the origins of language.

- Several areas of the brain play a specialized role in language production, and language function, like handedness, is highly lateralized in the brain.
- Changes in the anatomy of the throat in humans indicate that language ability compromises other functions, such as swallowing.
- Claims that hominid fossil remains can be used to reconstruct language ability have been made, but these claims should be regarded with caution.
- Many scenarios have been suggested for how and why language evolved.

BRAIN SIZE, LANGUAGE, AND INTELLIGENCE

14.3 Recognize the complex interaction between brain and language in the evolution of intelligence.

- Stone tools tell us a little directly about the intelligence or cognitive abilities of their makers.
- It makes little sense to rank either social or technical capabilities as being more critical in the evolution of human intelligence.

Review Questions

- 14.1 What has become functionally reorganized since humans split from the great apes?
- 14.2 What are the signs of spoken language evolution potentially available to anthropologists in the fossil record?
- 14.3 Why are symbols important in the evolution of brain and language?

Key Terms

cerebellum, p. 441
cerebral cortex, p. 441
cerebrum, p. 441

encephalization quotient (EQ), p. 443

hyoid bone, p. 459
language, p. 440
lunate sulcus, p. 450
neurons, p. 441

olfactory bulbs, p. 449
paleoneurology, p. 441
prefrontal region, p. 449

Chapter 15

Biomedical

Anthropology



Learning Objectives

- 15.1** Recognize the basic epidemiological rate statistics and how they are derived, and explain epidemiological transitions and their consequences.
- 15.2** Compare and contrast the biocultural and evolutionary approaches in biomedical anthropology.
- 15.3** Describe the unique challenges of human birth and summarize the stages of human

growth and development and the secular trend in growth.

- 15.4** Describe the human biological response to infectious disease and the ways cultural environments shape the arms race between humans and pathogens.
- 15.5** Compare and contrast Paleolithic and agricultural diets, and recognize the implications for switching from one to the other on human health.

Lunchtime on a late summer day 20,000 years ago in the southwestern part of what is now France: A small group of boys have been playing since midmorning, exploring the caves that are common in their region, looking for old stone tools that have been left behind by hunting parties. They are starting to get hungry. They do not head back to their village for food: The morning and evening meals will be provided by their parents and other adults in the tribe, but they are on their own between those two meals.

At this time of year, the boys do not mind foraging on their own. The summer has been rainy and warm, and a large variety of nuts, berries, and seeds are beginning to ripen. Because the summer growing season has been a good one, small game such as rabbits and squirrels are well fed and will make a good meal if the boys can manage to catch one. They spend an hour or two moving from site to site where food can be found, covering a couple of miles in the process. They see a rabbit and spend 20 minutes very quietly trying to sneak up on it before realizing that it is no longer in the area. Even without the rabbit, they are all happy with the amount of food they managed to find during their midday forage. In mid-afternoon, they stop by a stream for a rest, and then one by one they fall asleep.

Lunchtime on a late summer day in the early twenty-first century, at a middle school in the United States: A large group of children line up in the cafeteria to get their lunch. They have spent the morning behind desks, doing their school work. They have had one short recess, but they will not have another during the afternoon. They have a physical education class only once a week because budget cutbacks have meant that their school can afford only one gym teacher for more than 1,200 students.

As the children pass through the cafeteria line, most of them ignore the fruit, vegetables, and whole-wheat breads. Instead, they choose foods high in fat, salt, and sugar: chicken nuggets, fries, and cake. The children do not drink the low-fat milk provided but instead favor sweet sodas and fruit-flavored drinks. After they sit down, the children have 15 minutes to finish their meals. Most of them would say that they really like the food the cafeteria gives them. When they are finished, they return to their classrooms for more instruction.

At first glance, children in developed countries in the early twenty-first century are much healthier than their counterparts who lived 20,000 years ago. They are bigger and more physically mature for their age, and unlike their Paleolithic ancestors, they can reasonably expect to live well into their 70s. They have been vaccinated against several potentially life-threatening viral illnesses, and they need not worry that a small cut, a minor broken bone, or a toothache will turn into a fatal bacterial infection. They are blissfully free of parasites. For women, childbirth is not an event fraught with danger.

On the other hand, children from 20,000 years ago would have grown up more slowly than contemporary children, but upon reaching adulthood, they would have had a strong, lean bodies, with much more muscle than fat. They would not spend a lifetime consuming more calories than they expend. If they were lucky enough to avoid infectious disease, injury, and famine, in middle and old age they would have been less likely to suffer from heart disease, high blood pressure, diabetes, and even some kinds of cancer than would an adult living today.

Health and illness are fundamental parts of the human experience. The individual experience of illness is produced by many factors. Illness is a product of our genes and culture, our environment and evolution, the economic and educational systems

we live under, and the things we eat. When we compare how people live now to how they lived 20,000 years ago, it is apparent that it is difficult to define a healthful environment. Is it the quantity of life (years lived) or the quality that matters most? Are we healthier living as our ancestors did, even though we cannot re-create those past environments, or should we rejoice in the abundance and comfort that a steady food supply and modern technology provide us?

Biomedical anthropology is a subfield of biological anthropology concerned with issues of health and illness. Biomedical anthropologists bring the traditional interests of biological anthropology—evolution, human variation, genetics—to the study of medically related phenomena. Like medicine, biomedical anthropology relies on empiricism and hypothesis testing and, when possible, experimental research to understand human disease and illness. Biomedical anthropology is also like cultural medical anthropology in its comparative outlook and its attempt to understand illness in the context of specific cultural environments.

In this chapter, we will look at many aspects of human health from both biocultural and evolutionary perspectives. We will see how health relates to growth, development, and aging. We will then consider infectious disease and the problems associated with evolving biological solutions to infectious agents that can also evolve. Finally, we will examine the interaction between diet and disease and the enormous changes in diet our species has gone through since the advent of modern agriculture. But before going on to those topics, let us briefly consider some basic concepts from an allied discipline, epidemiology, which provides the quantitative foundations for population-level health research.

Epidemiology: Basic Tools for Biomedical Anthropology

15.1 Recognize the basic epidemiological rate statistics and how they are derived, and explain epidemiological transitions and their consequences.

Biomedical anthropology is concerned with understanding the expression and causes of disease at the population level. Another health science with a population-level outlook is **epidemiology**. Epidemiology is the quantitative study of the occurrence and cause of disease in populations. Compared with anthropologists, epidemiologists are “number-crunchers,” looking for broad-scale statistical associations between ill health and the factors that produce it in specific populations (Figure 15.1). In the same way that understanding the cell is essential for developing a proper understanding of anatomical structure, familiarity with some of the basic statistical tools of epidemiology is essential for the anthropologist’s understanding of the distribution of disease in human populations.

Rates: Mortality, Incidence, and Prevalence

The most basic epidemiological statistic is the *rate* of disease per 1,000 individuals, or even per 1 million individuals for rare conditions. We define rate as

$$\text{Rate} = \text{Events}/\text{Population at risk}$$

The *event* is the disease or condition you are interested in. It is important to specify the population at risk. For instance, we should calculate the ovarian cancer rate for adult women, not for the population as a whole.

biomedical anthropology

The subfield of biological anthropology concerned with issues of health and illness.

epidemiology

The quantitative study of the occurrence and cause of disease in populations.

Figure 15.1 Epidemiologists look for the causes of disease, such as toxic waste and industrial pollution, at the population level.



Mortality rates are measures of the probability of dying within a population over a given period of time. The *crude death rate* is defined as

$$\begin{aligned}\text{Crude death rate} &= (\text{All deaths during a calendar year}/\text{Population at midyear}) \times 1,000 \\ &= \text{Deaths per 1,000}\end{aligned}$$

We have to be wary in interpreting crude death rates. For example, in 2011 the crude death rate in Pennsylvania was 10.1/1,000, whereas in Utah it was only 5.4/1,000 (Hoyert and Xu, 2012). Does this mean that we would all be better off living in Utah rather than Pennsylvania? Not necessarily. Utah has a much higher birth rate and a higher proportion of young people than does Pennsylvania. Age is an important variable in determining a person's chance of dying in a given period of time. The different *age structures* of the two states undoubtedly explain much of the difference in crude death rate between them. Epidemiologists can take age into account when calculating death rate to produce an *age-adjusted* rate. Utah still is a bit better off than Pennsylvania, with an age-adjusted rate of 7.0/1000 versus 7.8/1000, but the difference is much less than the crude death rate on its own would indicate (U.S. national rate is 7.4/1,000).

Two of the most important epidemiological statistics are **incidence rate** and **prevalence rate**. They are defined as follows:

$$\text{Incidence rate} = (\text{Number of new cases of a disease}/\text{Total population})/\text{Period of time} \\ (\text{usually a year})$$

$$\text{Prevalence rate} = \text{Total number of cases of a disease at a given time}/\text{Total population}$$

Incidence rate is the occurrence of new cases of a disease. The higher the incidence rate, the more new cases are developing over a period of time. A change in incidence rate indicates a change in the balance of ecological factors that influence the expression of a disease, which could result from some naturally occurring factor or the development of an effective intervention program. Incidence rates of diagnosed cases of AIDS peaked in the United States in the early 1990s, with more than 106,000 new cases in 1993 (starting from only a handful of cases in 1981), and then leveled off to a steady 40,000 new cases per year starting in 1997 (Stine, 2009). This decline in incidence rate undoubtedly was caused by changes in behavior brought about by AIDS

incidence rate

The number of new occurrences of a disease over a given period of time divided by the population size.

prevalence rate

The number of existing cases of a disease divided by the population (or the population at risk).

education programs. If a vaccine for AIDS were developed, the incidence rate would plummet.

The prevalence rate is a function of both incidence and *duration*. Changes in the prevalence rate of a disease do not necessarily tell us anything about the incidence rate. For example, with the introduction of new drugs to treat AIDS, people who develop the condition are now surviving longer than ever. A person infected with HIV (the virus that causes AIDS) today can, with drugs and treatment, reasonably expect to survive for decades with the virus (Stine, 2009). Because the drugs only control the symptoms of AIDS and do not cure it, the prevalence rate may actually *increase* as a result of these new treatments with increased duration of illness, while the incidence rate remains the same. In contrast, a disease that kills quickly—or, looking on the bright side, is quickly cured—could have an incidence rate higher than its prevalence rate.

Epidemiological Transitions

In 1971, Abdel Omran coined the term *epidemiological transition* to describe changes in the patterns of disease and mortality in developed countries. In less developed societies, most deaths are caused by infectious diseases. In developed countries that have passed through the epidemiological transition of the twentieth century, the most common causes of death are chronic diseases of old age. Infectious disease rates dropped dramatically in developed countries thanks to better nutrition and hygiene, a better understanding of how infectious agents cause illness, and widespread use of antibiotics and vaccinations.

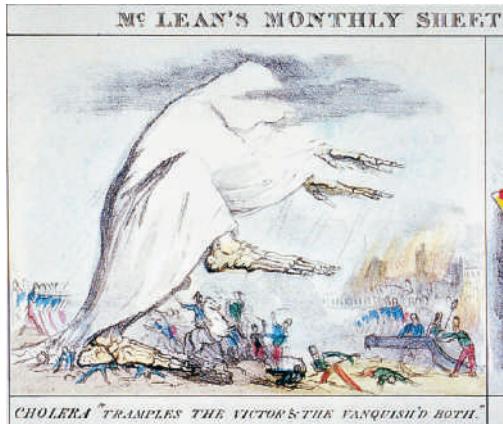
Table 15.1 lists the top ten causes of death in the United States in 1900 and 2000. The death rate from accidents holds almost the same position in both lists, although

Table 15.1 Top 10 Causes of Death in the United States, 1900 and 2000

| Rank | Cause of Death | Deaths per 100,000 | Percentage of All Deaths |
|-------------|-----------------------------|--------------------|--------------------------|
| 1900 | | | |
| 1 | Pneumonia | 202 | 12 |
| 2 | Tuberculosis | 194 | 11 |
| 3 | Diarrhea and enteritis | 140 | 8 |
| 4 | Heart disease | 137 | 8 |
| 5 | Kidney disease | 81 | 5 |
| 6 | Accidents | 76 | 4 |
| 7 | Stroke | 73 | 4 |
| 8 | Diseases of early infancy | 72 | 4 |
| 9 | Cancer | 64 | 4 |
| 10 | Diphtheria | 40 | 2 |
| 2000 | | | |
| 1 | Heart disease | 258 | 30 |
| 2 | Cancer | 201 | 23 |
| 3 | Stroke | 61 | 7 |
| 4 | Chronic respiratory disease | 44 | 5 |
| 5 | Accidents | 36 | 4 |
| 6 | Diabetes mellitus | 25 | 3 |
| 7 | Influenza and pneumonia | 24 | 3 |
| 8 | Alzheimer disease | 18 | 2 |
| 9 | Kidney disease | 14 | 2 |
| 10 | Septicemia | 11 | 1 |

SOURCES: R. D. Grove and A. M. Hetzel, *Vital Statistics Rates of the United States, 1940–1960* (Washington, DC: U.S. GPO 1988); U.S. National Center for Health Statistics, *National Vital Statistics Report*, 50 (15): 2002.

Figure 15.2 Before the advent of vaccinations and antibiotics, infectious diseases such as cholera were the scourge of human populations.



the death rate from accidents in 2000 was about half the 1900 rate. The three big causes of death in 2000—heart disease, cancer, and stroke—are all primarily diseases of old age, accounting for 60% of all deaths. In 1900, they accounted for only 16% of deaths. In 1900, people were at risk from a variety of infectious diseases. In 2000, the infectious diseases that made the top ten list—pneumonia, influenza, and septicemia—were all diseases to which older, chronically ill people are particularly vulnerable.

The concept of an epidemiological transition, which is based on an evolutionary and comparative view of diseases in populations, fits in well with much biomedical anthropological research. Anthropologist George Armelagos (1997) and others have argued that Omran's epidemiological transition is in fact the second epidemiological transition. The first occurred with the introduction of agriculture, which in turn led to the development of large urban populations. These larger populations became the setting for the spread of infectious diseases, many of which still plagued large cities in 1900 (Figure 15.2).

Biocultural and Evolutionary Approaches to Disease

15.2 Compare and contrast the biocultural and evolutionary approaches in biomedical anthropology.

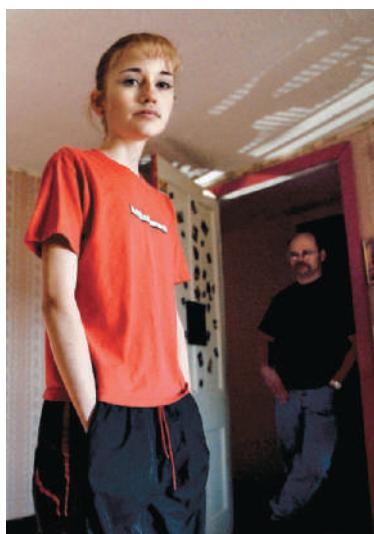
Epidemiology provides the quantitative foundation for biomedical anthropology's mission to understand the evolutionary and cultural factors underlying human disease. Although these factors are interrelated, within biomedical anthropology the biocultural and evolutionary approaches provide insights into the population-level expression of disease from somewhat different perspectives.

The Biocultural Approach

The *biocultural approach* recognizes that when we are looking at something as complex as human illness, both biological and cultural variables offer important insights. The biocultural view recognizes that human behavior is shaped by both our evolutionary and our cultural histories and that both our biology and behavior influence the expression of disease at both the individual and population levels (Wiley, 2004; Wiley & Allen, 2013).

An example of an illness that can be understood only in light of both biology and culture is *anorexia nervosa*, a kind of self-starvation in which a person fails to maintain a minimal normal body weight, is intensely afraid of gaining weight, and exhibits disturbances in the perception of his or her body shape or size (Figure 15.3) (American Psychiatric Association, 1994). The anorexic person fights weight gain by not eating, purging (vomiting) after eating, or exercising excessively. The prevalence rate for anorexia is about 0.5% to 1.0%; about 90% of sufferers are female. Anorexia is a serious illness with both long- and short-term increases in mortality. For example, at 6–12 years' follow-up after diagnosis, the mortality rate is 9.6 times the expected rate (Nielsen, 2001). This increase in mortality is caused by a wide range of health problems, potentially involving several organ systems (Mitchell & Crow, 2006). Based on family and twin studies, it is clear that genetics likely plays a role in the development of anorexia, but there has been little success in identifying specific genes or alleles that are involved (Starr & Kreipe, 2014). There is some evidence that anorexia and depression share some underlying genetic risk factors. At this point, the complex interplay between genes and the environment in causing anorexia poses a major clinical research problem.

Figure 15.3 A teenaged girl with anorexia.



An ideal of female attractiveness emphasizing thinness has long been thought to provide a cultural stress leading to the development of anorexia; however, anorexia nervosa was first described in the nineteenth century, long before thinness was a Western cultural ideal (Brumberg, 1989). It is clear that the thinness ideal shapes preferred body images today and is an important part of the Western cultural environment in which anorexia develops. Anorexia is also found in non-Western cultures. However, anorexic patients in Hong Kong, who may strive for thinness, tend not to have the “fat phobia” we associate with Western anorexia but rather exhibit a generalized avoidance of eating (Katzman & Lee, 1997). There is cross-cultural evidence that even though anorexia is not limited to Western cultures, the focus on fat is shaped by the Western cultural concerns with obesity, thinness, and weight loss. In the Pacific island nation of Fiji television was not introduced until the 1990s. For the first time, Western ideals of thinness and were made widely available to young Fijian women. Research in the years subsequent to the introduction of television has shown television was accompanied by increases in dieting and body dissatisfaction within this group (Becker, 2004).

Most young women maintain their body weight without starving themselves, habitually purging, or even dieting. In a 1-year longitudinal study of the eating and dieting habits of 231 American adolescent girls, medical anthropologist Mimi Nichter and colleagues (1995) showed that most of the subjects maintained their weight by watching what they eat and trying to follow a healthful lifestyle rather than taking more extreme measures. Anthropological studies such as this are important because clinicians are not as interested in what the healthy population is doing, and they help to provide a biocultural context for the expression of disease.

The Evolutionary Approach

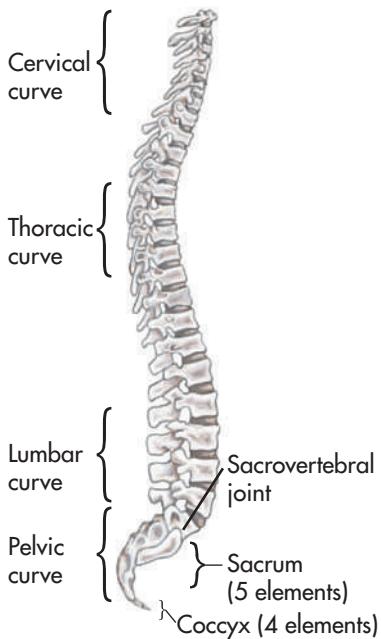
Biological anthropologists have long looked at disease from an evolutionary perspective. In the 1990s, Randolph Nesse and George C. Williams (1994) coined the term *evolutionary medicine* to describe a “Darwinian approach” to understanding disease. Nesse and Williams argued that the evolutionary perspective provides several insights into the expression of disease.

- *Defenses versus defects.* Every disease produces certain signs and symptoms. A *defect* results from the disease process itself, whereas a *defense* is a part of the body’s attempt to fight the disease. For example, a fair-skinned person with pneumonia may have a cough and darkening skin color. The darkening skin color is a defect, caused by the fact that the person’s hemoglobin is not carrying sufficient oxygen. The cough is a defense—an adaptation—that evolved as a mechanism to eject infectious material from the throat and lungs.
- *Infection and arms races.* The environment is filled with infectious agents or **pathogens**, such as bacteria and viruses. As our bodies evolve defenses to fight them, they too are evolving to combat our defenses. A familiar example is the evolution of *antibiotic resistance* in bacteria. Antibiotics were first introduced in the 1930s. By 1944, some strains of staphylococcal bacteria were showing signs of resistance to penicillin, and today 95% are penicillin resistant. As a result we have to use other antibiotics to fight them.
- *Environmental mismatch.* Human bodies did not evolve to deal with most aspects of modern life, including fatty diets, low reproductive rates, and noise. Thus certain diseases may be considered to be the result, in whole or part, of the mismatch between our bodies, adapted for life in a hunter-gatherer environment, and our contemporary environments. We will discuss examples of these diseases later in the chapter.
- *Pleiotropic gene effects.* We have many genes or alleles that probably did not lead to adaptations in past environments but were simply harmless. However, in

pathogens

Organisms and entities that can cause disease.

Figure 15.4 The S-curve in the human vertebral column—a result of the evolution of bipedality—makes humans highly susceptible to back injury and pain.



modern environments these genes may be expressed in new ways. For example, because we now live longer, we have to deal with genes that cause diseases such as Alzheimer disease and cancer, which are typically expressed only in old age.

- *Design compromises.* A classic example of an evolutionary design compromise leading to human suffering is back pain. The S-shaped spine we evolved in order to walk upright clearly predisposes us to developing back pain (Figure 15.4). This shape, combined with a sedentary lifestyle, causes 50% to 80% of all people in industrialized society to suffer from lower back pain at some point in their lives (Anderson, 1999).

Biomedical anthropology sits at the intersection of evolutionary and biocultural approaches to health and illness. A central concept of biomedical anthropology is adaptation. As we have discussed in previous chapters, an adaptation is a feature or behavior that serves over the long term to enhance fitness in an evolutionary sense. But we can also look at adaptation in the short term; this is known as *adaptability*. The life history stages that all people go through have been shaped by natural selection, but our biology must be flexible enough to cope with the different environmental challenges we will face over a lifetime.

Birth, Growth, and Aging

15.3 Describe the unique challenges of human birth and summarize the stages of human growth and development and the secular trend in growth.

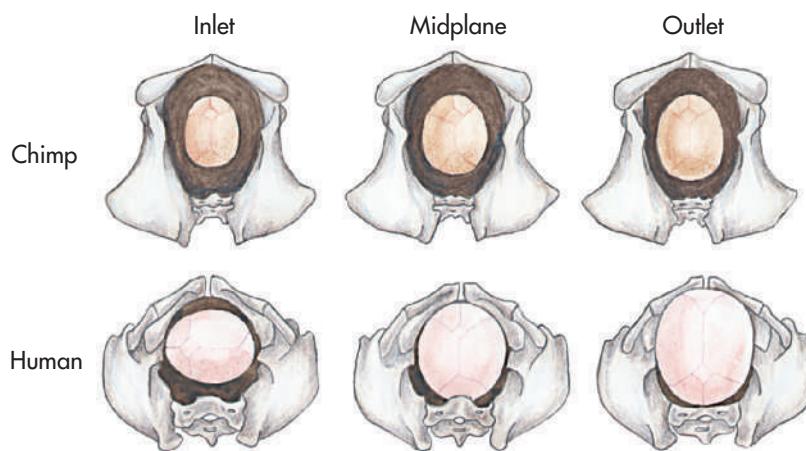
All animals go through the processes of birth, growth, and aging. Normal growth and development are not medical problems per se, but the process of growth is a sensitive overall indicator of health status (Tanner, 1990). Therefore, studies of growth and development in children provide useful insights into the nutritional or environmental health of populations.

Human Childbirth

Nothing should be more natural than giving birth. After all, the survival of the species depends on it. However, in industrialized societies birth usually occurs in hospitals. Of the more than 4 million births in the United States in 2000, more than 90% occurred in hospitals; between 1996 and 2009, Cesarean rates increased from 20.7% to 32.9% and has stabilized since (Kozhimannil et al., 2014). This rate is not extraordinary among developed countries: It is somewhat higher than those seen in Europe, but lower than rates in many parts of China and Latin America (Betrán et al., 2007). In 1900, only 5% of U.S. births occurred in a hospital (Wertz & Wertz, 1989). At that time, given the high risk of contracting an untreatable infection, hospitals were seen as potentially dangerous places to give birth.

Human females are not that much larger than chimpanzee females, yet they give birth to infants whose brains are nearly as large as the brain of an adult chimpanzee and whose heads are very large compared with the size of the mother's pelvis. The easiest evolutionary solution to this problem would be for women to have evolved larger pelvises, but too large a pelvis would reduce bipedal efficiency. Wenda Trevathan (1999) points out that the shape as well as the size of the pelvis is a critical factor in the delivery of a child. Not only is there a tight fit between the size of the newborn's head and the mother's pelvis, but the baby's head and body must rotate or twist as they pass through the birth canal, which is a process that introduces other dangers (such as the umbilical cord wrapping around the baby's neck). In contrast to humans, birth is easy in the great apes. Their pelvises are substantially larger relative to neonatal brain size, and the shape of their quadrupedal pelvises allows a more direct passage of the newborn through the birth canal (Figure 15.5).

Figure 15.5 Compared to a chimpanzee, the human newborn has relatively little room to spare as it passes through the birth canal.



In traditional cultures, women usually give birth with assistance from a midwife (almost always a woman). Trevathan observes that although women vary across cultures in their reactions to the onset of labor, in almost all cases, the reaction is emotion-charged and results in the mother seeking assistance from others. She hypothesizes that this behavior is a biocultural adaptation. A human birth is much more likely to be successful if someone is present to assist the mother in delivery. Part of the assistance is in actually supporting the newborn through multiple contractions as it passes through the birth canal, but much research has shown that the emotional support of mothers provided by birth assistants is also of critical importance (Klaus & Kennell, 1997). Such emotional support often is lacking in contemporary hospital deliveries, although there has been some effort in recent years to remedy this situation (Figure 15.6). It is very likely that birth for large-brained Neandertal babies was just as difficult as for modern humans (Ponce de León et al., 2008). It is interesting to consider the possibility that Neandertal mothers may have also received support from kin and others during birth.

Figure 15.6 Women giving birth in traditional cultures usually receive help from other women, or midwives. Midwife-assisted births are also becoming increasingly common in hospital settings.



Patterns of Human Growth

auxology

The science of human growth and development.

The study of human growth and development is known as **auxology**. All animals go through stages of growth that are under some degree of genetic control. However, the processes of growth and development can be acutely sensitive to environmental conditions.

Looking at human growth, we can imagine an optimal environment in which an individual will reach his or her genetic potential. However, most environments are not optimal. We can view growth responses to nonoptimal environments in two different ways (Schell, 1995). The anthropological model views the way humans grow in high-stress environments (with a lack of food, heavy infectious disease load, and pollution) in the context of nongenetic adaptation, or adaptability. Growth patterns are responses to environmental conditions, which may actually enhance survival. On the other hand, the medical approach assumes that any deviation from optimal growth patterns is evidence of ill health. The biomedical anthropological approach incorporates both these perspectives.

We chart growth and development using several different measures including height, weight, and head circumference. Cognitive skills, such as those governing the development of language, also appear in a typical sequence as the child matures. We can also assess age by looking at dentition or sexual reproductive capacity. Different parts of the body mature at different rates (Figure 15.7). For example, a nearly adult brain size is achieved very early, whereas physical and reproductive maturation all come later in childhood and adolescence.

Stages of Human Growth

In the 1960s, Adolph Schultz (1969) proposed a model of growth in primates that incorporated four stages shared by all primates (Figure 15.8). In general, as life span increases across primate species, each stage of growth increases in length as well.

THE PRENATAL OR GESTATIONAL STAGE The first stage of growth is the prenatal or gestational stage. This begins with conception and ends with the birth of the newborn. As indicated in Figure 15.8, gestational length increases across primates with increasing life span but is not simply a function of larger body size. Gibbons have a

Figure 15.7 Different parts of the body mature at different rates. “General” refers to the body as a whole: the major organ systems (nonreproductive), musculature, and blood volume.

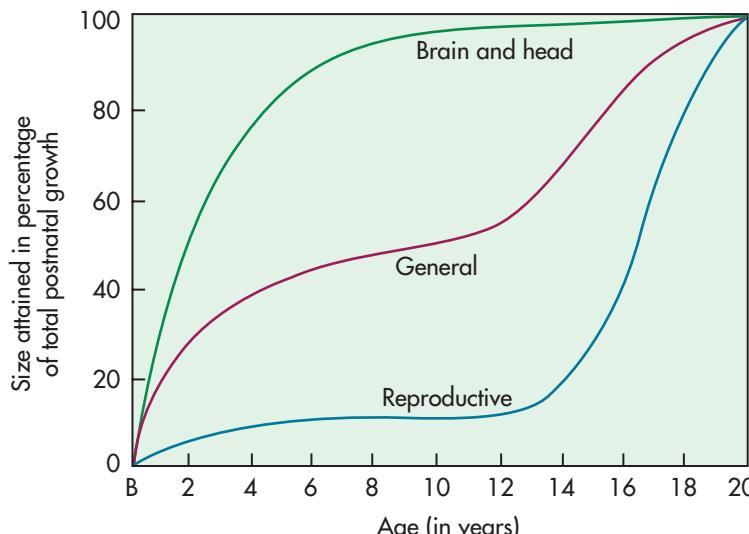
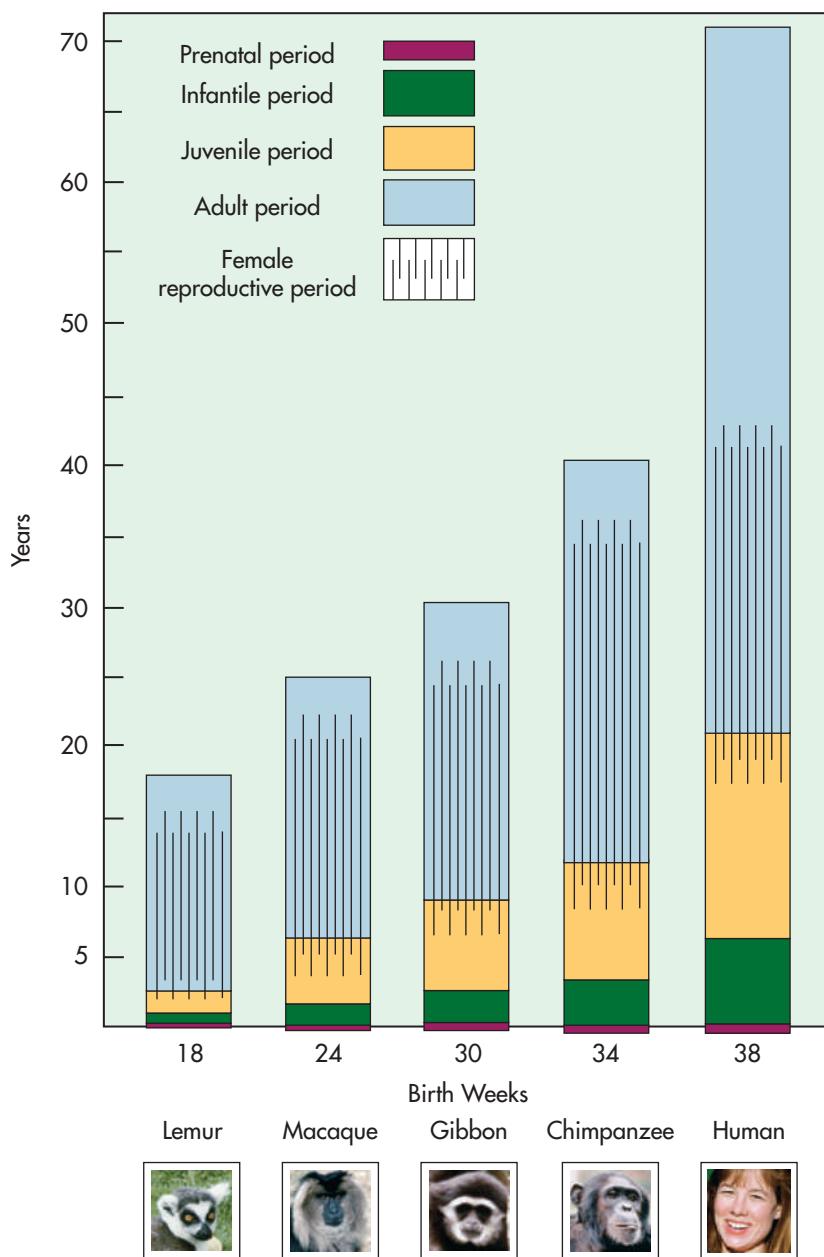


Figure 15.8 The four stages of life expressed in five different primates. Note that gestation length increases with increased life span, and the long postreproductive (female) life span observed in humans but not in other primates.



30-week gestation, compared with the approximately 25-week gestation of baboons, even though they are much smaller. Growth during the prenatal period is extraordinarily rapid. In humans, during the *embryonic stage* (first 8 weeks after conception), the fertilized ovum (0.005 mg) increases in size 275,000 times. During the remainder of the pregnancy (the *fetal period*), growth continues at a rate of about 90 times the initial weight (the weight at the end of the embryonic stage) per week, to reach a normal birth weight of about 3,200 g.

Although protected by the mother both physically and by her immune system, the developing embryo and fetus are highly susceptible to the effects of some substances in their environment. Substances that cause birth defects or abnormal development of the fetus are known as **teratogens**. The most common human teratogen is alcohol. *Fetal alcohol syndrome* (FAS) is a condition seen in children that results from

teratogens

Substances that cause birth defects or other abnormalities in the developing embryo or fetus during pregnancy.

excessive drinking of alcohol by the mother during pregnancy. At this point, it is not exactly clear what the threshold for excessive drinking is or whether binge drinking or a prolonged low level of drinking is worse for the fetus (Conover and Jones, 2012). Nonetheless, it is clear that heavy maternal drinking can lead to the development of characteristic facial abnormalities and behavioral problems in children. It is estimated that between 0.5 and 5 in 1,000 children in the United States have some form of alcohol-related birth defect. In some particularly high-risk groups, the rates are much higher. For example, surveys of Russian babies in orphanages suggest that 13% definitely have a facial phenotype consistent with FAS, while another 45% have intermediate phenotypes indicative of alcohol exposure *in utero* (Miller et al., 2006). Russia has some of the highest rates of alcohol consumption in the world.

Although they are not teratogens, other substances in the environment may affect the developing fetus. Pollutants such as lead and polychlorinated biphenyls may cause low birth weight and other abnormalities. Excessive noise in the environment has been conclusively linked to reduced prenatal growth (Schell, 1991).

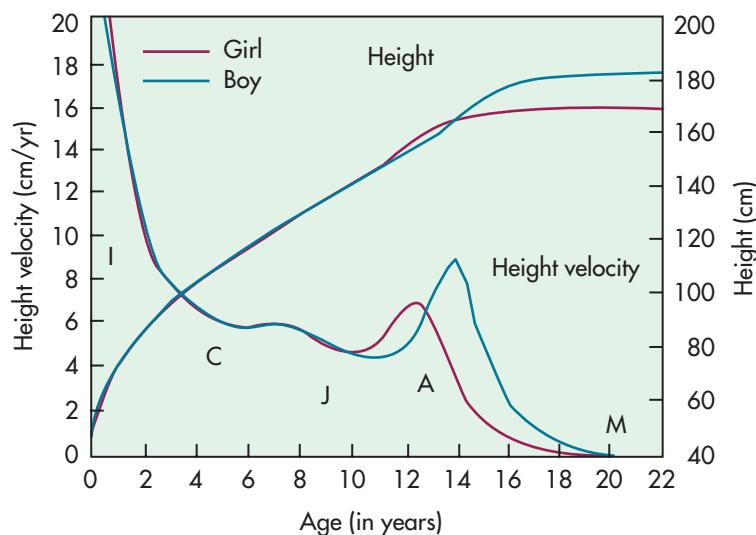
INFANCY, JUVENILE STAGE, ADOLESCENCE, AND ADULTHOOD Schultz defined the three stages of growth following birth—infancy, juvenile stage, and adulthood—with reference to the appearance of permanent teeth. Infancy lasts from birth until the appearance of the first permanent tooth. In humans, this tooth usually is the lower first molar, and it appears around 5 or 6 years of age. The juvenile stage begins at this point and lasts until the eruption of the last permanent tooth, the third premolar, which can occur anywhere between 15 and 25 years of age. Adulthood follows the appearance of the last permanent tooth.

Tooth eruption patterns provide useful landmarks for looking at stages of growth across different species of primates, but they do not tell the whole story. Besides length of stages, there is much variation in the patterns of growth and development in primate species. Barry Bogin (1999) suggests that the four-stage model of primate growth is too simple and does not reflect patterns of growth that may be unique to humans. In particular, he argues that in humans the juvenile stage does not take us all the way to adulthood. Instead we have an additional discrete stage, *adolescence*, when a growth spurt that reflects a species-specific adaptation occurs. There is a cost to a prolonged juvenile/adolescence stage because it delays the onset of full sexual maturity and the ability to reproduce. But the juvenile stage is also necessary as a training period during which younger animals can learn their adult roles and the social behaviors necessary to survive and reproduce within their own species. The evolutionary costs of delaying maturation are offset by the benefits of social life. Among mammals, the juvenile stage is longest in highly social animals, such as wolves and primates.

Bogin places the end of the juvenile period, and the beginning of adolescence, at the onset of puberty. The word *puberty* literally refers to the appearance of pubic hair, but as a marker of growth it refers more comprehensively to the period during which there is rapid growth and maturation of the body (Tanner, 1990). The age at which puberty occurs is tremendously variable both within and between populations, and even within an individual, different parts of the body may mature at different rates and times. Puberty tends to occur earlier in girls than it does in boys. In industrialized societies, almost all children go through puberty between the ages of 10 and 14 years (Figure 15.9). During adolescence, maturation of the primary and secondary sexual characteristics continues. In addition, there is an *adolescent growth spurt*. According to Bogin (1993, 1999), the expanding database on primate maturation patterns indicates that the adolescent growth spurt—and therefore adolescence—is most pronounced in humans.

Why do we need adolescence? Humans are the ultimate social animal. Bogin argues that the complex social and cultural life of humans, mediated by language, requires an adolescence, which is an extended period of social learning

Figure 15.9 The adolescent growth spurt in humans is seen as a “bump” in the height curve and a “spike” in the height velocity curve.

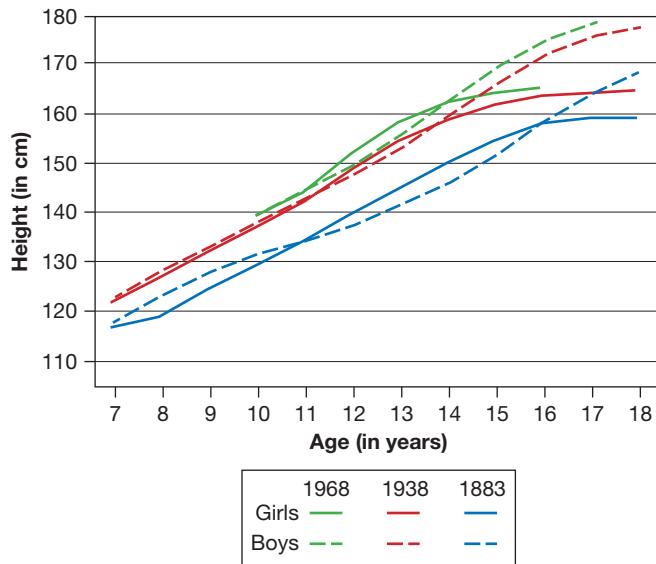


and development. In support of the view that adolescence is a period necessary for social learning, research on human brain growth has demonstrated that although approximate adult brain size is reached around 6 or 7 years of age, there is also an adolescent period of growth in the gray matter (neurons) of some parts of the brain, including the frontal and parietal lobes; lifetime peak gray matter volumes are reached at this time (Blakemore et al., 2010). The functional networks underlying social intelligence start to change during adolescence, as parts of the prefrontal cortex show an increase in activity between childhood and adolescence, followed by a decrease in the transition from adolescence to adulthood (Blakemore, 2008). This pattern suggests that with some mastery of social cognition, the networks involved become more efficient during adulthood, although there is a learning period at the onset of adolescence when they are less efficient and hence more active.

The Secular Trend in Growth

One of the most striking changes in patterns of growth identified by auxologists is the *secular trend in growth*. By using data collected as long ago as the eighteenth century, they demonstrated that in industrialized countries, children have been growing larger and maturing more rapidly with each passing decade, starting in the late nineteenth century in Europe and North America (Figure 15.10 on page 480). The secular trend started in Japan after World War II, and it is just being initiated now in parts of the developing world. In Europe and North America, since 1900, children at 5 to 7 years of age averaged an increase in stature of 1 to 2 cm per decade (Tanner, 1990). In Japan between 1950 and 1970, the increase was 3 cm per decade in 7-year-olds and 5 cm per decade in 12-year-olds. A more recent secular trend in growth has been seen in South Korea, where surveys of children conducted between 1965 and 2005 show a continuing increase in both height and weight (Kim et al., 2008). Twenty-year-old Korean men were 5.3 cm taller and 12.8 kg heavier than their 1965 counterparts; women were 5.4 cm taller and 4.1 kg heavier. The onset of puberty was clearly earlier in the 2005 group, since the greatest differences from the 1965 group were seen in the 10–15 year-old age groups. A secular trend in growth has also been documented among Bantu farmers in Cameroon in west-central Africa. Over the period 1911–2006, Bantu men increased in height from 159 cm to 172 cm, and women increased from 148 cm to 160 cm (Travaglino et al., 2011).

Figure 15.10 The secular trend in growth as measured in Swedish girls and boys between 1883 and 1968.



The secular trend in growth undoubtedly is a result of better nutrition (more calories and protein in the diet) and a reduction in the impact of diseases during infancy and childhood. We find evidence for this over the short term from *migration studies*, which have shown that changes in the environment (from a less healthful to a more healthful environment) can lead to the development of a secular trend in growth. Migration studies look at a cohort of the children of migrants born and raised in their new country and compare their growth with either their parents' growth (if the children have reached adulthood) or that of a cohort of children in the country from which they immigrated. Migration studies of Mayan refugees from Guatemala to the United States show evidence of a secular trend in growth (Bogin, 1995). Mayan children raised in California and Florida were on average 5.5 cm taller and 4.7 kg heavier than their counterparts in Guatemala.

The secular trend in growth in industrialized societies has been so pervasive that it tends to obscure variation within populations caused by socioeconomic factors (Tanner, 1990). However, we can measure the effect of the economy on child growth in some locales. Deborah Crooks (1999) looked at the growth of children in a rural, eastern Kentucky county at the edge of the Appalachian Mountains where 35% of the children live below the poverty level. Crooks found mild but persistent patterns of short stature among the children, with 21.7% of them having a stature below the fifteenth percentile of a broader U.S. sample. Among girls, stunted growth was about twice as common in this part of the county as elsewhere in the United States (9.1% versus 5%).

Although the secular trend in growth appears to highlight a straightforward relationship between increased stature and industrialization, the stature each individual achieves is the result of the complex interaction of genetics, economic status, and nutrition.

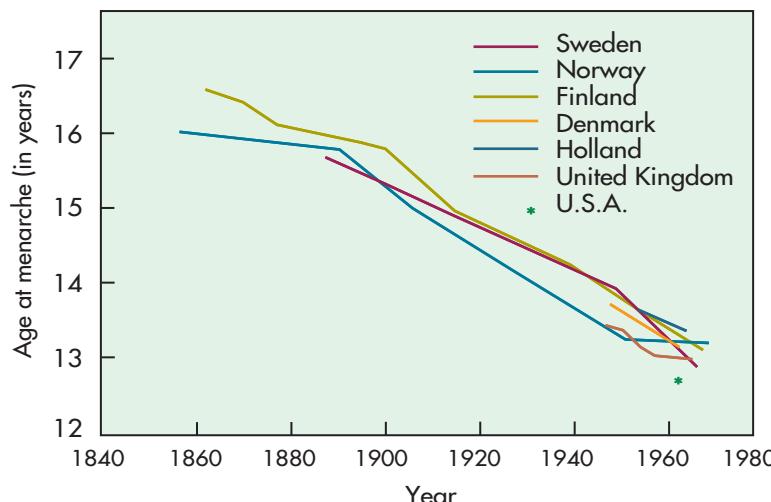
Menarche and Menopause

menarche

The onset of a girl's first menstrual period.

Another hallmark of the secular trend in growth is a decrease in the age of **menarche**—a girl's first menstrual period—seen throughout the industrialized world. From the 1850s until the 1970s, the average age of menarche in European and North American populations dropped from around 16 to 17 years to 12 to 13 years (Figure 15.11) (Tanner, 1990; Coleman & Coleman, 2002). A comprehensive study of U.S. girls

Figure 15.11 The declining age of menarche over the past 150 years has been measured in many European countries and has also been observed more recently in developing countries.



(sample size of 17,077) found that the age of menarche was 12.9 years for White girls and 12.2 years for Black girls (Herman-Giddens et al., 1997). This does not reflect a substantial drop in age of menarche since the 1960s.

In cultures undergoing rapid modernization, changes in the age of menarche have been measured over short periods of time. Among the Bundi of highland Papua New Guinea, age of menarche dropped from 18.0 years in the mid-1960s to 15.8 years for urban Bundi girls in the mid-1980s (Worthman, 1999). Over the long term, the rate of decrease in age of menarche in most of the population was in the range of 0.3 to 0.6 years per decade. For urban Bundi girls, the rate is 1.29 years per decade, which may be a measure of the rapid pace of modernization in their society.

Menarche marks the beginning of the reproductive life of women, whereas **menopause** marks its end. Menopause is the irreversible cessation of fertility that occurs in all women before the rest of the body shows other signs of advanced aging (Peccei, 2001a). Returning to Figure 15.8 on page 477, note that of all the primate species illustrated, only humans have a significant part of the life span that extends beyond the female reproductive years. In fact, as far as we know, humans are unique in having menopause (with the exception of a species of pilot whale). Menopause has occurred in the human species for as long as recorded history (it is mentioned in the Bible), and there is no reason to doubt that it has characterized older human females since the dawn of *Homo sapiens*. Although highly variable, menopause usually occurs around the age of 50 years.

Menopause occurs when women run out of eggs for ovulation. All the eggs a human female will ever have are produced during the fifth month of gestation. These eggs are in an arrested stage of meiosis and are known as *oocytes*. At birth a girl has 2 million oocytes in her ovaries, but that number drops to 400,000 at puberty. Over the course of her lifetime, a woman ovulates only about 400 mature eggs. The rest of the eggs are lost through programmed cell death or *atresia*. If human females maintained the rate of atresia they have for most of their adult life, they would have enough oocytes to last until they were 70 years old. However, the rate of atresia increases starting at age 40, with menopause resulting by about the age of 50. There is no strong evidence that the secular trend in growth has influenced the age of menopause in any way (Peccei, 2001b).

At first glance, menopause looks to be a well-defined, programmed life history stage. Why does it occur? Jocelyn Peccei (1995) suggests a combination of factors,

menopause

The postreproductive period in the lives of women, after the cessation of ovulation and menses.

Insights and Advances

Early Menarche and Later Health

An earlier age of menarche in girls is one consequence of the secular trend in growth. Many factors can influence the age at which a girl undergoes menarche. In general, the more nutritional energy available to a girl as she grows up, the earlier the age of menarche. Different amounts of calories in the diet can account for many of the differences in average age of menarche seen *between* different populations, especially comparing those that have or have not undergone a secular change in growth. Variation *within* a population, in which most people generally have access to abundant calories, can be influenced by many factors. Genetics certainly plays a role, and psychosocial stress (such as early sexual abuse) may lead to earlier menarche (Mishra et al., 2009).

Menarche is a critical developmental milestone, and the age at which it occurs is not simply a matter of personal significance for a girl: numerous studies show that earlier age of menarche increases the risk of developing a range of health problems later in life. A recent analysis of epidemiological studies looking at age of menarche and later risk of death found that each 1-year increase of age of menarche was associated with a 3% reduction in death from all causes (Charalampopoulos et al., 2014). Overall, there was a 23% higher relative risk of death for women who had early menarche (under 12 years of age), although there was not a protective effect for women who had late menarche. The increased risk of death may in part be due to a greater risk for cardiac disease, although the evidence for this is

not clear-cut. Women who had early menarche did have a 24% increased risk of coronary artery disease, but not other forms of cardiovascular disease, and this effect was only found to be true for nonsmokers.

Numerous studies have also shown that early age of menarche (among other developmental landmarks) is associated with a later increased risk of breast cancer (Vandeloo et al., 2007). This relationship may be mediated by childhood obesity, since obesity itself confers increased risk of developing breast cancer (as well as diabetes, another condition associated with early menarche). Earlier age of menarche is associated with higher body mass index (BMI), such that girls at the 75th percentile for BMI were 1.79 times as likely to have menarche before 11 years of age as girls in the lowest 25th percentile (Freedman et al., 2002). Lynn Ahmed and colleagues (2009) point out that hormonal triggers for early age of menarche may be set much earlier in development. Rapid weight gain during infancy and early childhood may program an early age of onset for puberty when a child is older.

Ahmed and colleagues acknowledge that the links between childhood obesity, early menarche, and later disease are correlational. However, these associations suggest the importance of hormonal factors in early childhood for the development of adult disease and point to potentially useful areas of investigation. A woman cannot change her age of menarche, but any woman who had an early menarche should recognize that she has an increased risk for developing some serious illnesses and may want to make lifestyle choices that serve to reduce the risk of developing those conditions.

including adaptation, physiological tradeoff, and an artifact of the extended human life span. Some adaptive models focus on the potential fitness benefits of having older women around to help their daughters raise their children, termed the *grandmothering hypothesis* (Hill & Hurtado, 1991). Kristen Hawkes (2003) proposes that menopause is the most prominent aspect of a unique human pattern of longevity and that this pattern has been shaped largely by the inclusive fitness benefits derived by postmenopausal grandmothers who contribute to the care of their grandchildren. There is some empirical support for this idea. For example, a study of Finnish and Canadian historical records indicates that women who had long postreproductive lives had greater lifetime reproductive success (Lahdenpera et al., 2004).

Peccei suggests that an alternative to the grandmothering hypothesis may be more plausible: the mothering hypothesis. She argues that the postreproductive life span of women allows them to devote greater resources to the (slowly maturing) children they already have and that this factor alone could account for the evolution of menopause. This hypothesis is supported by population data from Costa Rica covering maternal lineages dating from the 1500s until the 1900s (Madrigal and Meléndez-Obando, 2008). These data showed that the longer a mother lived, the higher her fitness; however, there was a negative effect on her daughter's fitness. Thus there was support for the mothering hypothesis but not the grandmothering hypothesis. Clearly, more research needs to be done in this area. The relationship between maternal

longevity and reproductive fitness is complex, and we will need data from many populations before there is a general perspective on that relationship in the human species as a whole.

Aging

Compared with almost all other animal species, humans live a long time, at least as measured by maximum life span potential (approximately 120 years). But the human body begins to age, or to undergo **senescence**, starting at a much younger age. Many bodily processes actually start to decline in function starting at age 20, although the decline becomes much steeper starting between the ages of 40 and 50 (Figure 15.12). The physical and mental changes associated with aging are numerous and well known, either directly or indirectly, to most of us (Schulz & Salthouse, 1999).

Why do we age? We can answer from both the physiological and the evolutionary standpoints (Figure 15.13 on page 484). From a physiological perspective, several hypotheses or models of aging have been offered (Nesse & Williams, 1994; Schulz & Salthouse, 1999). Some have focused on DNA, with the idea that over the lifetime, the accumulated damage to DNA, in the form of mutations caused by radiation and other forces, leads to poor cell function and ultimately cell death. Higher levels of DNA repair enzymes are found in longer-lived species, so there may be some validity to this hypothesis, although in general the DNA molecule is quite stable. Support for the DNA damage theory of aging comes from a rare (1 in 10 million people) autosomal recessive disorder known as *Werner syndrome* (Kirkwood, 2002). When they are young, people with this condition suffer from a variety of ailments that are common in the elderly (such as cataracts and osteoporosis). Werner syndrome is caused by an abnormal form of the enzyme *helicase*, which unwinds DNA during replication, repair, and gene expression.

Another model of aging focuses on the damage that *free radicals* can do to the tissues of the body (Finkel & Holbrook, 2000). Free radicals are molecules that contain at least one unpaired electron. They can link to other molecules in tissues and thereby cause damage to those tissues. Oxygen free radicals, which result from the process of oxidation (as the body converts oxygen into energy), are thought to be the main culprit for causing the bodily changes associated with aging. Antioxidants, such as vitamins C and E, may reduce the effects of free radicals, although there is no evidence

senescence

Age-related decline in physiological or behavioral function in adult organisms.

Figure 15.12 The effects of aging can be seen in the decline in function of many physiological systems.

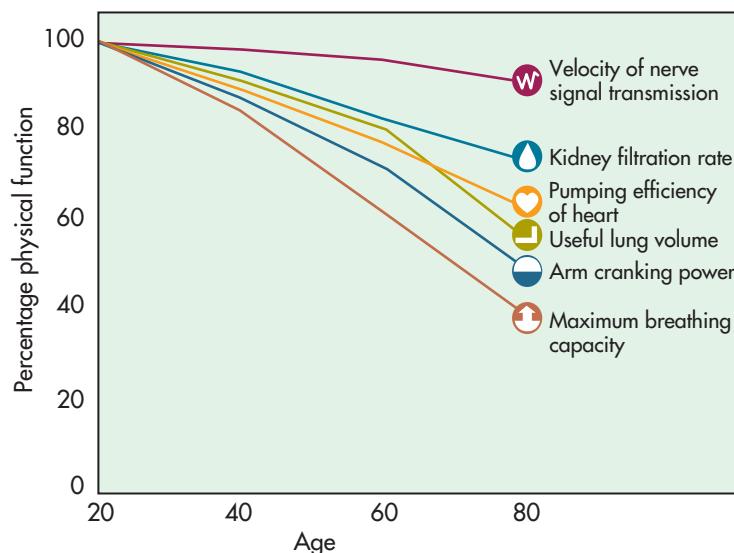
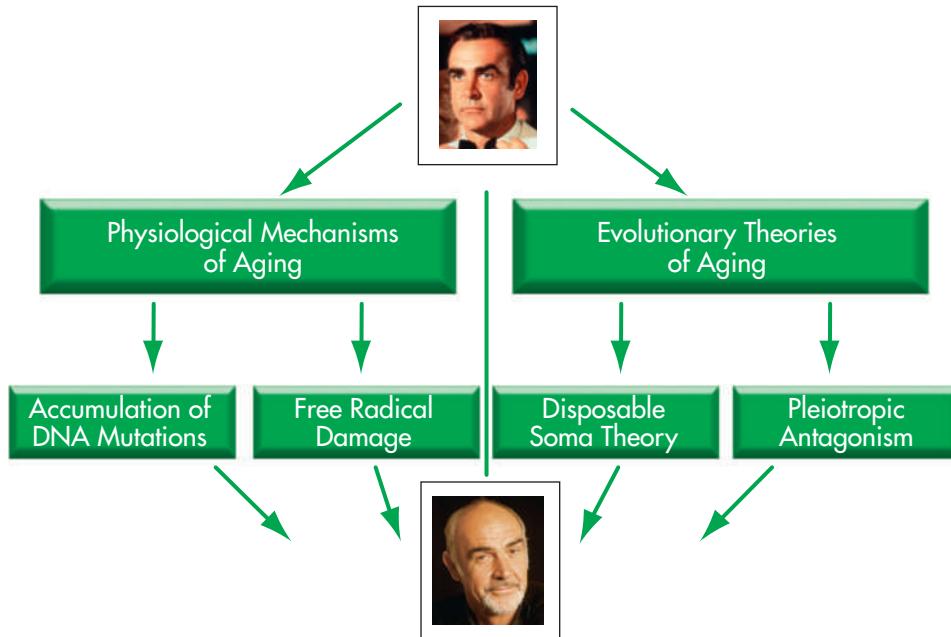


Figure 15.13 Physiological and evolutionary theories of aging.

as yet that they slow the aging process. Further evidence for the free radical theory of aging comes from diseases in which the production of the body's own antioxidants is severely limited. These diseases seem to mimic or accelerate the aging process. For example, an enzyme called *superoxide dismutase* (SOD) is an antioxidant usually produced by our bodies. People who do not make this enzyme (they are homozygous for an abnormal SOD gene) develop a familial form of the degenerative nerve disease *amyotrophic lateral sclerosis* (Lou Gehrig's disease). Both the DNA and free radical models of aging emphasize that the damage caused by these processes accumulates over the lifetime.

In wild populations, aging is not a major contributor to mortality: Most animals die of something other than old age, as humans did before the modern age. Thus aging per se could not have been an adaptation in the past because it occurred so rarely in the natural world (Kirkwood, 2002). Two nonadaptive evolutionary models of aging are the *disposable soma hypothesis* (Kirkwood & Austad, 2000) and the *pleiotropic gene hypothesis* (Williams, 1957; Nesse & Williams, 1994). Both take the position that old organisms are not as evolutionarily important as young organisms. The disposable soma theory posits that it is more efficient for an organism to devote resources to reproduction rather than to maintenance of a body. After all, even a body in perfect shape can still be killed by an accident, predator, or disease. Therefore, organisms are better off devoting resources to getting their genes into the next generation rather than fighting the physiological tide of aging.

The pleiotropic gene theory has a similar logic, although it comes at the problem from a different angle. *Pleiotropy* refers to the fact that most genes have multiple phenotypic effects. For all organisms, the effects of natural selection are more pronounced based on the phenotypic effects of the genes during the earliest rather than later phases of reproductive life. The simple reason for this is that a much higher proportion of organisms live long enough to reach the early reproductive phase than do the proportion who survive until the late reproductive phase. For example, imagine that a gene for calcium metabolism helps a younger animal heal more quickly from wounds and thus increase its fertility (Nesse & Williams, 1994). A pleiotropic effect of that

same gene in an older animal might be the development of calcium deposits and heart disease; this aged effect has little influence on the lifetime fitness of the animal. Aging itself may be caused by the cumulative actions of pleiotropic genes that were selected for their phenotypic effects in younger bodies but have negative effects as the body ages. A key point of the pleiotropic model of aging is that you cannot select against senescence because the effects of natural selection are always more pronounced earlier rather than later in the life span.

Infectious Disease and Biocultural Evolution

15.4 Describe the human biological response to infectious disease and the ways cultural environments shape the arms race between humans and pathogens.

Our bodies provide the living and reproductive environment for a wide variety of viruses, bacteria, single-celled eukaryotic parasites, and more biologically complex parasites, such as worms. As we evolve defenses to combat these disease-causing organisms, they in turn are evolving ways to get around our defenses. Understanding the nature of this arms race and the environments in which it is played out may be critical to developing more effective treatments in the future.

Infectious diseases are those in which a biological agent, or pathogen, parasitizes or infects a *host*. Human health is affected by a vast array of pathogens. These pathogens usually are classified taxonomically (such as bacteria or viruses), by their *mode of transmission* (such as sexually transmitted, airborne, or waterborne), or by the organ systems they affect (such as respiratory infections, encephalitis, or food poisoning for the digestive tract). Pathogens vary tremendously in their survival strategies. Some pathogens can survive only when they are in a host, whereas others can persist for long periods of time outside a host. Some pathogens live exclusively within a single host species, whereas others can infect multiple species or may even depend on different species at different points in their life cycle.

Human Behavior and the Spread of Infectious Disease

Human behavior is one of the critical factors in the spread of infectious disease. Actions we take every day influence our exposure to infectious agents and determine which of them may or may not be able to enter our bodies and cause an illness. Food preparation practices, sanitary habits, sex practices, whether one spends time in proximity to large numbers of adults or children—all these can influence a person's chances of contracting an infectious disease. Another critical factor that influences susceptibility to infectious disease is overall nutritional health and well-being. People weakened by food shortage, starvation, or another disease (such as cancer) are especially vulnerable to infectious illness (Figure 15.14). For example, rates of tuberculosis in Britain started to decline in the nineteenth century before the bacteria that caused it was identified or effective medical treatment was developed. This decline was almost certainly due to improvements in nutrition and hygiene (McKeown, 1979).

Just as individual habits play an important role in the spread of infectious disease, so can widespread cultural practices. Sharing a communion cup has been linked to the spread of bacterial infection, as has the sharing of a water source for ritual washing before prayer in poor Muslim countries (Mascie-Taylor, 1993). Cultural biases against homosexuality and the open discussion of sexuality gave shape to the entire AIDS epidemic, from its initial appearance in gay communities to delays by leaders in acknowledging the disease as a serious public health problem. A fascinating example of the influence of cultural practices on the spread of an infectious disease involves

Figure 15.14 A child suffering from malaria, one of the most common and deadly infectious diseases.



a condition known as *kuru* (see Insights and Advances: Kuru, Cannibalism, and Prion Diseases).

AGRICULTURE Agricultural populations are not necessarily more vulnerable to infectious disease than hunter-gatherer populations. However, larger and denser agricultural populations are likely to play host to all the diseases that affect hunter-gatherer populations and others that can be maintained only in larger populations. This is the basis of the first epidemiological transition discussed earlier. For example, when a child is exposed to measles, his or her immune system takes about 2 weeks to develop effective antibodies to fight the disease. This means that in order to be maintained in a population, the measles virus needs to find a new host every 2 weeks; in other words, there must be a pool of twenty-six new children available over the course of a year to host the measles virus. This is possible in a large agricultural population but almost impossible in a much smaller hunter-gatherer population (Figure 15.15).

Agricultural and nonagricultural populations also differ in that the former tend to be sedentary, whereas the latter tend to be nomadic. Large, sedentary agricultural populations therefore are more susceptible to bacterial and parasitic worm diseases that are transmitted by contact with human waste products. In addition, many diseases are carried by water, and agricultural populations are far more dependent on a limited number of water sources than nonagricultural populations. Finally, agricultural populations often have domestic animals and also play host to a variety of commensal animals, such as rats, all of which are potential carriers of diseases that may affect humans.

Specific agricultural practices may change the environment and encourage the spread of such infectious diseases as sickle cell and malaria. Slash-and-burn agriculture leads to more open forests and standing pools of stagnant water. Such pools are an ideal breeding ground for the mosquitoes that carry the protozoa that cause malaria. Agriculture that makes extensive use of irrigation and water damming brings people into contact with large flatworms of the genus *Schistoma*.

These flatworms cause a disease known as *schistosomiasis*, which is often characterized by blood in the urine. *Schistoma* species have an extraordinary life cycle that involves several distinct stages lived both inside and outside its two hosts: humans and a particular snail species. Schistosomiasis can damage the bladder, kidney, liver, spleen, and intestines. The World Health Organization estimates that 200 million people may be infected with the parasite (85% of whom live in Africa) and that 200,000

Figure 15.15 Risks of infectious disease increase in (a) high-density agricultural populations compared to (b) low-density, dispersed hunter-gatherer populations.



(a)



(b)

die annually from its effects (Figure 15.16). The genome of one of the flatworms that causes schistosomiasis (*Schistosoma mansoni*) has recently been sequenced, and it is hoped that this information will lead to the development of better medicines to treat this sometimes neglected tropical disease (Berriman et al., 2009).

MOBILITY AND MIGRATION The human species is characterized by its mobility. One price of this mobility has been the transmission of infectious agents from one population to another, leading to uncontrolled outbreaks of disease in the populations that have never been exposed to the newly introduced diseases. These are referred to as *virgin soil epidemics*.

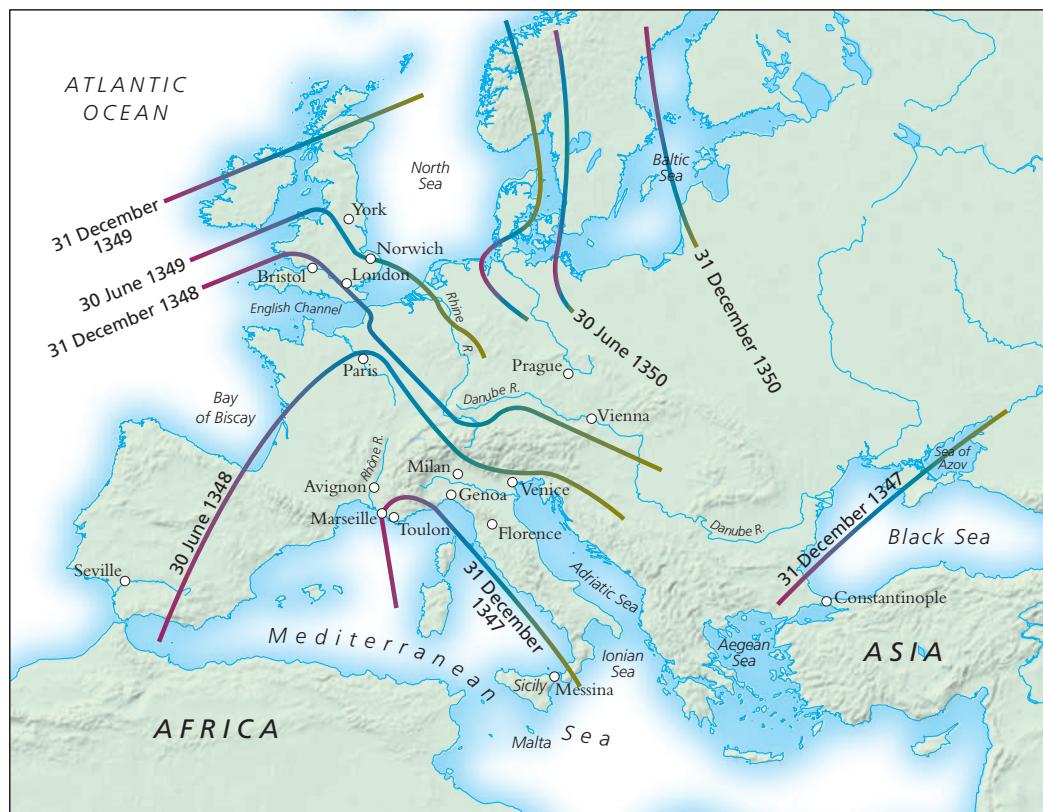
The Black Death in Europe (1348–1350) is one example of just such an outbreak (Figure 15.17). The Black Death was bubonic plague, a disease caused by the bacterium *Yersinia pestis*. The bacterium is transmitted by the rat flea, which lives on rats. When the fleas run out of rodent hosts, they move to other mammals, such as humans. The bacteria can quickly overwhelm the body, causing swollen lymph nodes (or *buboes*, hence the name) and in more severe cases lead to infection of the respiratory system and blood. It can kill very quickly. An outbreak of bubonic plague was recorded in China in the 1330s, and by the late 1340s it had reached Europe. In a single Italian city, Florence, a contemporary report placed the number dying between March and October 1348 at 96,000. By the end of the epidemic, one-third of Europeans (25–40 million) had been killed, and the economic and cultural life of Europe was forever changed.

Similar devastation awaited the native peoples of the New World after 1492 with the arrival of European explorers and colonists. Measles, smallpox, influenza, whooping cough, and sexually transmitted diseases exacted a huge toll on native populations throughout North and South America, the Island Pacific, and Australia. Some populations were completely wiped out, and others had such severe and rapid population

Figure 15.16 Two children with schistosomiasis.



Figure 15.17 The Black Death spread over much of Europe in a 3-year period in the middle of the fourteenth century.



Insights and Advances

Kuru, Cannibalism, and Prion Diseases

One of the most striking examples of a specific cultural practice contributing to the spread of an infectious disease is the case of *kuru*, a disease that once afflicted members of the Fore tribe in highland New Guinea (Gajdusek & Zigas, 1957; Goldfarb, 2002). *Kuru* is a progressive neuromuscular disorder that advances from tremors in the arms and legs to total paralysis over the course of a year (Figure A). Behavioral changes, such as dementia, accompany the physical changes.

The *kuru* epidemic among the Fore started in the early twentieth century, and by the mid-1940s there were more than 200 new cases a year appearing in a population of only about 12,000 individuals. Over the course of the epidemic, approximately 3,000 people were killed by *kuru*, all of them members of the Fore ethnic group or related in some way. About three-quarters of the victims were women, with children forming the next largest group afflicted.

Because *kuru* tended to appear in families, it was initially thought to be a genetic disease. Scientific investigation of *kuru* started in the late 1950s, which was about the same time as the sickle cell trait and anemia balanced polymorphism was being worked out. Therefore, it is not surprising that some investigators suggested *kuru* was also being maintained as a balanced polymorphism of some kind. They were shown to be wrong, however, when Carleton Gajdusek and colleagues (1966) demonstrated that they could transmit *kuru* to chimpanzees by injecting them with tissue extracts from *kuru* victims.

We now know that *kuru* is a *prion disease*, one of a family of diseases that affect the tissues of the brain leading to both muscular degeneration and behavioral

abnormalities (Sy et al., 2002). They are also called transmissible spongiform encephalopathy (TSE) diseases and are almost always fatal. All humans and many other mammals make the prion protein, especially in brain tissue. The exact function of the protein is still unknown.

Prion diseases can be genetic: A mutation in the prion gene can lead to familial versions of TSE diseases (such as *fatal familial insomnia*), and spontaneous mutations in the prion gene are also a major cause. However, the striking thing about prion diseases is that they are also communicable. If a person with a normal prion protein is exposed to the abnormal, disease-causing prion protein, the abnormal prion protein can “seed” a transformation of the normal protein to the disease-causing form, leading to the development of a TSE disease. Unlike bacteria or viruses, the prion is a transmissible infectious agent that spreads without the use of a nucleic acid.

Kuru in the Fore people probably can be traced back to a mutation that arose in the prion gene of a person living sometime at the end of the nineteenth century. But it did not spread through the population as a genetic disease would have. Instead, the transmission of *kuru* in the Fore was caused almost entirely by ritual cannibalism undertaken during funeral rites, usually by relatives of the deceased. Such rites were almost always directed by women, and cannibalism was considered to be in the women’s domain. Young children accompanying their mothers and other relatives also consumed human flesh (the youngest *kuru* victim recorded was 4 years old). Although other groups living near the Fore also practiced ritual cannibalism, the disease was found only among the Fore or those who were related to the Fore in some way.

The Fore stopped practicing cannibalism in the 1950s, and *kuru* has largely disappeared. No person born after 1960 has had the disease. However, sporadic cases occur from time to time in older individuals. This is an indication of the long latency period that can occur in these prion diseases. TSE diseases are quite rare, and although protein-based infectivity is biologically fascinating, there was no reason to view prion diseases as a public health threat. This all changed in the 1990s, when it was shown that *bovine spongiform encephalopathy* (BSE), or mad cow disease, can lead to the development of prion disease in humans who have consumed beef or other products derived from a cow with BSE. *Kuru* went from being an example of biomedical exotica of historical interest to a model for a disease with potentially major economic and public health ramifications (Lindenbaum, 2001).



Figure A A victim of *kuru*.

depletion that their cultures were destroyed. In North America, for example, many communities of native peoples lost up to 90% of their population through the introduction of European diseases (Pritzker, 2000). Infectious diseases often reached native communities before the explorers or colonizers did, giving the impression that North America was an open and pristine land waiting to be filled.

Infectious Disease and the Evolutionary Arms Race

As a species, we fight infectious diseases in many ways. However, no matter what we do, parasites and pathogens continuously evolve to overcome our defenses. Over the last 50 years, it appeared that medical science was gaining the upper hand on infectious disease, at least in developed countries. However, despite real advances, infectious diseases such as the viruses that cause AIDS and Ebola and antibiotic-resistant bacteria remind us that this primeval struggle will continue.

THE IMMUNE SYSTEM One of the most extraordinary biological systems that has ever evolved is the vertebrate immune system, the main line of defense in the fight against infectious disease. At its heart is the ability to distinguish self from nonself. The immune system identifies foreign substances, or **antigens**, in the body and synthesizes **antibodies**, which comprise a class of proteins known as **immunoglobulins**, which are specifically designed to bind to and destroy specific antigens (Figure 15.18).

Antibodies are produced by white blood cells known as *B lymphocytes*. These originate in the bone marrow and circulate between lymph tissue and the bloodstream. Another class of lymphocytes, *T cells*, is also critical in the immune response. *Helper T cells* lead to the activation of *B lymphocytes* to produce antibodies and stimulate the production of specialized cells called *phagocytes*, which destroy infectious agents, such as viruses, by engulfing and destroying them. One of the most extraordinary qualities of the immune system is its ability to remember previous exposures to an antigen, thus priming the system for future exposures to the antigen. This is the immunological basis of *vaccination* (discussed in more detail in the next section), whereby exposure to

antigens

Whole or part of an invading organism that prompts a response (such as production of antibodies) from the body's immune system.

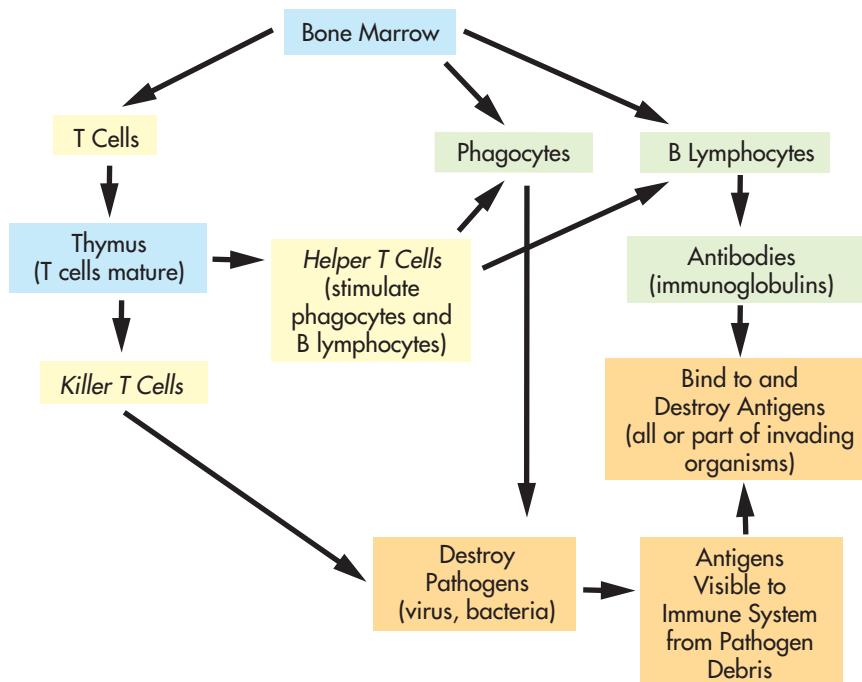
antibodies

Proteins (immunoglobulins) formed by the immune system that are specifically structured to bind to and neutralize invading antigens.

immunoglobulins

Proteins produced by B lymphocytes that function as antibodies.

Figure 15.18 The immune system has several different components that work in concert.



a killed or inactivated form of an antigen, such as a virus, protects an individual from developing an illness upon later exposure to the active form of the antigen. The memory function of the immune system is carried out by specialized T and B lymphocytes.

The immune system is a complex mechanism that has evolved to deal with the countless number of potential antigens in the environment. An example of what happens when just one of the components of the immune system is not functioning occurs in AIDS. The *human immunodeficiency virus* (HIV) that causes AIDS attacks the helper T cells. As mentioned earlier, the helper T cells respond to antigens by inducing the B lymphocytes to produce antibodies, leading to the production of phagocytes; when their function is compromised, the function of the entire immune system is also compromised. This leaves a person with HIV infection vulnerable to a host of opportunistic infections, a condition that characterizes the development of full-blown AIDS.

CULTURAL AND BEHAVIORAL INTERVENTIONS Although the immune system does a remarkable job fighting infectious disease, it is obviously not always enough. Even before the basis of infectious diseases was understood, humans took steps to limit their transmission. Throughout the Old World, people with leprosy were shunned and forced to live apart from the bulk of the population. This isolation amounted to *quarantine*, in recognition of the contagious nature of their condition.

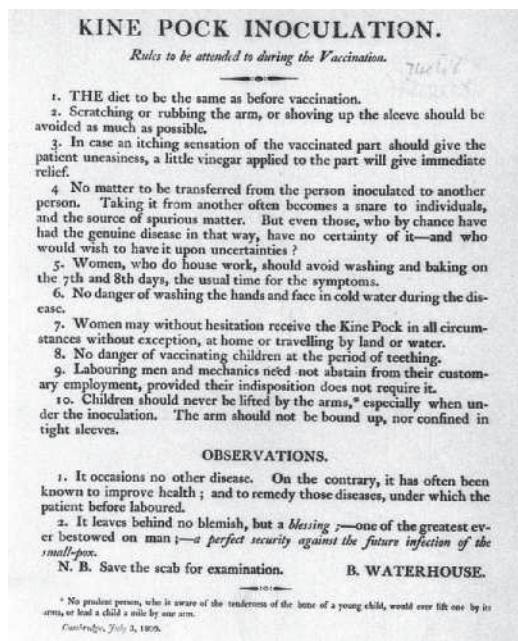
One of the most effective biocultural measures developed to fight infectious diseases is vaccination. The elimination of *smallpox* as a scourge of humanity is one of the great triumphs of widespread vaccination. Smallpox is a viral illness that originated in Africa some 12,000 years ago and subsequently spread throughout the Old World (Barquet & Domingo, 1997). It was a disfiguring illness, causing pustulant lesions on the skin, and it was often fatal. Smallpox killed millions of people upon its introduction to the New World; in the Old World, smallpox epidemics periodically decimated entire populations. In A.D. 180, a smallpox epidemic killed between 3.5 and 7 million people in the Roman Empire, precipitating the first period of its decline.

Numerous remedies were used to combat the spread of smallpox. In some cultures, children were exposed to people with mild cases of smallpox in the hopes that it would strengthen their resistance to the disease. In China, powdered scabs of smallpox sores were blown into the nostrils of healthy people. Women in the harems of the Turkish Ottoman Empire were inoculated on parts of their body where the smallpox scars (which result in the area of the vaccination) could not be seen. The Turkish method was to make four or five small scratches on the skin and introduce some pus from an infected person into them. This method was introduced to England (and Western medicine) in the early eighteenth century, and early medical statisticians verified its success at preventing the development of serious forms of the illness (although 23% of the people vaccinated by this method died). We now have much safer forms of vaccination against smallpox, which have led to the total eradication of this horrible disease (Figure 15.19).

The most recently developed forms of intervention against infectious disease are drug based. The long-term success of these drugs will depend on the inability of the infectious agents to evolve resistance to their effects. Overuse of anti-infectious drugs may actually hasten the evolution of resistant forms by intensifying the selection pressures on pathogens.

EVOLUTIONARY ADAPTATIONS The immune system is the supreme evolutionary adaptation in the fight against infectious disease. However, specific adaptations to disease that do not involve the immune system are also quite common (Jackson, 2000). For example, a class of enzymes known as *lysozymes* attacks the cell wall structure of some bacteria.

Figure 15.19 Early instructions for administration of the smallpox vaccine. Note in the last lines that the vaccine was considered to be a blessing.



Lysozymes are found in high concentrations in the tear ducts, salivary glands, and other sites of bacterial invasion.

The sickle-cell allele has spread in some populations because it functions as an adaptation against malaria. Another adaptation to malaria is the Duffy blood group (see Chapter 5). In Duffy-positive individuals, the proteins Fya and Fyb are found on the surface of red blood cells. These proteins facilitate entry of the malaria-causing protozoan *Plasmodium vivax*. Duffy-negative individuals do not have Fya and Fyb on the surface of their red blood cells, so people with this phenotype are resistant to vivax malaria. Many Duffy-negative people are found in parts of Africa where malaria is common; others, who live elsewhere, have African ancestry.

Diet and Disease

15.5 Compare and contrast Paleolithic and agricultural diets, and recognize the implications for switching from one to the other on human health.

It seems that there are always conflicting reports on what particular parts of our diet are good or bad for us. Carbohydrates are good one year and bad the next. Fats go in and out of fashion. Cholesterol has gone from being just a molecule to being a nutritional boogeyman, to be avoided via the consumption of low-cholesterol and cholesterol-free foods. From a biocultural anthropological perspective, American attitudes toward diet and health at the turn of the twenty-first century provide a rich source of material for analysis (Allen, 2012).

Despite all the confusion about diet, we all have the same basic nutritional needs. We need energy (measured in calories or kilojoules) for body maintenance, growth, and metabolism. Carbohydrates, fat, and proteins are all sources of energy. We require protein for tissue growth and repair. In addition to energy, fat provides us with essential fatty acids important for building and supporting nerve tissue. We need vitamins, which basically are organic molecules that our bodies cannot synthesize yet are essential in small quantities for a variety of metabolic processes. We also need a certain quantity of inorganic elements, such as iron and zinc. For example, with insufficient iron, the ability of red blood cells to transport oxygen is compromised, leading to anemia. Finally, we all need water to survive.

Over the past three decades, scientists have tried to reconstruct a typical *Paleolithic diet*, which theoretically reflects the kinds of foods people ate during the pre-agricultural part of human history. Many researchers believe that our bodies are evolved for functioning in this kind of nutritional environment. From the perspective of the human diet, agriculture changed everything. New foods were introduced, but variety was lost, and problems associated with specific dietary deficiencies (other than total calories) became common in some agricultural populations. Ultimately, however, the legacy of modern agriculture is not scarcity but abundance, and, as a species, we are not particularly well adapted to living in an environment of continuous nutritional abundance.

The Paleolithic Diet

For most of human history, people lived in small groups and subsisted on wild foods that they could collect by hunting or gathering. Obviously, diets varied in different areas: Sub-Saharan Africans were not eating the same thing as Native Americans on the northwest Pacific coast. Nonetheless, S. Boyd Eaton and Melvin Konner (Eaton & Konner, 1985; Eaton et al., 1999) argue that we can reconstruct an *average* Paleolithic diet from a wide range of information derived from paleoanthropology, epidemiology, and nutritional studies. A comparison of the average Paleolithic and contemporary diets is presented in Table 15.2 on page 492 (Eaton et al., 1999).

Table 15.2 Comparison of Paleolithic and Contemporary Diets

| Dietary Component | Paleolithic Diet | Contemporary Diet |
|---|--|---|
| Energy (calories) | High caloric intake and expenditure to support active lifestyle and large body size. | More sedentary lifestyle uses fewer calories, yet caloric consumption often exceeds expenditure. |
| Micronutrients (vitamins, antioxidants, folic acid, iron, zinc) | High consumption (65–70% of diet) of foods rich in micronutrients, such as fruits, roots, nuts, and other noncereals. | Low consumption of foods rich in micronutrients. |
| Electrolytes (sodium, calcium, and potassium, needed for a variety of physiological processes) | High consumption of potassium relative to sodium (10,500 mg/day vs. 770 mg/day). High blood pressure is rare in contemporary hunter-gatherers with high potassium/sodium ratios. | Low consumption of potassium relative to sodium (3,000 mg/day vs. 4,000 mg/day). High sodium intake from processed foods is associated with high blood pressure. |
| Carbohydrates | Provide about 45–50% of daily calories, mostly from vegetables and fruits, which are rich in amino acids, fatty acids, and micronutrients. | Provide about 45–50% of daily calories, mostly from processed cereal grains, sugars, and sweeteners, which are low in amino acids, fatty acids, and micronutrients. |
| Fat | Provides about 20–25% of daily calories, mostly from lean game animals, which have less fat and saturated fat than domestic animals, leading to lower serum cholesterol levels. | Provides about 40% of calories, mostly from meat and dairy products. Some contemporary diets, such as from Japan and the Mediterranean region, are low in total or saturated fat and are associated with lower heart disease rates. |
| Protein | High consumption, providing about 30% of daily calorie intake, mostly from wild game that is low in fat. | Recommended daily allowance about 12% of total calories. High protein intake has been associated with higher heart disease rates, probably because contemporary high-protein diets also tend to be high in fat. |
| Fiber | 50–100 g/day. High-fiber diets sometimes are considered risky because of loss of micronutrients, but this would be less of a worry in a Paleolithic diet rich in micronutrients. | 20 g/day. |

The contemporary diet is not simply a more abundant version of the hunter-gatherer diet. It differs fundamentally in both composition and quality. Compared with contemporary diets, the hunter-gatherer diet can be characterized as being high in micronutrients, protein, fiber, and potassium and low in fat and sodium. Total caloric and carbohydrate intake is about the same in both diets, but hunter-gatherers typically were more active than contemporary peoples and thus needed more calories, and their carbohydrates came from fruits and vegetables rather than processed cereals and refined sugars.

The comparison between hunter-gatherer and contemporary diets indicates that increasing numbers of people are living in nutritional environments for which their bodies are not necessarily well adapted. With few exceptions (such as the evolution of lactose tolerance) there has not been enough time, or strong enough selection pressures, for us to develop adaptations to this new nutritional environment. Indeed, because most of the negative health aspects of contemporary diets (obesity, diabetes, cancer) become critical only later in life, it is likely that health problems associated with the mismatch between our bodies and our nutritional environment will be with us for some time.

To circumvent this problem, some people today are trying to live their lives as cavemen and cavewomen in the supermarket, adopting a Paleolithic-type diet in the contemporary world. Dozens of self-help books with titles such as *Neanderthin* and *The Paleo Solution* have been published in support of these modern, stone-age eaters. There is nothing particularly wrong with this, it is probably quite healthy in the long run (Lindeberg, 2012), and as with any particular diet, whether it is deemed a success or failure depends on an individual's experience with it. One difficulty with the paleo diet is that the Paleolithic itself represents only a small part of human evolutionary history. Our diets and food-associated behaviors evolved over millions of years primate evolution in general. The sensory, physiological, and cognitive bases of human eating therefore evolved over a much longer time period than the Paleolithic, and while our bodies may be suited to paleo eating, our minds may not be (Allen, 2012).

Agriculture and Nutritional Deficiency

Agriculture allowed the establishment of large population centers, which in turn led to the development of large-scale, stratified civilizations with role specialization. Agriculture also produced an essential paradox: From a nutritional standpoint, most agricultural people led lives that were inferior to the lives of hunter-gatherers. Agricultural peoples often suffered from *nutritional stress* as dependence on a few crops made their large populations vulnerable to both chronic nutritional shortages and occasional famines. The “success” of agricultural peoples relative to hunter-gatherers came about not because agriculturalists lived longer or better lives but because there were more of them.

An example of the decline in health associated with the intensification of agriculture comes from paleopathological research in the Illinois Valley (Cook, 1979; Cook & Buikstra, 1979). Over the period A.D. 600–1200, the people in the Illinois Valley went from lives that were characterized predominantly by subsistence based on hunting and gathering (with some trade for agricultural products) to an agricultural economy with significant maize production. Population centers increased in size. However, at the same time, signs of malnutrition also increased. Enamel defects in tooth development became more common and are associated with higher death rates during the weaning years (Figure 15.20). Skeletal growth rates slowed. Specific skeletal lesions associated with malnutrition also increased in frequency.

With their dependence on a single staple cereal food, agricultural populations throughout the world have been plagued by diseases caused by specific nutritional deficiencies. As in the Illinois Valley, many populations of the New World were dependent on maize as a staple food crop. Dependence on maize leads to the development of *pellagra*, a disease caused by a deficiency of the B vitamin *niacin* in the diet. Symptoms of pellagra include a distinctive rash, diarrhea, and mental disturbances, including dementia. Ground corn is low in niacin and in the amino acid tryptophan, which the body can use to synthesize niacin. Even into the twentieth century, poor sharecroppers in the southern United States and poor farmers in southern Europe, both groups that consumed large quantities of cornmeal in their diets, were commonly afflicted with pellagra. Some maize-dependent groups in Central and South America were not so strongly affected by pellagra because they processed the corn with an alkali (lye, lime, ash) that released niacin from the hull of the corn.

In Asia, rice has been the staple food crop for at least the last 6,000 years. In China, a disease we now call *beriberi* was first described in 2697 B.C. Although it was not recognized at that time, beriberi is caused by a deficiency in vitamin B₁ or *thiamine*. Beriberi is characterized by fatigue, drowsiness, and nausea, leading to a variety of more serious complications related to problems with the nervous system (especially tingling, burning, and numbness in the extremities) and ultimately heart failure. Rice is not lacking in vitamins; however, white rice, which has been polished and milled to remove the hull, has been stripped of most of its vitamin content, including thiamine. Recognition of an association between rice overdependence and beriberi began to develop in the late nineteenth century, when the Japanese navy reported that beriberi could be eliminated among its sailors (half of whom contracted the disease) by increasing the meat, vegetables, and fish in their diets.

Agriculture and Abundance: Thrifty and Nonthrifty Genotypes

The advent of agriculture ushered in a long era of nutritional deficiency for most people. However, the recent agricultural period, as exemplified in the developed nations of the early twenty-first century, is one of nutritional excess, especially in terms of the consumption of fat and carbohydrates of little nutritional value other than calories. The amount and variety of foods available to people in contemporary societies are unparalleled in human history.

Figure 15.20 Enamel defects due to malnutrition in a child from the Illinois Valley (A.D. 600–1200).



Figure 15.21 Pima Indian woman receiving an eye exam. Eye problems are a common result of diabetes.



In 1962, geneticist James Neel introduced the idea of a *thrifty genotype*, a genotype that is very efficient at storing food in the body in the form of fat, after observing that many non-Western populations that had recently adopted a Western or modern diet were much more likely than Western populations to have high rates of obesity, diabetes (especially Type 2 or non-insulin-dependent diabetes), and all the health problems associated with those conditions (see also Neel, 1982). Populations such as the Pima-Papago Indians in the southwest United States have diabetes rates of about 50%, and elevated rates of diabetes have been observed in Pacific Island-, Asian-, and African-derived populations with largely Western diets (Figure 15.21).

According to Neel, hunter-gatherers needed a thrifty genotype to adapt to their nonabundant nutritional environments; in contrast, the thrifty genotype had been selected against in the supposedly abundant European environment through the negative sequences of diabetes and obesity. The history of agriculture and nutritional availability in Europe makes the evolution of a *non-thrifty genotype* unlikely (Allen & Cheer, 1996); Europe was no more nutritionally favored than other agricultural or hunter-gatherer populations.

However, the notion of a thrifty genotype retains validity. At its heart is the idea that we are adapted to a lifestyle and nutritional environment far different from those we find in contemporary populations.

Douglas Crews and Linda Gerber (1994; Gerber & Crews, 1999) have proposed a refinement and expansion of the thrifty genotype model that they call the *thrifty-pleiotropic genotype* model. Whereas Neel concentrated primarily on energy intake, they point out that the thrifty genotype should apply to any nutrient in the environment that is (or was) potentially scarce. Thus we should expect negative health consequences for the overconsumption of a variety of nutrients: Excess cholesterol consumption leads to heart disease, excess salt consumption leads to high blood pressure, and so on. The deficiency syndromes of agriculture are part of this adaptive balance: Too little of a nutrient can also lead to disease. The pleiotropic aspect of Crews and Gerber's model is based on the observation that most of the diseases associated with overconsumption are chronic illnesses that have their effects late in life; they are to some extent a consequence of aging. If the efficiency of the thrifty genotype increases reproductive fitness early in life, the negative pleiotropic consequences in middle and old age will not be selected against, even in an environment of nutritional abundance.

Biomedical anthropology is interested in understanding the patterns of human variation, adaptation, and evolution as they relate to health issues. This entails an investigation of the relationship between our biologies and the environments we live in. Understanding environmental transitions helps us understand not only the development of disease but also the mechanisms of adaptation that have evolved over thousands of years of evolution. Change is the norm in the modern world. In the future, we should expect human health to be affected by these changes. By their training and interests, biological anthropologists will be in an ideal position to make an important contribution to understanding the dynamic biocultural factors that influence human health and illness.

Summary

EPIDEMIOLOGY: BASIC TOOLS FOR BIOMEDICAL ANTHROPOLOGY

15.1 Recognize the basic epidemiological rate statistics and how they are derived, and explain epidemiological transitions and their consequences.

- Incidence rate is the rate at which new cases of a disease appear in a population over a certain period of time.

- The prevalence rate is the total number of cases divided by the population size at any given time.
- Prevalence is a function of both the incidence and duration of a disease.
- For example, a disease with a low incidence rate but a long duration could have a higher prevalence rate than a disease with a high incidence rate that is cured or quickly fatal.

BIOCULTURAL AND EVOLUTIONARY APPROACHES TO DISEASE

15.2 Compare and contrast the biocultural and evolutionary approaches in biomedical anthropology.

- The biocultural approach recognizes that both biological and cultural variables are important for understanding human disease.
- Evolutionary or “Darwinian” medicine looks at health and disease from the perspective of adaptation and adaptability, design compromises, and competition between hosts and infectious organisms.
- Organisms adapted for one environment may suffer health consequences when living in an environment different from the one for which they are adapted.

BIRTH, GROWTH, AND AGING

15.3 Describe the unique challenges of human birth and summarize the stages of human growth and development and the secular trend in growth.

- Patterns of growth and development are a direct reflection of health status in a population, as evidenced by the secular trend in growth.
- Birth is a biocultural process in humans, in which the large head of newborns may have selected for the practice of midwifery or birth assistance.
- Growth in humans is characterized by stages that are seen in other primates, but which are each longer to accommodate the learning required of the large human brain.
- Adolescence and the adolescent growth spurt may be unique to humans.
- Menopause may be an aging-associated adaptation, although most evolutionary models of aging see it as a by-product of physiology.

INFECTIOUS DISEASE AND BIOCULTURAL EVOLUTION

15.4 Describe the human biological response to infectious disease and the ways cultural environments shape the arms race between humans and pathogens.

- The spread and severity of infectious disease is influenced by a wide range of biological and cultural factors.
- The development of agriculture leading to the establishment of large, high-density populations fundamentally changed the infectious disease profile for the human species.
- Increases in human mobility and migration have facilitated the spread of infectious disease to immunologically vulnerable populations.

DIET AND DISEASE

15.5 Compare and contrast Paleolithic and agricultural diets, and recognize the implications for switching from one to the other on human health.

- There are fundamental differences between the contemporary diet and that of hunter-gatherers (the Paleolithic diet).
- Although they may support larger populations, agricultural diets are associated with specific and general nutritional deficiencies.
- The mismatch between the diet we evolved with and that we currently have may be one of the cause of increases in diseases associated with lifestyle.

Review Questions

- 15.1 How does biomedical anthropology differ from clinical approaches to disease?
- 15.2 How do incidence and prevalence rates differ from one another?
- 15.3 What are five concepts that define the evolutionary approach in medical anthropology?
- 15.4 Under what circumstances do populations typically demonstrate a secular trend in growth?
- 15.5 How have agriculture and increased mobility shaped changes in how infectious diseases spread among and affect human populations?
- 15.6 What does it mean to eat like a caveman, and is that really something that people should be doing today?

Key Terms

antibodies, p. 489
antigens, p. 489
auxology, p. 476
biomedical anthropology, p. 469
epidemiology, p. 469

immunoglobulins, p. 489
incidence rate, p. 470
menarche, p. 480
menopause, p. 481
pathogens, p. 473

prevalence rate, p. 470
senescence, p. 483
teratogens, p. 477

Chapter 16

The Evolution of Human Behavior



Learning Objectives

- 16.1** Define the four approaches used to study the evolution of human behavior, and explain how cross-cultural research can inform evolutionary perspectives on behavior.
- 16.2** Discuss how ecological studies of human behavior can be used to test evolutionary predictions about human behavior, and illustrate the relationship between progesterone and testosterone to human reproductive behavior.
- 16.3** Understand sexual selection and how it has influenced some aspects of human reproductive behavior and patterns of sex differences in human behavior.
- 16.4** Recognize how motherese and basic color terms reveal the biological influences on language expressed in a cultural context.
- 16.5** Discuss how human behavioral diseases are culturally universal and how conditions such as addiction and depression are related to adaptive aspects of cognition.

In early 1978, the American Association for the Advancement of Science held a meeting in Washington, D.C., which attempted to bring together representatives from all sides in what came to be called “the sociobiology debate.” Two of the most prominent scientists to attend the meeting were Edward Wilson, a proponent of the evolutionary study of human behavior (which was then called sociobiology), and Stephen Jay Gould, who cautioned that arguments about the biological basis of human behavior historically had been used to justify racist and sexist ideologies. Many of Wilson’s critics accused him of arrogance for suggesting that evolutionary explanations of human behavior would come to dominate thinking in the traditional social sciences. In contrast, proponents of sociobiology felt that Wilson and other workers in the field were being unfairly accused of holding political and ideological views that they themselves found to be repugnant. Advocates on both sides of the debate were fueled by arrogance and righteousness, a volatile combination.

Sociologist of science Ullica Segerstråle attended this landmark meeting. She describes the extraordinary scene when Wilson faced some of his more enthusiastic critics:

“The two-day symposium featured about twenty speakers in all. As a member of the audience, I can say that for those who anticipated a public showdown, it was somewhat disappointing to sit through rather technical talks dealing with animal sociobiology. . . . But there was anticipation in the air, particularly in the session where both Wilson and Gould were to speak. The ballroom was filled to capacity. Would Gould demolish sociobiology? Would Wilson stand up to Gould? By now, the audience wanted some action. The result exceeded anybody’s expectation.”

“What happens is a total surprise. The session has already featured Gould, among others, and Wilson is one of the later speakers. Just as Wilson is about to begin, about ten people rush up on the speaker podium shouting ‘Racist Wilson you can’t hide, we charge you with genocide!’ While some take over the microphone and denounce sociobiology, a couple of them rush up behind Wilson (who is sitting in his place) and pour a pitcher of ice-water over his head, shouting ‘Wilson, you are all wet!’ Then they quickly disappear again. Great commotion ensues but things calm down when the session organizer steps up to the microphone and apologizes to Wilson for the incident. The audience gives Wilson a standing ovation. Now Gould steps up to the microphone saying that this kind of activism is not the right way to fight sociobiology—here he has a Lenin quote handy, on ‘radicalism, an infantile disorder of socialism.’ For his valiant handling of the situation, Gould, too, gets a standing ovation. (The audience does not quite know how to react to any of this but applauding seems somehow right). Wilson—still wet—gives his talk, in spite of the shock of the physical attack. . . . his calmly delivered talk is something of an anticlimax.”

(Segerstråle, 2000)

We are fortunate that most debates about the evolution of human behavior do not end (or begin) with someone being doused with water. But the incident provides an indication of just how heated these debates can become. They reflect a basic conflict over whether human behavior is in the genes or is a product of our culture and upbringing: the old *nature versus nurture* debate. The nurture, or cultural, side accuses the nature, or evolutionary, side of being *genetic determinists*, people who believe that all observed behavioral differences between individuals, the sexes, or populations can be ascribed only to differences in genetics. The genetic side accuses the cultural side of embracing the logic of creationism: That once culture evolved, the rules of the game changed,

human behavior became shaped only by culture, and we were no longer subject (at the behavioral level) to the forces of evolution, which are so readily apparent in the animal world.

As you might expect, neither of these two extreme positions reflects the views of most biological anthropologists. Biological anthropologists, with their appreciation for the biology and behavior of our closest primate relatives, understand that human bodies and human behavior evolved. On the other hand, biological anthropologists also recognize that human behavior is not genetically determined but is the product of the interaction of genes and cultural environments. Although behaviors do not fossilize, we can draw inferences about how they may have evolved by examining contemporary human and nonhuman primate behavior and biology. Many behavioral scientists today believe that although humans are capable of a wide range of behaviors, some patterns of behavior we observe across cultures and populations are most directly explained by evolution and natural selection.

To understand the evolutionary foundations of contemporary human behavior we need to apply the same logic and inferences that we use when studying other evolutionary phenomena. We can use the vast amount of information we have about human behavior and look for patterns that are consistent with evolutionary models. We can also take advantage of natural experiments that provide unusual combinations of variables and allow us to gain new perspectives on human behavior. The same principles that we use to make inferences about the phylogenetic relationships of the Old World monkeys, the adaptive value of the trunk of an elephant, the plumage of the male peacock, or the social behavior of prairie dogs can also guide our inferences about the evolution of human behavior. However, human behavior occurs in a cultural context. Like the biomedical anthropology approach to health and illness, a comprehensive understanding of the evolution of human behavior entails a biocultural perspective.

In this chapter, we will address several aspects of human behavior from an evolutionary perspective. These include the ecology and demography of traditional human societies, patterns of human behavior that have been shaped by sexual selection, the interaction between culture and biology in the expression of language, and the emergence of behavioral disease in an evolutionary context. We recognize, of course, that each of these topics can be productively analyzed from a cultural or nonevolutionary perspective; however, as we have emphasized throughout this text, the biological anthropological approach is defined both by evolutionary theory and by the quest to understand the human species in a biocultural context. Therefore, this chapter focuses on these evolutionary and biocultural explanations of human behavior.

Studying the Evolution of Human Behavior

16.1 Define the four approaches used to study the evolution of human behavior, and explain how cross-cultural research can inform evolutionary perspectives on behavior.

The publication of G. C. Williams's book *Adaptation and Natural Selection* in 1966 was a landmark in the study of the evolution of behavior. Williams saw the evolution of social behavior in terms of benefits not to the group as a whole (that is, for the good of the species) but to the individuals (and their genes) who made up the group. Following on this work and others, in 1975 zoologist Edward O. Wilson published a

sociobiology

Name popularized by E. O. Wilson for the evolutionary study of animal social behavior.

book called *Sociobiology: The New Synthesis*. For a variety of social and political reasons, which are beyond the scope of this text (see Segerstråle, 2000; Alcock, 2001), Wilson's book became a lightning rod for critics of evolutionary interpretations of human behavior. Wilson defined **sociobiology** simply as the science of the biological basis of social behavior. Only a small part of his book was dedicated to humans—social insects were the main focus of Wilson's own research—but his brief exploration of human sociobiology drew the most attention.

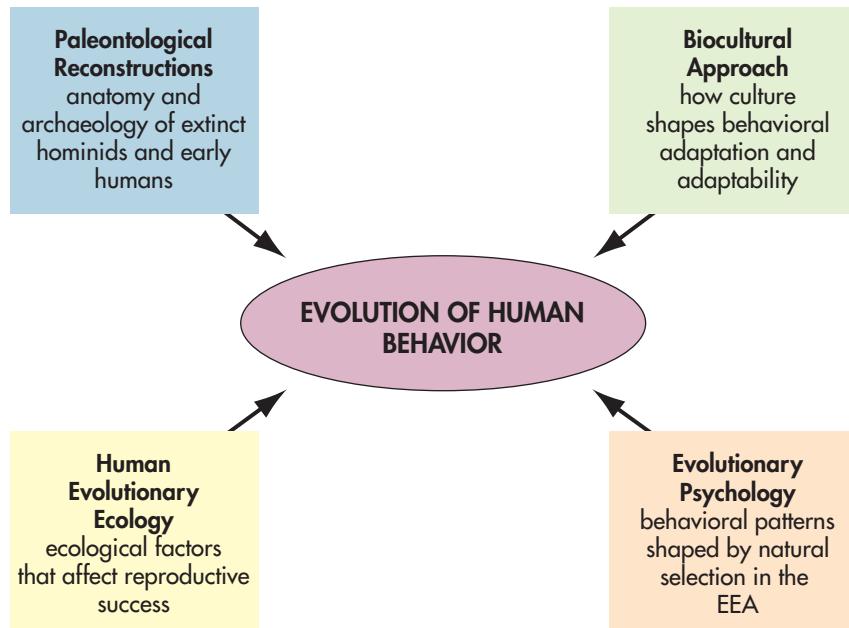
Critics of sociobiology, such as the paleontologist and writer Stephen Jay Gould, claimed that sociobiology in general was not good science and was susceptible to political misapplication. Mindful of these criticisms, the field of the evolution of human behavior has moved away from Wilson's grand vision of human sociobiology (that it would subsume all the social sciences) and embraced several different, sometimes competing approaches to human behavior, which are seen to be complementary to or a part of traditional human behavioral sciences.

The Evolution of Human Behavior: Four Approaches

Anthropologists and other scientists use varied approaches to study the evolution of human behavior, depending on their particular research interests and training (Figure 16.1). Four of the most common approaches are paleontological reconstructions of behavior, biocultural approaches, evolutionary psychology, and human evolutionary (or behavioral) ecology. The examples covered in this chapter make use of the latter three approaches.

PALEONTOLOGICAL RECONSTRUCTIONS OF BEHAVIOR Earlier we discussed several reconstructions of the behavior of earlier hominins. These reconstructions were based on the anatomy of extinct hominins and, when present, the archaeological remains with which they were associated. They were also based on correlations among behavior, anatomy, and ecology we have observed in nonhuman primate species and in contemporary humans, especially those living under traditional hunter-gatherer conditions. Any reconstruction of the behavior of our hominin ancestors is a synthesis of both paleontological and contemporary data.

Figure 16.1 Four approaches to studying the evolution of human behavior.



BIOCULTURAL APPROACHES It is clear that human cultural behavior has influenced human evolution. For example, the adoption of slash-and-burn agriculture had an indirect effect on the evolution of the sickle cell polymorphism, and the development of dairying in some populations was a direct selective factor in the evolution of lactose tolerance. Our biological and evolutionary heritage may have shaped several patterns of behavior that are expressed in a cultural context. One aspect of human behavior that we have already discussed in detail—language—is a prime example.

EVOLUTIONARY PSYCHOLOGY An adherence to three main principles characterizes **evolutionary psychology**. First, human and animal behavior is not produced by minds that are general purpose devices. Rather, the mind is composed of *cognitive modules*, which are assumed to have an underlying neuroanatomical basis. These modules express specific behaviors in specific situations. Second, cognitive modules are complex design features of organisms. Because natural selection is the only way to evolve complex design features, evolutionary psychology focuses on understanding behaviors or cognitive modules as adaptations. Third, for most of our history, humans and hominins have lived in small groups as hunter-gatherers. Evolutionary psychologists believe that our evolved behavior may reflect or should be interpreted in terms of this hypothetical **environment of evolutionary adaptedness (EEA)**.

Evolutionary psychologists acknowledge that some behaviors, like some physical features, are the by-products of other evolutionary forces and therefore should not be considered adaptations (musical ability may be such a behavior, for example). Furthermore, although the EEA figures prominently in their interpretation of behavioral data, most evolutionary psychologists study the behavior of contemporary humans living in developed countries, via surveys, psychological experiments, and observations of people in day-to-day settings. This is not simply a matter of convenience: Evolutionary psychologists seek species-wide adaptations, which can be examined in any cultural setting (although data from cross-cultural studies is always helpful). They use such data to uncover the adaptations that characterized life in the EEA, whatever that may have been. Over the past two decades the principles of evolutionary psychology have been elucidated by two of its main proponents, anthropologist John Tooby and psychologist Leda Cosmides (Barkow et al., 1992; Tooby & Cosmides, 2000).

HUMAN EVOLUTIONARY (OR BEHAVIORAL) ECOLOGY In contrast to evolutionary psychology, which focuses more on psychological experiments and surveys of people living in developed countries, **human evolutionary ecology** focuses on the ecological factors that influence reproductive success in the few remaining hunter-gatherer populations. Among the groups studied most intensely have been the Yanomamö of Amazonia (Chagnon, 1988, 1997), the Aché of Paraguay (Hill & Hurtado, 1996), and the Hadza of Tanzania (Hawkes et al., 2001). Topics of interest to human evolutionary ecologists include the relationship between status and reproductive success, demographic effects of tribal warfare and aggression, and the underlying social impact of hunting and food sharing. Researchers use data on contemporary hunter-gatherer groups to refine models that purport to reconstruct the behavior of extinct hominins (Marlowe, 2005).

evolutionary psychology

Approach to understanding the evolution of human behavior that emphasizes the selection of specific behavioral patterns in the context of the environment of evolutionary adaptedness.

environment of evolutionary adaptedness (EEA)

According to evolutionary psychologists, the critical period for understanding the selective forces that shape human behavior; exemplified by hunter-gatherer lifestyles of hominins before the advent of agriculture.

human evolutionary ecology

Approach to understanding the evolution of human behavior that attempts to explore ecological and demographic factors important in determining individual reproductive success and fitness in a cultural context.

Behavioral Patterns and Evolution

Human behavior can be observed at the individual, cultural, or even species-wide levels. To understand the natural history of human behavior, it is important to remember the mosaic nature of its evolution. Just as different parts of the human body evolved at different points in our past, different aspects of human behavior may reflect different evolutionary periods.

cognitive universals

Cognitive phenomena such as sensory processing, the basic emotions, consciousness, motor control, memory, and attention that are expressed by all normal individuals.

COGNITIVE UNIVERSALS As a species we share many behaviors by virtue of our shared biology. These **cognitive universals** include behaviors studied by cognitive scientists, such as sensory processing, the basic emotions, consciousness, motor control, memory, and attention (Gazzaniga et al., 2008). Language also is typically included among the cognitive behaviors shared by all people. At a biological level, we share the neurological mechanisms underlying some of these cognitive universals with many other mammalian species. For example, much of what we know about the specifics of visual processing comes from experimental work on cats and monkeys. Other universals, such as language, clearly have emerged fully only in the hominin lineage (although we may study its biological antecedents by looking at other species).

Given the universal, and in many cases cross-species, expression of these cognitive processes, it is reasonable to assume they are biological adaptations that have been shaped by natural selection. Although cognitive universals have a basic common expression in all people, we often see variation in the way they are expressed. It is likely that this variation results from both environmental and genetic factors, in the same way, for example, that variation in stature arises within and between populations.

cross-cultural universals

Behavioral phenomena, such as singing, dancing, and mental illness, that are found in almost all human cultures, but are not necessarily exhibited by each member of a cultural group.

CROSS-CULTURAL UNIVERSALS When we look across the diverse cultures of the world, it is easy to notice that many commonalities emerge, which can be called **cross-cultural universals** (Brown, 1991). For example, all cultures have a language. We also find that each culture develops rituals and traditions to mark and recognize status. They develop systems for identifying and naming kin. They organize social and occupational roles along sex and gender lines. Standards of sexual attractiveness and beauty may show common patterns across cultures. Many biological anthropologists argue that common cultural practices did not develop independently over and over again but rather reflect underlying genetic factors that are widely distributed in our species. If we cannot find a common cultural origin for a widespread behavioral pattern observed across cultures, then it is reasonable to hypothesize that the pattern may reflect a common biological origin. This is especially true if we find the behavior in a majority of human cultures or if we can show it to be associated with a common ecological variable. One way to look at this is that we are not hardwired to develop these behaviors but rather are “prewired” to express them given a proper ecological or cultural environment (Marcus, 2004).

Remember that cross-cultural universals are *not* individual universals. For example, we could say that singing and dancing are cross-cultural universals, but that does not mean that all members of every culture sing and dance. Similar forms of behavioral disease are found in different cultures, so in one sense we can say that mental illnesses are a cross-cultural universal, even if only a small proportion of the population develops these conditions.

WITHIN-CULTURE VARIATION Male and female mammals may adopt different sexual and reproductive strategies because they invest different amounts of time and energy in each offspring. How has this mammalian pattern been rendered in a human cultural context? Do we see evidence that humans have evolved away from typical primate patterns? If so, how and why has this within-culture variation happened? Variation in behavior correlated with age may also have been shaped by evolutionary pressures. For example, is the young, risk-taking male a Western cultural construct or a cross-cultural phenomenon amenable to evolutionary theorizing? Although age and sex are the primary biological variables that figure into studies of the evolution of within-culture variation, we can study other aspects of within-culture variation from an evolutionary perspective.

BIOLOGICAL CONSTRAINTS ON HUMAN BEHAVIOR People are capable of doing just about anything, and any number of behaviors shaped by culture are not

easily explained in a bioevolutionary context. On the other hand, when we look across cultures, there seem to be some constraints on what people do, which in turn lead to behavioral convergences across cultures. A nonbehavioral example of a behavioral convergence is footwear. Footwear tends to converge on a similar basic shape, which is functionally constrained by the shape and action of the human foot. In a similar fashion, human behavior may be channeled into similar patterns by constraints imposed by our neurobiology. A basic issue in the evolution of behavior is determining whether any given behavior is an adaptation or simply the result of a biological constraint on behavior. Of course, similar debates arise about anatomical features as well.

Traditional Lives in Evolutionary Ecological Perspective

- 16.2** Discuss how ecological studies of human behavior can be used to test evolutionary predictions about human behavior, and illustrate the relationship between progesterone and testosterone to human reproductive behavior.

Human behavior emerges from the interplay of biological and cultural factors. Over the past four decades, human evolutionary ecologists have undertaken intensive study of traditional cultures to understand how human behavior evolved biologically in the context of culture. Studies of traditional hunter-gatherers and traditional agricultural cultures are important because their lifestyles reflect more closely the natural selection environments (the EEA) that shaped hominin evolution, until the advent of large-scale, complex societies starting less than 10,000 years ago.

Evolutionary ecology represents a profound theoretical departure from traditional cultural anthropology. Investigating the interplay between behavior, culture, and ecology, evolutionary ecologists typically live for extended periods of time with the groups they are studying, as cultural anthropologists do (Figure 16.2). However, they differ from other cultural anthropologists in their reliance on quantitative research methods, which are necessary to test evolutionary hypotheses.

Quantification in Evolutionary Ecology Research

To rigorously test evolutionary hypotheses and to discover how ecological factors affect human behavior, evolutionary ecologists must collect quantifiable data. These data include birth, death, and marriage statistics (that is, demographic variables); nutritional data; and calculations of daily energy expenditure. Some evolutionary ecologists use sophisticated mathematical models to try to understand human cultural behavior in an evolutionary context (Boyd & Richerson, 1988; Richerson & Boyd, 2004). Others use data from multiple cultures to look at how ecological and environmental variables interact to potentially influence the behavior of hunter-gatherers (Marlowe, 2005).

WEALTH, REPRODUCTIVE SUCCESS, AND SURVIVAL
One of the basic tenets of human evolutionary ecology is that cultural success should be related to increased fitness

Figure 16.2 Evolutionary ecologists live and do research in contemporary cultures that maintain all or some aspects of their traditional lifeways, such as these tribespeople from New Guinea.



Figure 16.3 Male Turkmen in the wealthier half of the population had higher fertility rates than those in the poorer half.

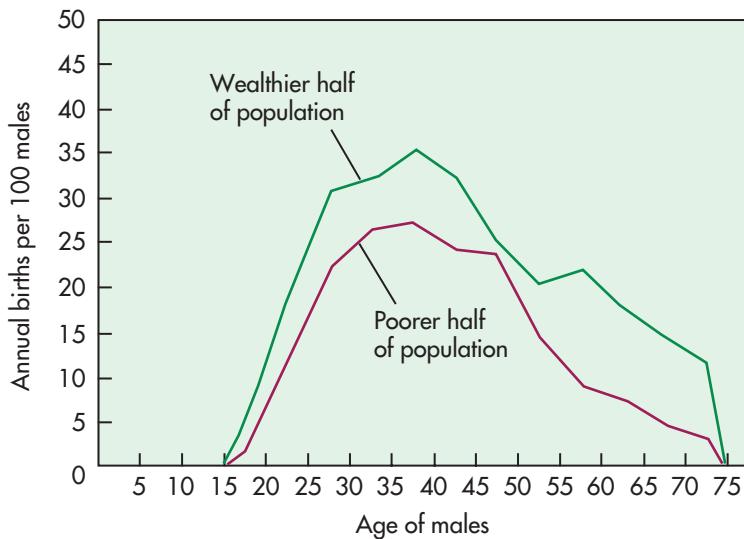


Figure 16.4 The Kipsigis of Kenya.



bridewealth

Payment offered by a man to the parents of a woman he wants to marry.

tion between number of offspring and acres of land owned (Figure 16.5). Ownership of 30 acres correlated to having fifteen to twenty surviving offspring, whereas men with 90 acres had twenty-five to thirty offspring. In general, the fertility of the wives of richer and poorer men was approximately the same. Wealthier men have more children because they can have more wives, being able to afford more bridewealth payments. And although larger families may lead to increased wealth, Borgerhoff Mulder found no evidence that this was the causal direction: Wealthier men were able to afford large families, not the other way around.

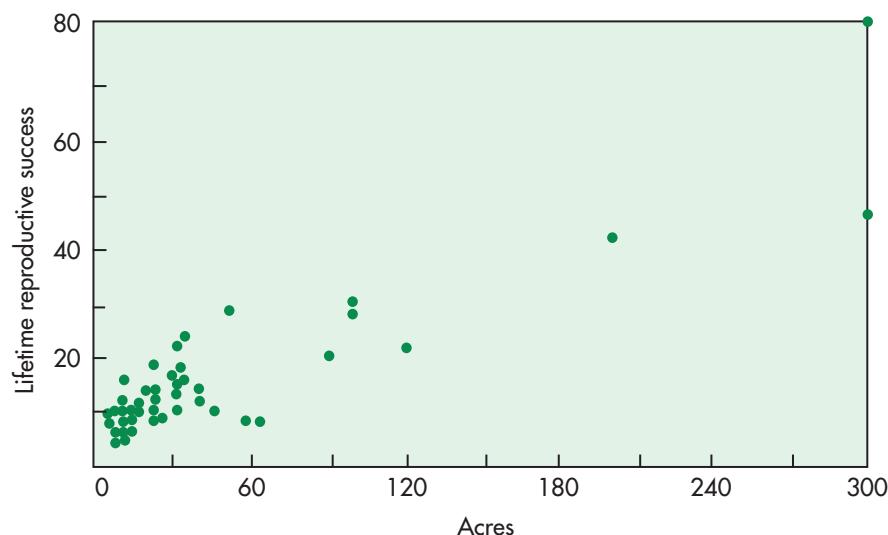
The Turkmen and Kipsigis studies, and others done elsewhere, support the hypothesis that one measure of cultural success—wealth—correlates with reproductive success. However, this correlation does not generally hold for developed, urbanized, capitalist cultures, where higher socioeconomic status typically is not associated with a higher birth rate. This is an important example of the kind of fundamental biocultural change that can occur in a society when it transforms from an undeveloped to a developed economy.

(Irons, 1979). William Irons tested this hypothesis in a study of fertility and mortality among the tribal Turkmen of Iran. In this culture, wealth (in terms of money, jewelry, and consumable goods) is a primary measure of cultural success. Irons found that for men, fertility and survivorship were higher for the wealthier half of the population than for the poorer half (Figure 16.3); survivorship was significantly higher for the wealthier women, but there was no difference in fertility. He also found that reproductive success was more variable among men than among women (that is, the difference between the richer and poorer halves was more pronounced for men than for women), as predicted by sexual selection theory.

Monique Borgerhoff Mulder (1987, 1990) looked at the relationship between wealth and reproductive success in a different population, the Kipsigis of Kenya (Figure 16.4). The Kipsigis are a pastoral people who moved into Kenya from northeastern Africa in the late eighteenth century. The wealth of a Kipsigis man is defined in terms of his land holdings, the number of animals he has, and his household possessions. Borgerhoff Mulder found that all these measures correlate strongly to amount of land owned, so she used that as her primary statistic of wealth.

The Kipsigis practice polygyny, which means that a man can have more than one wife at a time. When a man wants to marry a young woman, he approaches her parents with an offer of **bridewealth**, a payment that can equal up to a third of an average man's wealth. Borgerhoff Mulder looked at wealth and reproductive success among Kipsigis men in a series of different age groups and found a strong correlation between wealth and number of offspring. For example, in a group of forty-four men who were circumcised between 1922 and 1930 (circumcision marks coming of age), there was a very high correlation

Figure 16.5 The relationship between number of acres a Kipsigis man owns and the number of offspring he has during his lifetime.



PHYSIOLOGY AND ECOLOGY Another method for quantifying the relationship between cultural and ecological factors in human behavior is to look at the way physiological measures vary across ecological contexts. For example, Peter Ellison (1990, 1994) developed a method of measuring levels of reproductive hormones in saliva as a noninvasive means to assess reproductive function in women living in diverse environments.

Progesterone is a steroid hormone produced by the corpus luteum and the placenta that prepares the uterus for pregnancy and helps maintain pregnancy once fertilization has occurred. Progesterone levels measured in saliva correlate with ovarian function. Ellison and his colleagues found that salivary progesterone levels are strongly correlated with age over the course of a woman's reproductive life (between about ages 15 and 50 years). Progesterone levels increase from a baseline level at the end of puberty, peaking between 25 and 30 years of age and dropping off thereafter. Ellison suggests that ovarian function matures at approximately the same age as the pelvis becomes structurally mature (early to mid-20s).

Studies among two traditional agricultural groups, the Lese of Zaire and the Tamang of Nepal, and women from the Boston area, showed that the basic age-dependent curve of salivary progesterone production was the same in all three populations (Figure 16.6 on page 506). Ellison believes that this pattern probably represents a fundamental feature of human reproductive physiology. This discovery refines our view of the female reproductive years as an evolved life history stage (beginning at menarche and ending at menopause).

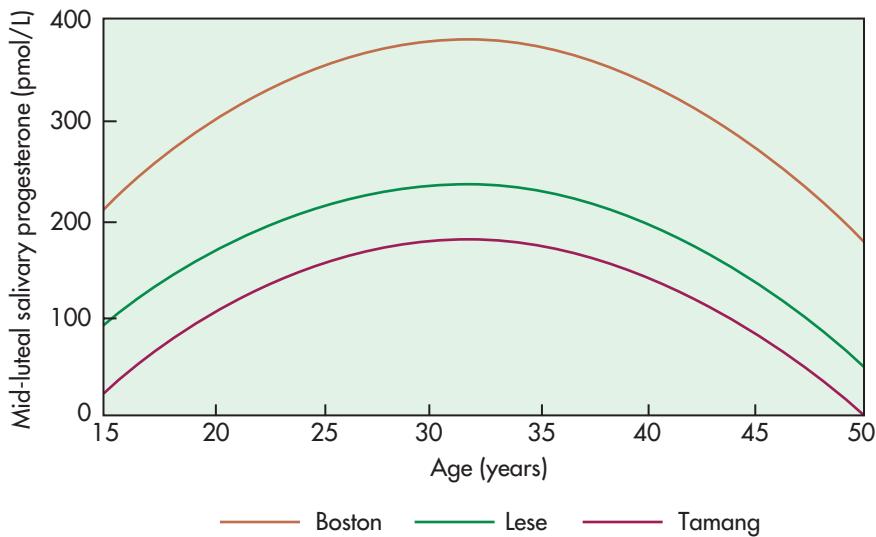
Although the shapes of the progesterone-versus-age curves were the same in Boston, Lese, and Tamang women, the amount of progesterone produced varied among the groups. Boston women, who presumably had the most nutritionally rich environment with few infectious diseases, had higher progesterone levels at every age than were found in the other two populations. Ellison suggests that chronic stress that delays growth and maturation, such as nutritional deficiencies, could lead to lower levels of ovarian function throughout the lifetime. Such a stress-response relationship could be adaptive because in a stressful environment it may be better to devote more effort and energy to body maintenance and survival rather than reproduction.

Progesterone levels not only vary over the course of a woman's life, but also monthly as part of her *menstrual cycle*. Progesterone levels peak after ovulation, during

progesterone

A steroid hormone produced by the corpus luteum and the placenta, which prepares the uterus for pregnancy and helps maintain pregnancy once fertilization has occurred.

Figure 16.6 The age-dependent curve of salivary progesterone levels in three populations.



the luteal phase, which helps prepare the endometrium of the uterus for implantation of the fertilized egg. Researchers have long noted that the onset of *premenstrual syndrome* (PMS) accompanies this increase in progesterone levels in the body. PMS is associated with mild depression, anxiety, and other negative changes in mood. About 80% of women experience PMS symptoms at some point, with up to 18% needing some kind of medical assistance (Halbreich, 2003). Direct and consistent evidence linking PMS with progesterone levels has been hard to come by, but in a large-scale study of salivary progesterone levels in a large group of young, healthy women, it was found that women with low levels of PMS symptoms (specifically, intensity of aggressive behavior and fatigue) had 20–25% higher levels of progesterone than women with high levels of symptoms (Ziomkiewicz et al., 2012). The regulation of mood by progesterone during the menstrual cycle (which involves other hormones and factors, of course) demonstrates one way that human behavior is influenced by our physiology.

testosterone

A steroid produced primarily in the testes and ovaries, and at a much higher level in men than in women. Responsible for the development of the male primary and secondary sexual characteristics. Strongly influences dominance and reproductive behavior.

Another steroid hormone whose levels can be measured in saliva is **testosterone**. Testosterone is produced primarily in the testes and ovaries; it is known as the “male hormone” since the testes produce about 10 times as much as the ovaries, and testosterone is primarily responsible for the development of the primary male sexual characteristics in the fetus and the secondary characteristics at puberty. It has also been hypothesized that testosterone is an important modulator of behavior, especially in the context of male dominance and reproductive behavior. Much evidence for this hypothesis has been gathered from studies of numerous mammal species, but what is the situation in humans?

One way to test the hypothesis claiming that testosterone influences behaviors related to male–male competition and mate-seeking behavior is to compare testosterone levels in men who are in a committed relationship with those who are single. T. C. Burnham (2003) and his colleagues found that in a sample of 122 American business school students, men who were married or in a committed relationship had 21% lower salivary testosterone levels than those who were single. Peter Gray and his colleagues (2006) looked at testosterone levels in a group of men in Beijing, China, and they found that married non-fathers had slightly lower levels than unmarried men but the difference did not reach statistical significance; however,

they did find that married fathers had significantly lower levels than either of the other two groups. In a study in East Africa, Martin Muller and his colleagues (2009) compared testosterone levels between non-fathers and fathers in Hadza foragers and in Datoga pastoralists. Hadza fathers are much more involved in paternal care than Datoga fathers, thus Muller and his colleagues predicted that in the Hadza, testosterone levels should be lower in fathers rather than non-fathers, while in the Datoga, there should be no difference. This is exactly what they found: The intensive childcare given by Hadza fathers appears to suppress testosterone production. Note that there was no overall difference in testosterone levels between the Hadza and Datoga men.

These studies demonstrate that testosterone levels vary in human males according to their marital/parental status, and that these patterns can be observed in a variety of biological and cultural groups. They support the hypothesis that testosterone level is a modulator of, or reacts to, an individual male's reproductive situation. Burnham and colleagues (2003) point out that since testosterone may impair immune function and encourage risk-taking, lower levels of testosterone in married men may help explain the fact that married men generally are healthier and have lower mortality than unmarried men.

Hunting, Gathering, and the Sexual Division of Labor

Ecological research on contemporary hunter-gatherer groups has revolutionized our knowledge of how people without agriculture acquire the food they eat. This knowledge has informed models of how hunting and gathering patterns in hominins may have evolved. It has become increasingly clear that earlier speculations were based on inadequate understanding of hunter-gatherer lifeways (Lee & DeVore, 1968). The concept of "man the hunter, woman the gatherer" reflects a division of labor between the sexes in all human cultures, but it is all too easy to turn it into a simplistic, stereotypical picture of evolved, hardwired gender roles (Bird, 1999; Panter-Brick, 2002). Furthermore, observing sex differences in food acquisition practices is not the same as explaining why they exist.

In almost every traditional foraging culture, both men and women devote a substantial portion of their time and energy to the search for and acquisition of food. And in almost every culture, despite the fact that they live in the same environment, men and women exploit different aspects of that environment when acquiring food. This difference (along with the fact that women have responsibility for child bearing and rearing) underlies the traditional sexual division of labor, although not necessarily along the simplistic division that "men hunt and women gather." For example, among the aboriginal peoples of Mer Island in the Coral Sea, both men and women forage for food on the coral reef. Men concentrate on using large spears to kill large fish swimming around the edges of the reef while women walk the dry part of the reef, collecting shellfish or catching small fish or octopus with small spears. Women almost always succeed in bringing home a reasonable amount of food, whereas the men have much more variable success (Bird, 1999). In the Hadza of Tanzania, men concentrate on large game hunting while women focus almost exclusively on foraging for berries, nuts, fruits, and roots (O'Connell et al., 1992; Hawkes et al., 1997) (Figure 16.7 on page 508).

There are several models for the origins of the sexual division of labor. The *cooperative provisioning model*, based on the study of monogamous birds, predicts that the sexual division of labor occurred as a result of the evolution of monogamous relationships, because it would allow the pair to more fully exploit the environment if they

Figure 16.7 The evolutionary significance of “Man the Hunter” has been debated for decades.



plants (Weiner, 1988). Big yams aside, animals provide protein and fat in quantities not available from any other source, and animal food is almost always highly prized in human cultures. As Hilliard Kaplan and colleagues (2000, p. 174) state, “The primary activity for adult males is hunting to provide nutrients for others. . . [Hunting] is a fundamental feature of the human life-history adaptation.” But why do males provide nutrients for others?

WHY DO MEN HUNT AND SHARE MEAT? As we discussed earlier, male cooperative hunting and meat sharing, which we see in chimpanzees, may have a long history in hominin evolution. As hominins became more adept at hunting larger game that could not be butchered, transported, or consumed by a single individual, meat sharing may have become a central component of human culture. Sharing large game may have been the basis for food sharing in general becoming an important part of cultural unity and identity (Jones, 2007). A fascinating aspect of big game hunting in many cultures is that the hunter or hunters most responsible for the catch may have little to say about how the meat is distributed. Research among the Hadza in Tanzania shows that

did not compete with each other for resources (see discussion of Lovejoy’s model previously). An alternative model, the *conflict model*, suggests that hominin males and females were already exploiting the environment in fundamentally different ways before males began contributing energy and resources to females and their young (Bird, 1999). The sexual division of labor is not really a division but reflects the fact that males and females have different problems to overcome (conflicts) in the course of mating, reproduction, and parenting.

It is nonsensical to ask whether hunting or gathering is more important. Neither provides more energy than the other on a regular basis. The productivity of hunting and gathering varies by season, environment, and a host of other factors (Kaplan et al., 2000). Women and men do vary in the *package size* of the food they focus on acquiring (obviously, we are not talking here about packages in the supermarket). Women concentrate on small foodstuffs that tend to be predictable, immobile, and obtainable while caring for infants and young children. Even though she almost always receives assistance from others, including female relatives and the father of her children, an individual woman is responsible primarily for feeding herself and her children.

Men concentrate on obtaining foods in large sizes that they cannot consume at once by themselves and that they redistribute to families or the larger social group. These foods almost always come in the form of dead animals, which may be obtained by hunting, trapping, fishing, or even scavenging. In some Melanesian societies, however, men compete to grow the largest yams, which, although they are too fibrous to eat, can be distributed and used for propagation of new

a successful hunter may not even be able to recoup his losses via reciprocal altruism later (Hawkes et al., 2001).

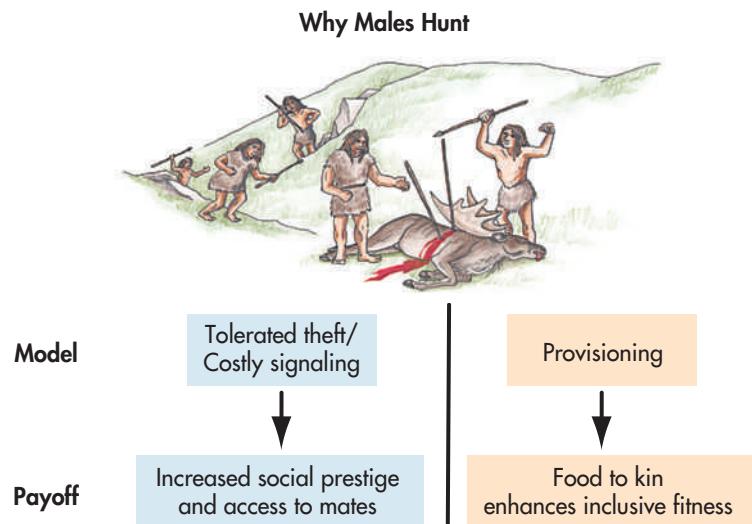
The *tolerated theft model* of hunting and meat sharing explains meat sharing in part by suggesting that defending a large kill takes more energy than it is worth; in other words, it may pay off in the long run to tolerate the “theft” of meat (that is, sharing) rather than to work hard to defend a kill (which may be too large for a single individual to consume). The reward for hunting would come not from the meat itself but from the increase in social status and prestige, which reflects on family members as well (Figure 16.8). In effect then, large animal hunting becomes a form of *costly signaling* (Bird, 1999), which ultimately increases the opportunities for males to acquire new mates. In the tolerated theft model, large game hunting did not evolve primarily as a means of paternal provisioning, although females and their young definitely benefit from males’ hunting activity.

Critics of the tolerated theft or costly signaling model argue that because most of the food that is shared after a hunt goes to close kin or reproductive partners, sharing enhances the fitness of the male hunter and therefore should be considered an adaptation (Hill & Kaplan, 1993). They suggest that the provisioning itself, not the costly signaling, is the fitness-enhancing aspect of the behavior. Kaplan and colleagues (2000) propose that hunting and meat sharing intensified in hominin evolution in the context of a pair bond and paternal investment in the young. Part of their evidence for this hypothesis is that reproductive-age women in hunter-gatherer populations almost always receive nutritional support from men. Because most of that support comes in the form of animals that have been hunted, and such altruistic behavior is much more likely to have evolved in the context of provisioning kin, paternal investment via hunting may be an adaptation, not simply a secondary result of hunting for social prestige.

In the costly signaling model, hunting by men and meat sharing evolved in the context of sexual selection. Hunting itself is not seen as a critical behavior in hominin evolution, and nutritional benefits to children may be an incidental outcome of the process (Bird, 1999). In contrast, advocates of the provisioning model give hunting and meat sharing a central role in hominin evolution: They argue that it was a prime impetus in the evolution of a larger brain and increased longevity (Kaplan et al., 2000). Proficient hunting can take a long time to learn, and studies of the Aché in Paraguay show that hunters do not achieve peak hunting proficiency until they are in their 40s (Walker et al., 2002). In the provisioning model, hunting and meat eating are coupled with learning and brain development to form the evolutionary basis of human society.

Resolution of the debate about why men hunt—for mates and prestige, or to provision—will require further study. Michael Gurven and Kim Hill (2009) have proposed a more comprehensive model of male hunting. They argue that the ultimate fitness benefits of hunting are the product of multiple potential proximate benefits (for example, mating opportunities, help with childcare, trade opportunities) coupled with the psychological and status benefits that accompany being a successful hunter. Gurven and Hill argue that male hunting may be ubiquitous in human cultures because there are multiple paths by which it can become an adaptive behavior. More data are needed, but unfortunately, the limited number of cultures that still practice a hunter-gather lifestyle (mostly in marginal environments) may make obtaining

Figure 16.8 Models for the evolution of hunting by males.



new data on the issue difficult. Obviously there is merit to both the costly signaling and provisioning views, but they cannot both be correct because they posit divergent views on the adaptive importance of hunting in hominin evolution.

Sexual Selection and Human Behavior

16.3 Understand sexual selection and how it has influenced some aspects of human reproductive behavior and patterns of sex differences in human behavior.

The study of human sexual behavior has been revolutionized over the past 30 years by the development of an evolutionary perspective on human reproductive strategies, sex and gender differences in behavior, and cross-cultural patterns of attractiveness and mate selection (Symons, 1979; Fisher, 1992; Buss, 2003). This evolutionary perspective is based in large part on the fact that humans are mammals. Male and female mammals vary profoundly in their energetic investment in producing offspring. Female mammals provide not only eggs but also a body in which fetal growth takes place. After birth, they are obligated to provide milk and care for offspring until the age of weaning. Males are obligated to provide sperm at the time of conception, and that is all. Subsequent investment, which can take the form of provisioning a pregnant or lactating female or providing food for the young, is not required, and in many species, including most primate species, males do not directly participate or invest in rearing of young.

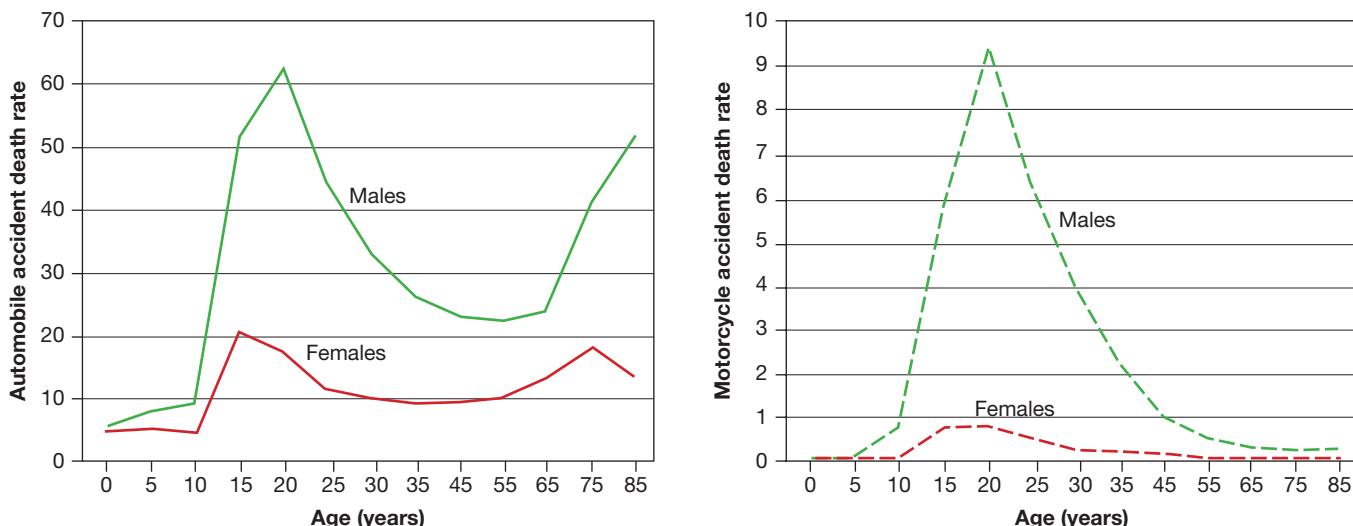
Mammalian males and females also vary in their reproductive potential. The energetic costs of gestation and lactation constrain a female mammal's reproductive potential; she can only have a limited number of offspring in her lifetime. On the other hand, sperm production does not impose much of a limit on a male mammal's reproductive potential. Given their energetic investment in reproduction, we would expect mammalian females to be choosier when selecting mates than males would be. Males should also be choosy, but if they are successful in impregnating a large number of females, choosing a specific, high-quality mate is less of an issue. In general, mammalian males compete for access to females, and mammalian females should choose high-quality males, however that is defined. We can also expect males to vary more in their reproductive success than females. For example, there may be a large number of males that never reproduce, whereas almost every female will find a reproductive partner.

Research on human mate selection and standards of attractiveness in different cultures indicates that women tend to value resource-providing ability in their partners, whereas men tend to value youth and appearance (indicators of reproductive potential) in their potential partners (Buss, 2003). These observations are consistent with predictions derived from mammalian evolutionary biology. Of course, these are statistical patterns generated from surveys of large numbers of individuals. Obviously, different cultures define sexual attractiveness differently, and there is much individual variation in sexual preferences. Nonetheless, according to many evolutionary researchers, the statistical patterns of sexual behavior that are observed across cultures are not easily explained by cultural convergence. Instead, they may reflect underlying behavioral trends that have been shaped by natural selection.

Risk-Taking Behavior

Sex difference in risk-taking behavior has long been recognized and found in several different behavioral domains. When we look across human cultures, we find that as a group young adult males (ages 15–29) have the highest death rates from accidents or violence (Figure 16.9). For example, death rates in motor vehicle accidents

Figure 16.9 Risk of death from passenger car accidents (solid lines) and motorcycle accidents (dashed lines) per 100,000 U.S. population during 1980–1986 for males (green lines) and females (maroon lines).



for 20-year-old Americans are three to four times higher in men than women (Hill & Chow, 2002). Young males do not die from accidents more often because they are unlucky but because they are more likely to put themselves in risky situations (Figure 16.10). Beyond accidents, young, single males take greater financial risks with their money compared to their female counterparts (Jianakoplos & Bernasek, 1998). In addition, laboratory studies (in which risk taking is assessed with a simulation) suggest that men respond to an acute stress by increasing risk-taking behavior, while women become more risk-aversive (Lighthall et al., 2009). Proclivity toward risk-taking behavior in males may reflect a significant sex difference in human behavior, which may have a long evolutionary history (Low, 2000).

Why should males engage in risk-taking behavior more than females? Bobbi Low (2000) argues that the reason goes back to general sex differences in mammalian biology. For a female mammal, the costs associated with risk-taking behavior are unlikely to outweigh the benefits. She is likely to be able to find mates and fulfill her reproductive potential throughout her lifetime, so she has no particular need to engage in risk-taking behavior to acquire mates. On the other hand, male mammals vary much more in reproductive success. A male mammal may engage in high-risk, potentially very costly (even life-threatening) activities because such behaviors could have a potentially high reproductive benefit. For example, aggressive behavior between male mammals over access to females is very common; it has clearly been selected for in the context of sexual access to mates. Females may also find risk-taking in males to be attractive because they may consider it a manifestation of ambition or “good genes” or a proxy for the ability to provide resources for the female and her offspring.

Elizabeth Hill and Krista Chow (2002) suggest that risky or binge drinking may also be understood in the context of sexual selection for risk-taking behavior. First, among college-age people, risky drinking is about 50% more common in men than women (48% versus 33%, although figures vary depending on criteria for defining a binge), and males are more likely to engage in driving after drinking. The peak age for alcohol abuse in males is 15 to 29 years. College men who were not married were twice as likely to engage in binge drinking as those who were married. These aspects of risky drinking in young men suggest to Hill and Chow that it is another manifestation of the evolved pattern of risk-taking behavior. They argue

Figure 16.10 Risk-taking behavior by young males.



that risk-taking behaviors are not deviant but that we should recognize them as an evolved response to environmental instability. With specific reference to risky drinking at the individual level, Hill and Chow suggest that dealing with instability in the person's family or work life may be one avenue of therapy for the treatment for alcohol abuse.

One possible evolutionary prediction based on the fact that men, especially young men, are especially prone to risk-taking and aggressive behavior is that when there are too many men in a population (as a proportion), then there will be more violence (Schact et al., 2014). This is also what one might predict by numerical common sense, and it is also supported by sociological studies that have shown high rates of murder in societies with male-biased sex ratios. Ryan Schact and colleagues, however, reviewed and analyzed sex-ratios and male violence in a range of cultures. They found that there is no evidence for male-biased populations to have more violence. In fact, female-biased populations may have an excess of violence, especially violence directed against women. In populations with an excess of females, males are more promiscuous and less involved in parenting, suggesting an increased intensity in male-male competition. Schact and colleagues argue that there are many factors influencing intra-sexual competition and violent behavior at a societal level. Sexual selection may underlie much of this behavior, but not in the classical and simple sense that more males means more competition and therefore more violence.

Inbreeding Avoidance and Incest Taboos

Evolutionary factors may have played an important role in shaping not only mate choice preferences but also mate choice aversions. Inbreeding is defined as reproduction between close relatives. Close inbreeding has several major biological costs (Rudan & Campbell, 2004). A highly inbred population or species loses genetic variability over time. Reduced variability means that the population cannot respond quickly via natural selection to environmental change. Populations with reduced variability also have fewer opportunities to evolve balanced polymorphisms maintained by heterozygous advantage.

The likelihood that lethal or debilitating recessive alleles will be expressed is increased when close relatives interbreed. Because relatives share a high percentage of their alleles, there is a greater chance (compared to unrelated individuals) that they will both possess the same lethal recessives that may be passed on to their offspring. Inbred individuals suffer from greater mortality or loss of fitness relative to less-inbred individuals in the same species; this phenomenon is known as **inbreeding depression** (Mettler et al., 1988). Studies of inbreeding in humans clearly demonstrate the potentially harmful effects of reproduction between first-degree relatives (such as father and daughter or sister and brother) and between relatives who share 25% of their alleles (such as uncle and niece or grandparent and grandchild). Offspring of first-degree relatives (who share 50% of alleles) are far more likely than other children to be stillborn or to die within the first year of life, and physical and mental abnormalities are much more common among them. Even in situations where inbreeding is less close than among first-degree relatives (such as in the many societies where first-cousin marriage is prescribed), there are costs to inbreeding in the form of higher rates of genetic disorders (Overall et al., 2002) and perhaps an increased accumulation of genetic risk factors for late-onset conditions such as heart disease and diabetes (Rudan & Campbell, 2004).

Up to half of all traditional cultures prescribe some form of *consanguineous* marriage, usually between first or second cousins or in some cases uncle-niece (Bittles et al., 1991). Alan Bittles and his colleagues argue that understanding the

inbreeding depression

Lesser fitness of offspring of closely related individuals compared with the fitness of the offspring of less closely related individuals, caused largely by the expression of lethal or debilitating recessive alleles.

effects of inbreeding requires looking at it in a broader social and demographic context. For example, women in consanguineous marriages typically start to reproduce at an earlier age, and thus their longer reproductive lives may compensate to some extent for the loss of fitness due to inbreeding depression. Estimates for increases in mortality of the offspring of first-cousin marriages are between 1.0 and 6.4%. This is a substantial increase, especially in a developed country, but as Bittles and colleagues point out, in a traditional setting with a high load of infectious and nutritional disease, the relative cost would not be as great, at least in the short term.

It is important to remember that only a very small proportion of all human births are the result of matings between first-degree relatives. Sexual contact between close relatives is rare, and the proportion of those contacts in which pregnancy could occur (in which both parties are sexually mature and sexual intercourse takes place) is also very small (Van den Berghe, 1983). Across the world's cultures, 2 to 3% allow matings between first-degree relatives, but this is usually only among elites, and it has the primary goal of consolidating resources or political power.

INBREEDING AVOIDANCE AND INCEST RULES All human cultures have rules and traditions that regulate sexual contact and reproductive relationships. **Incest** is any violation of such rules by members of a kin group. Incest rules are sometimes explicit (stated in legal or customary form) and sometimes implicit (followed but not overtly stated or codified). Definitions of kin vary from culture to culture and do not always closely follow biological patterns of relatedness. For example, in American culture, sexual contact between stepparents and stepchildren is generally regarded as being incestuous, although from a biological standpoint a pregnancy that resulted from such a mating would not constitute inbreeding.

incest

A violation of cultural rules regulating mating behavior.

Both cultural and biological scientists agree on the universality of cultural rules governing sexual relations between close kin—the *incest taboo*—but they differ on why it exists. For many years, Freudian ideas dominated cultural explanations of the incest taboo: Incest rules were necessary to prevent people from acting on their natural desire to commit incest. The evidence that people innately desire to commit incest is very slight, and the Freudian viewpoint, despite its historical popularity, has little cross-cultural, empirical support (Thornhill, 1991). Biological theories of inbreeding avoidance have focused on the fact that mechanisms that encourage outbreeding should be selected for; the cross-cultural universality of the incest taboo, which is essentially a mechanism for outbreeding, is taken to be evidence that such an adaptive mechanism may be present in the human species as a whole.

A basic social science criticism of the biological evolutionary view of inbreeding avoidance asks, Why do cultures make laws against it? If it is biological, the argument goes, then there should be no need to have cultural laws or institutions to prevent it. Nancy Thornhill's (1991) analysis of incest rules suggests that most of them are more concerned with regulating sexual (and economic and power) relationships between more distantly related kin; incest taboos among close relatives are more likely to be implicit than explicit. Thus the assumption that most cultures regulate inbreeding between close relatives using explicit cultural rules is unfounded.

BROTHER-SISTER INBREEDING AND THE WESTERMARCK HYPOTHESIS Finnish anthropologist Edvard Westermarck (1891) long ago suggested, in what became known as the *Westermarck hypothesis*, that siblings raised together develop an aversion to seeing each other as reproductive partners when they are adults. In order for the aversion to develop, siblings must be in proximity to one another during a *critical period*, usually thought to encompass the first 5 years of life. The psychological

Figure 16.11 Children in a kibbutz.



mechanism governing this aversion may be an adaptation because it was probably selected for as a mechanism to promote outbreeding.

Evidence for the Westermarck hypothesis comes from a variety of sources, including some natural experiments. In the mid-twentieth century, the *kibbutz* movement in Israel led to the establishment of numerous small, independent communities dedicated to socialist and egalitarian principles. Similarly aged boys and girls were raised communally in children's houses in some of these kibbutzim (Sheper, 1983) (Figure 16.11). In his groundbreaking study, anthropologist Joseph Sheper found that of 2,769 marriages between children raised in kibbutzim, only 14 united couples had been reared in the same children's house. Sheper interpreted these results as strong evidence for the Westermarck hypothesis. The child-rearing arrangement in the kibbutz "fooled" biology (and the psychological mechanism leading to sexual aversion) by bringing unrelated children into close proximity with one another during the critical period. In usual circumstances, children raised in close proximity to one another are close relatives, and there should be strong selection pressures against them mating with one another. Thus kibbutz children raised in the same children's house saw each other as siblings and did not see their housemates as potential spouses.

Similar evidence supporting the Westermarck hypothesis has been obtained from the study of *sim-pua* marriages in Taiwan (Wolf, 1966, 1970). *Sim-pua* is a form of arranged marriage whereby a girl is adopted into a household at a young age and then later expected to marry a biological son of the same family when they are older. These marriages were found to have much higher rates of divorce and lower numbers of offspring than non-*sim-pua* marriages. Anthropologist Arthur Wolf, who conducted the research, suggests that these marriages often failed because of a sexual aversion that developed between the adopted sister and her brother/groom who were raised in close proximity during the critical period.

The Westermarck hypothesis is supported by evidence from these diverse natural experiments and is based on a strong theoretical foundation in the context of the biological costs of close inbreeding (although see Shor & Simchai, 2009, for a critique). It applies only to sibling inbreeding avoidance, of course. Clearly, different biological or cultural mechanisms would have to regulate intergenerational inbreeding avoidance.

Language-Related Cross-Cultural Behaviors

16.4 Recognize how motherese and basic color terms reveal the biological influences on language expressed in a cultural context.

Earlier, we discussed the evolution of language, a behavior (in a very large sense) that almost all scientists agree is a biological universal in our species (see Insights and Advances: The Evolution of Languages on page 516–517). It is not surprising that something as pervasive and essential as language has multiple effects on several aspects of human behavior. Many anthropologists believe that language is what makes human culture possible. Indeed, when we look at the central place of language in defining a specific culture, we could argue that cultural diversity is inevitable given that languages themselves evolve and diverge. And yet, even beyond the basic biology and structure of language, cross-cultural patterns emerge that we can best explain from a broader evolutionary perspective.

motherese (infant-directed speech)

Emotive spoken language used by mothers and other adults when addressing prelinguistic babies and children.

Motherese or Infant-Directed Speech

Human infants are remarkably proficient at acquiring language. If they are placed in an environment where language is used, they will pass through a series of stages that, typically by the age of 3 years, result in a fully linguistically competent human being (Pinker, 1994). *Language development* entails training of both the mind and the body: the body to produce sounds and the mind to put them in the correct order to produce language. A critical stage in language development in babies is *babbling*. Starting at about 7 to 8 months of age, babies start to say syllables such as *ba-ba* or *da-da*. This is the beginning of the production of spoken language. Even babies who are born deaf babble with their hands as they learn sign language (Petitto & Marentette, 1991) (Figure 16.12).

The stages of language development that babies go through form a kind of cross-cultural behavioral universal. But language development is so clearly biologically hardwired, and babies have so little cultural exposure, that it does not make much sense to think of it in terms of cross-cultural universals. In contrast, the way adults talk to babies seems to be much more of a culturally influenced behavior.

As we look at how adults talk to babies in different cultures with very different languages, we find striking similarities in their use of **motherese or infant-directed speech** (Ferguson, 1964; Fernald et al., 1989). Compared with adult-directed speech, speech directed at infants tends to be slower, higher-pitched, and more repetitive, with shorter utterances and longer pauses. Most of us are familiar with what baby talk sounds like; it tends to sound the same in a wide variety of languages (Figure 16.13). In fact, one study has shown that native English-speaking mothers could differentiate between adult- and infant-directed Hindi language song excerpts with much greater success than chance suggests (Trehub et al., 1993).

Although *motherese* is not universal, it is widespread and found in diverse cultures that do not share a recent common origin. One

Figure 16.12 A deaf baby attempting to sign.



Figure 16.13 Motherese may be just one of many ways the emotional bond between mother and child is reinforced.



Insights and Advances



Sir William Jones

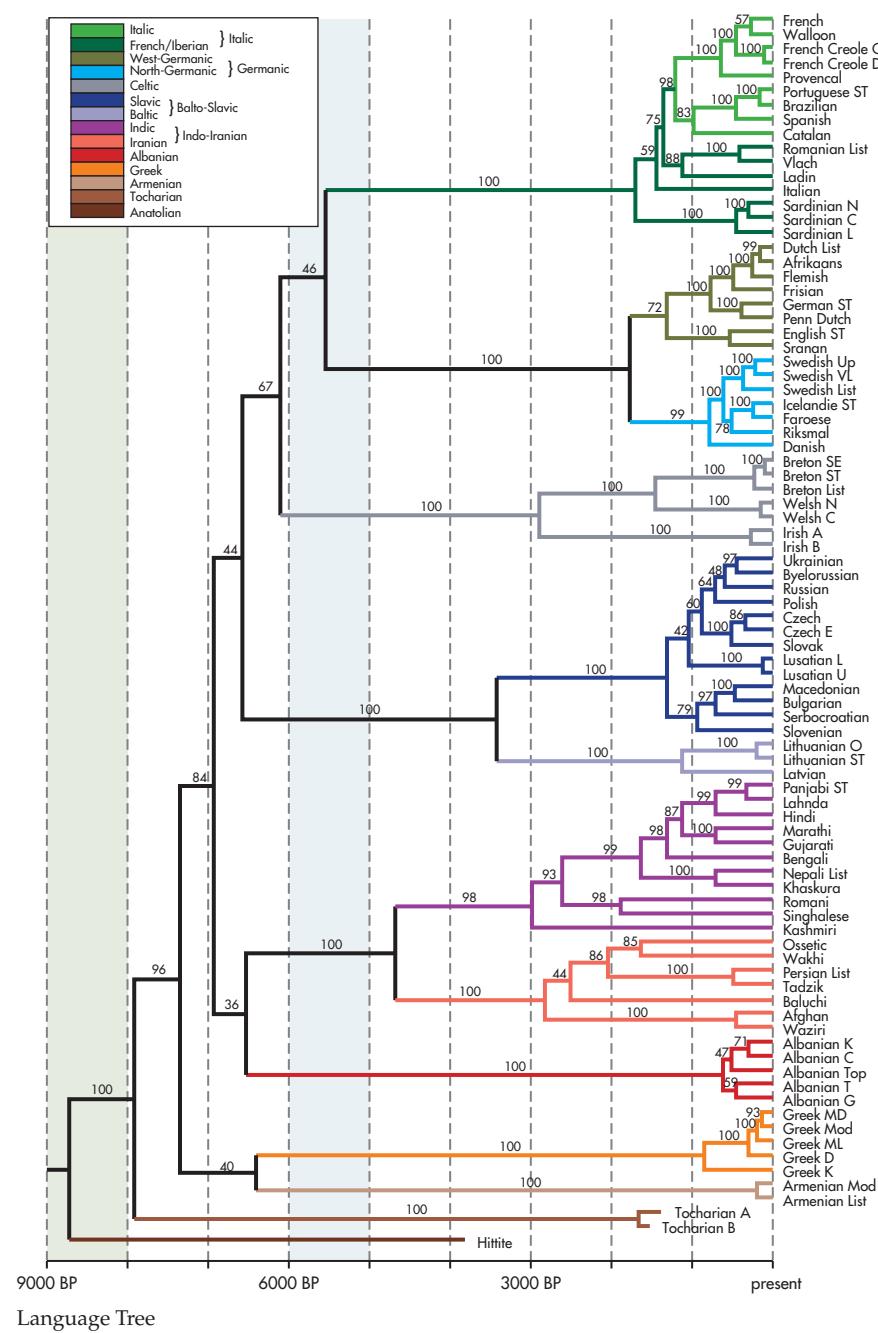
The Evolution of Languages

The earliest scientific application of evolutionary logic was not produced by a biologist trying to understand the origins of a species or how a particularly interesting adaptation arose. Instead, linguists trying to figure out how languages such as Greek, Latin, Sanskrit, and several others could have so many similarities, despite such apparently diverse cultural sources, were really the first evolutionists. In 1786, William Jones, a British lawyer working in India, suggested that these languages arose from a single common language in the past, one that no longer existed. Eventually, this language family would be called *Indo-European* and the source language became known as *proto-Indo-European*. The basic framework of descent and diversification from an extinct ancestor represents a thoroughly evolutionary way of thinking, long before Darwin published *On the Origin of Species* in 1859. During the 1850s and 60s, a German linguist named August Schleicher presented evolutionary relationships among Indo-European languages in tree-like form; he was the first to illustrate evolutionary relationships of any kind in this way. Darwin famously included only one evolutionary tree in the first edition of *On the Origin of Species* (between pages 117 and 118), and it was not really a phylogenetic tree at all but an illustration of theoretical species diversification.

Over the past 150 years or so, evolution has of course come to be more closely associated with biology rather than linguistics, although the field of historical linguistics has continued to explore language relationships and diversification. In recent years, there has been renewed interest in using evolutionary methods in the reconstruction of language relationships. Specifically, the sophisticated methods of phylogenetic reconstruction developed for analyzing genomic and other kinds of voluminous genetic data can be applied to languages and language families with much apparent success.

For example, phylogenetic reconstructions of the relationships within the Indo-European and Austronesian language families have served to help illuminate the distant histories and prehistories of their speakers (Gray and Atkinson, 2003; Gray et al., 2009, 2011). Archaeological and other sources of information can be used to support two alternative locations for the origins of the Indo-Europeans. One model suggests that the proto-Indo-European peoples emerged from the pastoralist Kurgan culture of southern Russia and Ukraine, when this group of semi-nomadic, warrior-horsemen rapidly expanded out of their homeland 5,000–6,000 years ago. An alternative model puts the origins of the Indo-Europeans at an earlier date, 8,000–9,500 years ago, with a source population in Anatolia (present-day Turkey). This expansion was a result of a wave of agriculturalists moving outwards from Anatolia and into Europe. Using standard evolutionary methods, Russell Gray and his colleagues created a phylogenetic tree of eighty-seven Indo-European languages, ranging from Icelandic to Hindi. They found that the consensus tree they created for Indo-European languages was much more consistent with an Anatolian origin of Indo-Europeans; however, the tree also indicated a great diversification of languages 6,000–7,000 years ago, which could align with Kurgan expansion. Gray and colleagues' evolutionary analysis of Indo-European thus revealed support for both archaeological models (with support for ultimate origins in Anatolia), which are not actually mutually exclusive. Their analysis of Austronesian languages, which originated in Taiwan about 5,000 years ago and spread out through the Philippines, island Southeast Asia, Oceania, New Guinea, and Polynesia, and even all the way to Madagascar, suggests a series

idea about motherese is that it is not directly related to teaching language but instead strengthens the emotional bond between mother and infant (Fernald, 1992). Compared with adult-directed speech, infant-directed speech is less emotionally inhibited; more emotional forms of adult-directed speech more closely resemble infant-directed speech (Trainor et al., 2000). There can be no doubt that babies do not understand the words in baby talk, but it clearly provokes some response or adults would not persist with it. Anne Fernald argues that motherese helps establish emotional communication between the mother and infant before the development of verbal language.



of “pulses and pauses” leading to a complex pattern of colonization and expansion of Austronesian speakers.

Both the Indo-European and Austronesian language trees reflect relatively recent evolutionary events, at least in the broader context of human evolution. Theoretically,

Baronchelli and colleagues do not see a universal grammar, but a brain that is universally capable (at least in childhood) of learning many different languages and their very diverse grammars.

since spoken language presumably started somewhere at some time, with a specific group of people or proto-people, we might be able to use contemporary languages to trace back to the original language, just as we can use Indo-European languages to reconstruct proto-Indo-European. Some linguists have attempted to do this, or at least attempted to create higher level, super-groups of related languages. Most linguists and other interested scholars remain highly skeptical of our ability to reconstruct a “proto-human” language, however. Languages are simply too diverse and change too quickly for reconstructive efforts to be successful going all the way back to the beginning (which is now known to be on the order of 200,000 years ago for modern humans, rather than the 50,000 years that was once thought to be a reasonable estimate).

The great extent of language diversity and the speed with which languages change pose an interesting evolutionary problem: How can humans basically share a biological foundation for spoken language, yet manage to deal with the great cultural diversity of languages in general? Andrea Baronchelli and colleagues (2012) suggest that the rapid pace of cultural evolution in the hominin lineage has selected for biological adaptations for flexible learning. There has been an ongoing feedback in the evolution of language (in the biological sense) and languages (in the cultural) sense, such that the cultural adaptation of language has “recruited” pre-existing brain regions for the production of language.

As we learned earlier, the mother–infant relationship is the fundamental relationship in primate societies, and it is based in part on the development of a strong emotional bond between mother and child. Motherese may serve as an adaptation to facilitate the emotional development of the mother–infant bond, which is expressed through the mother’s spoken language. Anthropologist Dean Falk (2004) sees an even greater significance for the communication between primate mother and infant—that in early hominins, this relationship may have served as an evolutionary nursery (so to speak) for the development of language. Falk notes that chimpanzees and bonobos

use a variety of vocalizations and gestures for communication between mothers and infants. She argues that these vocalizations and gestures became more elaborate and important in early hominin evolution. With the adoption of bipedality and expanded foraging ranges, combined with the fact that human babies are relatively helpless and unable to cling to mothers as other primate infants do, Falk suggests that the elaboration of ape-like motherese was necessary for mothers to soothe and comfort their infants for the increasing amount of time of separation between the mother and child. She hypothesizes that the beginnings of language can be traced to this essential relationship.

Basic Color Terms

A trip to the paint store or a glance at a large box of crayons could lead you to believe that there is an almost unlimited number of color names. But if we look beyond the “peach parfaits” and “iceberg whites” of the world, we see that we can limit the number of *basic color terms* to a much smaller number. Anthropological linguists Brent Berlin and Paul Kay published a groundbreaking study in 1969 in which they analyzed color terms used by native informants speaking a wide range of languages and found significant constraints on the ways in which languages identify color. Color term data on more than 100 languages are now available (Kay & Berlin, 1997).

Berlin and Kay defined basic color terms as single words used to describe colors that can be applied to a wide range of objects, that are widely known within a culture, and that are not subsumed into a more inclusive color category (for example, *green* is a basic color term but *lime* is not). Berlin and Kay did not find that the actual words used to describe colors are similar cross-culturally; rather, the naming of colors appears to follow a systematic and perhaps evolved or evolutionarily constrained pattern. In cultures that identify only two *focal colors*, or colors that exemplify the basic color categories, these always correspond to black and white (light and dark). In cultures that have three color terms, the named colors are always black, white, and red. In cultures with four terms, the colors are black, white, red, and blue/green/yellow. Above four color terms, patterns are still evident, although they are more variable and complex. The cross-cultural distribution of color terms suggests a cultural evolutionary scenario for developing color terms: The black-versus-white distinction came first, followed by the addition of red and then other colors.

English has eleven focal colors: black, white, red, yellow, green, blue, brown, purple, pink, orange, and gray. In contrast, the Dani of New Guinea recognize only two colors: *mola* for bright, warm colors and *mili* for dark colors (Figure 16.14). Although these are the only two color terms that the Dani use, the color terms themselves do not constrain the Dani perception of the variety of colors in the world. In a series of studies, psychologist Eleanor Rosch (Heider) found that Dani people have no trouble remembering or differentiating between colors or hues for which they have no name (Heider, 1972).

Color naming patterns probably are constrained by factors related to the physiology of color vision and perception (Dedrick, 1996). Color vision is extremely important to anthropoid primates, including human beings, and our color vision system reflects a long evolutionary history; it comes as no surprise that cultural color naming behaviors might be strongly influenced by this adaptation to the environment. Since 1969, a vast amount of research has been done on color naming, and the cross-cultural sequence of acquiring color terms probably is more complicated than outlined above especially as we get beyond four color terms. Nonetheless, given the infinite number of colors and names that human perception and language could generate, there can be little doubt that this cultural behavior is constrained by some aspect of our perceptual biology.

Figure 16.14 English and Dani basic color terms.

| English Color Terms | Dani Color Terms |
|------------------------|---------------------|
| | black |
| | white |
| | red |
| | yellow |
| | green |
| | blue |
| | brown |
| | purple |
| | pink |
| | orange |
| | gray |

mili

mola

Behavioral Disease

16.5 Discuss how human behavioral diseases are culturally universal and how conditions such as addiction and depression are related to adaptive aspects of cognition.

Anthropologists and psychiatrists once thought mental illnesses and behavioral diseases were limited to civilized cultures (Allen, 1997). However, studies of the cross-cultural distribution of mental illness show that many behavioral diseases are expressed in much the same way in different cultures (Murphy, 1976) (Figure 16.15). In modern biological psychiatry, mental illnesses are considered to result primarily from the interaction of genetic predispositions and environmental factors. Because many genetically influenced behavioral disorders are common, and we cannot explain their prevalence by mutation rate or environmental factors alone, it is reasonable to explore the evolutionary factors that may underlie their distribution. Note that this does *not* mean we should necessarily consider the behavioral diseases themselves to be adaptive, but rather that we may better understand them in the context of behavioral phenotypes shaped by natural selection.

Figure 16.15 A Yoruban with a psychotic disorder.



Depression and Natural Selection

Psychiatrists define *mood* as a persistent emotional state. Over the course of a lifetime, all people go through periods of high or low mood. Changes in mood in response to the environment or particular events are only natural. For example, low mood, or *minor depression*, is a perfectly reasonable response to an unhappy event, such as the death of a loved one. On the other hand, when depression gets out of hand and strongly affects a person's ability to function or care for himself or herself, then it is clearly not an adaptive behavioral phenotype. Psychiatrists say that a person has *major depression* if he or she suffers from 2 or more weeks of depressed mood or impaired enjoyment, disturbed sleep and appetite, psychomotor changes (such as restlessness or feeling slowed down), reduced concentration, excessive guilt, or suicidal thoughts or actions (American Psychiatric Association, 1994). Major depression is surprisingly common, with about 16.2% of Americans suffering from it at some point in their lives (Kessler et al., 2003).

Why is major depression so common? In its severe form, depression is clearly not adaptive because it not only leads to increased mortality via suicide but also diminishes a person's ability to respond to all kinds of environmental and social stimuli. The genetics underlying mood are undoubtedly complex, but many studies have shown that there is a genetic component to developing major depression, and several candidate alleles have been identified (Lohoff, 2010). It is likely that, as with other phenotypes influenced by multiple genes (such as stature), there is a normal distribution in the expression of mood, with people at one extreme suffering from major depression.

MINOR DEPRESSION AS AN ADAPTATION Evolutionary psychiatrist Randolph Nesse (2000) suggests that, in general, minor depression, or low mood, is a psychological and physiological mechanism that regulates our behavior when we are placed in any situation that might constitute an adaptive challenge. Minor depression is common because decreased motivation or activity is beneficial in many situations. For example, over the course of hominin evolution, the loss of a loved one probably signaled a number of things: a dangerous situation, loss of information, loss of a contributing member to the community or family, and loss of future contributors to the community (in the case of children) (Figure 16.16 on page 520). Whatever the particular situation, temporary low mood would encourage the surviving individuals to disengage from activity in the short term, allowing them to establish new goals and directions.

Figure 16.16 Grieving behavior can have common expressions in different cultures.



Major depression is increasing in developed countries and becoming a larger health problem. Why? Nesse suggests that another possible adaptive function of low mood is to dissuade people from wasting energy in the pursuit of unreachable goals. Most people living in hierarchical societies (in which resources and power are not distributed equally) face an ongoing conflict between their knowledge of a more prosperous life and their inability to achieve it. According to Nesse, the contemporary media culture exacerbates this conflict by presenting a range of unachievable goals while promoting the pursuit of such goals as a cultural ideal.

In the environments in which it evolved, low mood is a short-term adaptation to a transient challenge; once the challenge or event is over, mood improves. However, in contemporary urbanized societies, people live in an environment in which challenges to status or goal achievement are ongoing, encouraging the development of persistent low mood. This persistent low mood can slip into major depression in genetically susceptible individuals.

Of course, Nesse's hypothesis on the adaptive nature of depression is speculative. However, we know that mood is important in all social primates: Whether or not we want to say they are "happy" or "sad," it is clear that we can see social primates exhibiting high or low mood. Mood has been shaped by millions of years of evolution in a social context. Thus sociocultural factors, such as the development of a media culture, may indeed be playing a role in the expression of mood and the increased development of major depression.

Schizophrenia

Schizophrenia is the chronic brain disease most typically associated with cultural notions of crazy behavior or insanity. It is found in almost all human cultures, with a lifetime prevalence typically estimated to be somewhere between 0.5 and 1.0% (Jablensky et al., 1992). Although that percentage seems low, it translates into nearly 3 million people with schizophrenia in the United States alone. Schizophrenia is characterized by several symptoms, including delusions (often of a paranoid nature), auditory hallucinations, disorganized speech, grossly disorganized or catatonic behavior, and negative symptoms, which are characterized by emotional flattening, not talking, or not moving (American Psychiatric Association, 1994). Age of onset typically is the late teens into the twenties (usually a bit later in females than males), and the course of illness is highly variable.

Schizophrenia is clearly a genetic disease. Evidence of its origin comes from a variety of sources; among them is the fact that a family history of schizophrenia is associated with a much higher risk of developing the disease. However, concordance rates for identical twins tend to be no higher than 50% (Gottesman & Shields, 1982), indicating that some people carry the alleles that predispose development of

schizophrenia but do not develop the illness. Recent genomic research has revealed that there is a large number of diverse alleles associated with the condition; there is some evidence (still controversial) that a large number of common alleles with small individual effects can explain a reasonable proportion of the heritability for schizophrenia (Mowry and Gratten, 2013).

WHY IS SCHIZOPHRENIA SO COMMON? The basic evolutionary question about schizophrenia is, Why is it so common? The estimated prevalence rate of 1% is much higher than can be maintained via mutation rate alone, whether schizophrenia is caused by the effect of a single major allele or of multiple alleles. In addition, numerous studies conducted over the past century have shown that people with schizophrenia, particularly males, have reduced fertility and fitness (Nimagaonkar et al., 1997). This is not surprising because the disease strikes at an age when people are entering their reproductive years.

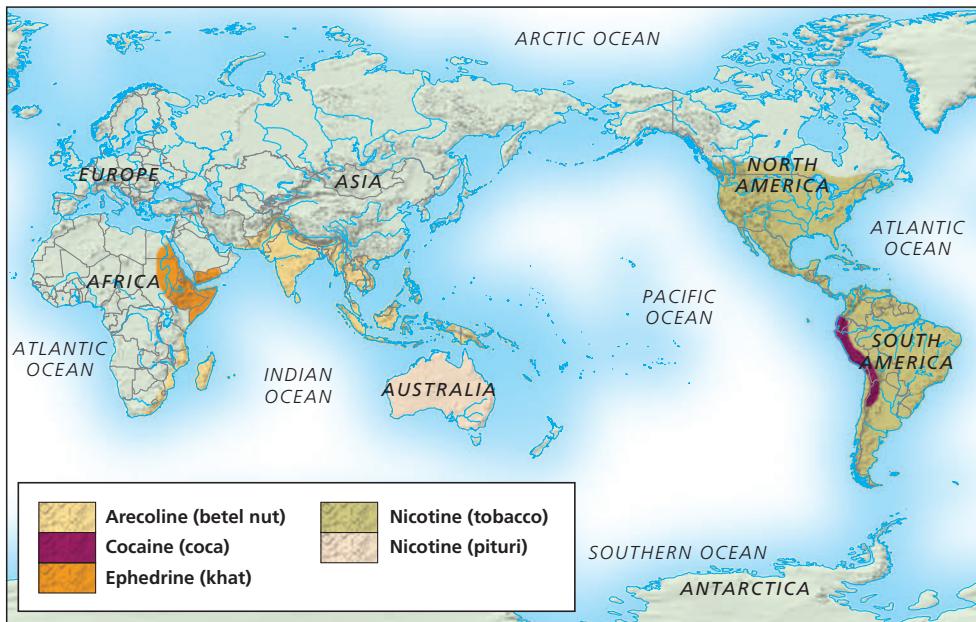
Because schizophrenia is associated with reduced fertility and is a genetic condition, the alleles underlying the condition eventually should be eliminated from the population by negative selection. This does not seem to be happening. If anything, over the past 200 years schizophrenia seems to be getting more rather than less common, and it may be more common in large, developed societies than in traditional ones (Allen, 1997). The clinical schizophrenia phenotype itself obviously is not adaptive because it leads to demonstrably reduced fitness. Individuals who carry schizophrenia-causing alleles but who do not develop the disease may have some characteristics that help them to reproductively compensate for the loss of alleles in individuals who have full-blown schizophrenia.

Since the 1960s, numerous theories have been offered to explain the evolution of schizophrenia (see Polimeni & Reiss, 2003, for a review). Given the reduced fitness of individuals who have schizophrenia and the current understanding of the genetics underlying the condition, it is reasonable to suggest that schizophrenia alleles are being maintained in human populations as a balanced polymorphism (Huxley et al., 1964; Allen and Sarich, 1988). Although some argue that schizophrenia is simply a by-product of human brain evolution or of a combination of genetic load and mutation (Keller and Miller, 2006), several researchers have looked at the alternative phenotypes associated with the schizophrenia genotype to explain how a small reproductive advantage (on the order of 5% [Kidd, 1975]) in the healthy relatives of schizophrenic patients could maintain the alleles in the population. What exactly that advantage might be has yet to be determined. It could be physiological, behavioral, or even some combination of several factors.

Psychoactive Substance Use and Abuse

The consumption of *psychoactive substances* (drugs) seems to be a cross-cultural human universal, and its history dates back tens of thousands of years. The most commonly consumed psychoactive substances are alcohol, tobacco, betel nut (used throughout south and Southeast Asia and Oceania), opium and its derivatives, coca and cocaine (coca leaves are a mild stimulant when chewed; cocaine is a concentrated form of the active ingredient), cannabis (marijuana), caffeine, and khat (chewed in East Africa) (Smith, 1999; Sullivan & Hagen, 2002) (Figure 16.17 on page 522). Contemporary psychoactive drugs for the most part appeared with the development of agriculture, starting between 10,000 and 15,000 years ago. Pre-agricultural peoples undoubtedly used available psychoactive substances in plants, although large and steady quantities of such substances did not become available until the development of agriculture (Smith, 1999).

Psychoactive drugs generally work by mimicking the effects of neurotransmitters found in the nervous system or by stimulating the production of neurotransmitters that influence behavior or mood. Biological research on *drug addiction*, or *substance dependence*, indicates that both genetic and environmental factors play key roles in the

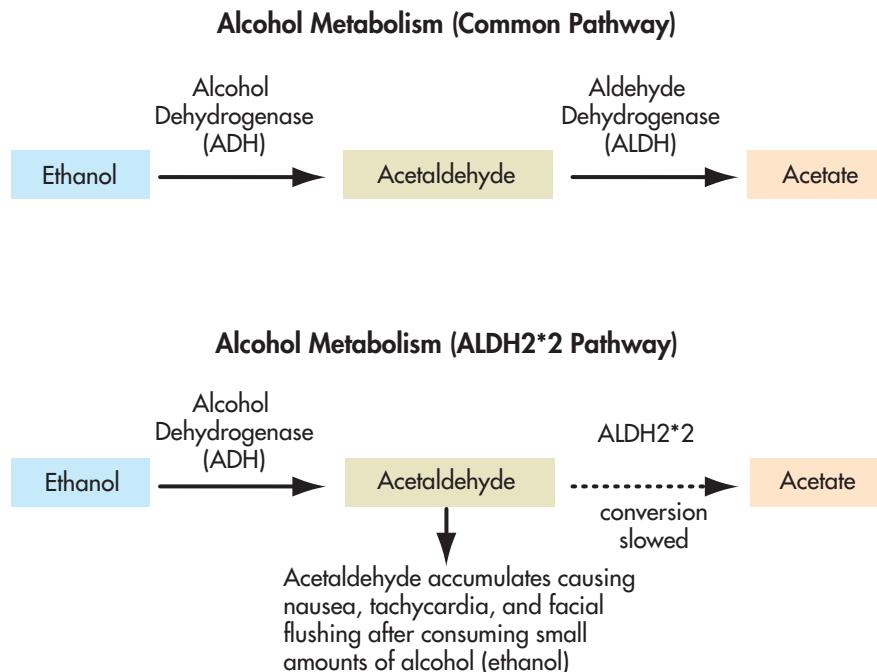
Figure 16.17 Worldwide map of traditional psychoactive substance use.

development of drug dependence. A person with a substance dependence problem exhibits the following: tolerance to the effects of a drug, leading to the use of increasing amounts; psychological or physiological withdrawal if the drug is removed, making giving up the drug difficult; and use of the drug despite knowledge of the negative consequences of continued usage.

GENETIC POLYMORPHISMS ASSOCIATED WITH PSYCHOACTIVE SUBSTANCE DEPENDENCE Much biological research on drug dependence has focused on the neurotransmitter *dopamine*. Dopamine is an important component of the pleasure and reward system in the brain. Stimulants, opiates, nicotine, and THC (the active ingredient in marijuana) all affect this neurotransmitter system (Enoch & Goldman, 1999). A whole range of addictive behaviors (including drug addiction, gambling addiction, and so on) may be related to polymorphisms in dopamine receptor genes (Blum et al., 1996). Specifically, individuals with severe addiction problems may be much more likely to carry an allele associated with a reduction in the total number of dopamine receptors. These individuals appear to need more of a stimulus (drug or activity) to derive a sense of reward or pleasure. Therefore, they are at higher risk for increased drug usage and ultimately substance dependence. Although there is controversy over whether eating should be associated with addiction, there is evidence that dopamine-mediated food reward pathways in the brain are different in obese and normal weight individuals (Allen, 2012).

In contrast to reward deficiency syndrome, a different polymorphism may make addiction to a specific drug—alcohol—less likely than usual (Enoch & Goldman, 1999). *Ethanol* (the alcohol we consume) is metabolized first to acetaldehyde by the enzyme *alcohol dehydrogenase* (ADH) and then to acetate by *aldehyde dehydrogenase* (ALDH). Acetaldehyde is the chemical that produces facial flushing, tachycardia (increased heart rate), and nausea in some people after the consumption of alcohol. In most people acetaldehyde does not accumulate in the body because it is quickly converted to acetate (Figure 16.18). However, alleles found in some East Asian populations lead to a buildup of acetaldehyde in the body, either increasing its rate of synthesis or decreasing its rate of conversion to acetate. For example, an allele *ALDH2*2* (due to a single amino acid substitution in ALDH) is found with a frequency of 35%

Figure 16.18 Genetic variation in the metabolism of alcohol.



in the Japanese population. This allele causes a buildup of acetaldehyde in the body, leading to facial flushing and other unpleasant side effects after even modest alcohol consumption. *ALDH2*2* heterozygotes and homozygotes both experience facial flushing; their risk of developing alcoholism is one-tenth to one-fourth that of those who do not possess the allele. No *ALDH2*2* homozygote individual has ever been observed to be an alcoholic, presumably because their physiology prevents them from ever consuming enough alcohol to become dependent on it.

EVOLUTIONARY PSYCHOLOGY THEORIES ABOUT PSYCHOACTIVE SUBSTANCE USE AND ABUSE Randolph Nesse and Kent Berridge (1997) have taken the view that psychoactive substances are an evolutionarily novel feature of the contemporary environment. They argue that psychoactive drug use cannot be adaptive because it so fundamentally disrupts longstanding emotional mechanisms that have been shaped by natural selection. Drugs that simulate positive emotions (heroin, cocaine, alcohol, marijuana, and amphetamine) send false signals of fitness benefit, which in turn has the potential to disrupt a person's entire biological system of "wants" and "likes." Drugs that block negative emotions or reduce anxiety are potentially even more disruptive because they remove the body's signals to take action or to avoid potential threats.

Roger Sullivan and Ed Hagen (2002) provide a different evolutionary analysis of human psychoactive substance use. They argue that hominins have probably had a long-term evolutionary relationship with psychoactive substances. With the exception of alcohol, most of the active ingredients of commonly used psychoactive drugs are formed naturally in plants and are similar to neurotransmitters found in the brain. Sullivan and Hagen argue that we benefit from consuming small quantities of these neurotransmitter-like chemicals in the same way that we need to consume small quantities of essential vitamins and minerals. An interesting point raised by Sullivan and Hagen is that in many traditional cultures, no distinction is made between drugs and food. People consume food for sustenance and to have more energy; for example, some traditional cultures classify tobacco as a food. Much psychoactive substance use in traditional cultures is associated not with developing a hedonic rush

(“getting high”) but with gaining increased stamina in a marginal environment (such as the Australian desert or Andean mountains). Even today, nonhedonic substances constitute most drug consumption (caffeine, nicotine, arecoline in betel nuts). Sullivan and Hagen hypothesize that psychoactive drug use in past environments could have been adaptive (providing increased stamina and neurotransmitters), although it may not be so in contemporary environments, which are characterized by easy access to both food and psychoactive substances.

Human behavior is remarkably diverse. An evolutionary perspective is one of many complementary ways to understand why people do what they do. It is not sufficient on its own to serve as a comprehensive explanation for human behavior, but millions of years of evolution have shaped our behavior in ways both subtle and profound. The evolution of human behavior is a relatively new academic field, so there is still much work to be done on this intriguing topic.

Summary

STUDYING THE EVOLUTION OF HUMAN BEHAVIOR

16.1 Define the four approaches used to study the evolution of human behavior, and explain how cross-cultural research can inform evolutionary perspectives on behavior.

- The complexity of human behavior requires different perspectives to understand its evolution.
- Paleontological reconstructions, ecological studies of people living in traditional settings, modeling the interaction between biology and culture, and psychological approaches are all used to understand the evolution of behavior.

TRADITIONAL LIVES IN EVOLUTIONARY ECOLOGICAL PERSPECTIVE

16.2 Discuss how ecological studies of human behavior can be used to test evolutionary predictions about human behavior, and illustrate the relationship between progesterone and testosterone to human reproductive behavior.

- Human ecologists study traditional societies that may more reasonably reflect the conditions under which human behavior evolved rather than contemporary societies.
- Associations between economic success and increased fitness may have been important in human evolution.
- Links between physiology and behavior have been studied by looking at hormonal profiles in males and females.

SEXUAL SELECTION AND HUMAN BEHAVIOR

16.3 Understand sexual selection and how it has influenced some aspects of human reproductive behavior and patterns of sex differences in human behavior.

- The sexual division of labor is found in almost all human cultures.
- Evolutionary models to explain its evolution focus variously on cooperation and competition between the sexes.
- Increased risk-taking behavior in males (especially younger ones) and females may have an evolutionary basis and myriad social implications.
- Studies of inbreeding avoidance suggest that human reproductive and sexual behavior are shaped by a range of biological and cultural factors.

LANGUAGE-RELATED CROSS-CULTURAL BEHAVIORS

16.4 Recognize how motherese and basic color terms reveal the biological influences on language expressed in a cultural context.

- Motherese is a form of communication that adults use when speaking to infants; it is observed in cultures throughout the world. One hypothesis is that the origins of language may be traced to verbal communication between mothers and their infants in early hominin evolution.
- Basic color terms in different languages may reflect physiological constraints related to visual color processing.

BEHAVIORAL DISEASE

16.5 Discuss how human behavioral diseases are culturally universal and how conditions such as addiction and depression are related to adaptive aspects of cognition.

- Although major depression is a serious and debilitating condition, minor depression may be adaptive in the sense that reduced motivation or activity may be a reasonable response to a variety of situations.
- Human variation in alcohol metabolism influences individual risk for becoming alcoholic.
- Psychoactive substance use may have a long history in human evolution, although the widespread availability of large quantities of these substances in the current environment may be unprecedented, leading to their abuse.

Review Questions

- 16.1 How do universal cognitive patterns give us insights into the evolution of human behavior?
- 16.2 How does parenthood affect testosterone levels in men?
- 16.3 How does risk-taking behavior potentially relate to evolved reproductive strategies?
- 16.4 What is special about infant-directed speech?
- 16.5 How are some behavioral diseases related to broader aspects of human behavioral evolution?

Key Terms

bridewealth, p. 504
cognitive universals, p. 502
cross-cultural universals, p. 502
environment of evolutionary adaptedness (EEA), p. 501

evolutionary psychology, p. 501
human evolutionary ecology, p. 501
inbreeding depression, p. 512
incest, p. 513

motherese (infant-directed speech), p. 514
progesterone, p. 505
sociobiology, p. 500
testosterone, p. 506

Chapter 17

Bioarchaeology and Forensic Anthropology



Learning Objectives

- 17.1** Describe how bioarchaeologists and forensic anthropologists relate aspects of life, death, and the skeleton.
- 17.2** Explain the archaeological field recovery methods used to process a site/scene.
- 17.3** Describe what is involved in laboratory processing, curation, and chain of custody including how these differ in bioarchaeology and forensic work.
- 17.4** Understand what the biological profile is and how it is used by forensic anthropologists and bioarchaeologists.
- 17.5** Discuss how taphonomy is used to understand events that happened around the time of death.
- 17.6** Explain the role that DNA, kinship, and identity play in archaeological and forensic investigations.

17.7 Describe the techniques used to assess identification in forensic anthropology.

17.8 Discuss how archaeology and the skeleton are used in bioarchaeology and population change.

17.9 Describe the approaches used in forensic anthropology of mass disasters, war crimes, and human rights.

It had been raining across the heartland for months. Every day, day in, day out—the Mississippi and Missouri rivers were swollen, the land waterlogged, and the rain just kept on. It had been one bad hair day after another all Spring. Little did we know it was about to get much much worse. . . .

Unlike every other year, the Spring rains never stopped. Throughout the summer a steady rain continued, sometimes in great torrents. More than 150 river systems were simultaneously above flood stage. There was nowhere for the water to go. Levees breached and streams and rivers flooded as more than 24 inches of rain fell from June to August in northern Missouri—more than twice the summer average.

The Great Flood of 1993 devastated nine Midwestern states. Fifty people lost their lives and tens of thousands more were displaced as at least 15 million acres of farmland flooded and 10,000 homes were destroyed. The Great Flood also produced one of the most unusual of mass disaster incidents when a levee breach in early July inundated the cemetery of Hardin, Missouri. The rushing waters created a 50-foot deep lake on the cemetery grounds, dislodged headstones, caskets, and burial vaults and carried away 769 of Hardin's ancestors—some from pre-Civil War graves.

As flood waters began to recede, state and local officials, volunteers, and the region 7 Disaster Mortuary Operational Response Team (D-MORT) recovery workers waded through waist-high water, scrambled up trees to recover stranded body parts, and systematically surveyed corn and soybean fields for bones. The surreal recovery area encompassed 26 square miles. By that Fall, D-MORT forensic experts including anthropologists, dentists, radiologists, finger print analysts, and more gathered at a temporary morgue on the county fairgrounds to systematically evaluate and identify remains. D-MORT anthropologists from the Smithsonian Institution and Armed Forces Institute of Pathology examined complete skeletons, isolated crania, and over 3,500 isolated bones to glean information that was compared with details about the decedents collected from family members.

Five months after the flooding, one of the strangest mass disaster incidents was closed. Although a few individuals remained unaccounted for and many others were not positively identified, in November 1993, the Hardin ancestors were reinterred on a newly purchased plot of land and the town could begin to move on. Nonetheless, the re-emergence of their loved ones had awoken many old memories for those who survived.

Our skeleton tells a tale about the evolution of our species and of the life (and death) of an individual. So far, we have used the skeleton to understand the evolution of our distant ancestors. But skeletal clues can be used, as they were by the forensic anthropologists working for D-MORT in the Hardin Cemetery disaster, to identify the age and sex of an individual, recognize idiosyncratic features that might help with identification, and understand events in his or her life possibly related to death. In this chapter we consider how two groups of biological anthropologists, bioarchaeologists and forensic anthropologists, use skeletal remains to understand our more recent evolution. We consider the basic methods used by these two disciplines to recover

remains and to construct a biological profile of an individual. We look at the special importance of taphonomy for differentiating between events that occurred around the time of death and those that occurred well after death. Then we examine ancillary techniques, such as DNA technology, that each group employs to better answer the question at hand. Finally, we consider the special applications of these disciplines ranging from understanding the origin of agriculture to helping bring war criminals to justice.

Life, Death, and the Skeleton

17.1 Describe how bioarchaeologists and forensic anthropologists relate aspects of life, death, and the skeleton.

bioarchaeologist

A biological anthropologist who uses human osteology to explore the biological component of the archaeological record.

Bioarchaeologists and forensic anthropologists are specialists in human osteology who use the theory and method of biological anthropology to answer questions about how recent humans lived and died. Bioarchaeologists study skeletal remains from archaeological sites in the Holocene (the last 10,000 years) to reveal the history of human populations and individual humans. Forensic anthropologists study skeletal remains from crime scenes, war zones, and mass disasters within the very recent past to reveal the life history of the individual, to identify that individual, and to understand something about the context in which death occurred. Both specialists rely on the same fundamental core of expertise, osteological identification and archaeological field methods, to retrieve remains from the field and to develop a profile of the age, sex, and other biological attributes of an individual. Because the shape of the skeleton of a human or any other animal is dictated mostly by its function in life and its evolutionary history, the bioarchaeologist and forensic anthropologist can reconstruct the probable age, sex, and sometimes ancestry of an individual from his or her skeletal remains. They can observe the influence of certain kinds of diseases on the skeleton, and they can assess some aspects of what happened to an individual just before, around the time of, and after his or her death.

Each specialist then combines this fundamental information with other areas of inquiry to understand, for example, population-level biological changes that occurred when societies shifted from hunting and gathering to farming, or the influence of the number of bodies on the rate of decomposition in a mass grave. Bioarchaeologists take a population perspective combining the biological profiles of a number of individuals to understand patterns of disease and behavior in the past (Larsen, 1999). They pay particular attention to cultural attributes when trying to understand past behavior from the skeleton, combining osteological inquiry with the evaluation of associated archaeological remains that tell them about past cultures. For example, bioarchaeologists might use the age, sex, and distribution of grave goods found with skeletons in a prehistoric cemetery to consider patterns of social stratification in the past. Or they might use the mechanical properties of bone combined with the archaeological indicators that mark a shift from hunting and gathering to farming in order to understand the influence of these changes in activity on the lifeways of the individual.

Forensic anthropologists, on the other hand, use the principles of skeletal biology in legal or criminal investigations. They reconstruct the circumstances not only of homicides but also of accidental deaths, suicides, mass disasters, war crimes, and combat deaths. They might use information from the skeleton to compare with antemortem medical records to assist in the positive identification of a serviceman missing in action. Or they may examine the physical traces of a knife wound on a dismembered arm or leg bone to identify the type of weapon used. Their work helps bring closure to grieving relatives and bring criminals to justice.

Given the nature of their investigations, forensic anthropologists differ from bioarchaeologists in that they work in a more recent context—usually within the last 50 to 100 years, although this varies by jurisdiction—and with a greater primary focus on the individual. But unlike pathologists and medical examiners, forensic anthropologists bring an anthropological perspective and a hard-tissue focus to investigations of skeletal remains. Both bioarchaeologists and forensic anthropologists bring to their work a broad perspective that encompasses natural human variation, human osteology, and natural selection.

Field Recovery Methods

17.2 Explain the archaeological field recovery methods used to process a site/scene.

Results of bioarchaeological and forensic investigations rely on good contextual information (Figure 17.1). Things like body position, relationship to nearby items such as bullets or grave goods, and structures near the individual—such as ancient hearths or recent buildings—require precise and thorough documentation in the field. Without such documentation, we would not know if the bullet recovered at the scene was 10 feet from the individual, or within the victim’s chest cavity. We would not be able to reconstruct from the bones alone whether the skeleton clutched a decorated scepter, or whether the artifact lay in a pile of items some distance from the individual. These associations are crucial for inferring the meaning of a burial and the circumstances surrounding the death of an individual. So to ensure full recovery and good contextual information from the field, whether it be a crime scene or a prehistoric site, both specialists rely on archaeological techniques to find, document, and remove remains from the site.

The site might be found in any number of ways. In forensic anthropology, sites are often accidentally encountered by a passerby, during a walk in the woods, for example, or information from an informant who knows of a crime may lead to a site. Because many body dumps are very recent, cadaver dogs may be useful in finding forensic sites. Bioarchaeologists may also encounter sites accidentally, Kennewick man was found in the Columbia River by two passersby for example, but often the identification of sites is based on a survey of an area of interest, an evaluation of air or satellite photos, or other directed measures. Once identified, the area is cordoned off to limit disturbance.

By whatever means the area of interest is identified, once on site the anthropologist systematically surveys the area for additional remains to determine the scope of the area to be investigated. Such surveys most commonly include visual surveys in which an individual or team of investigators walk a systematic path over an area searching for remains, associated items, or evidence of burial (Figure 17.2). Other noninvasive technology like ground-penetrating radar (GPR) may also be used to identify subsurface structures. In particular instances, GPR can identify possible burials for future excavation, but this equipment is expensive and requires an expert operator.

Figure 17.1 Biological anthropologists map skeletal remains from a prehistoric site.



Figure 17.2 The first step in field recovery involves surveying the site, sometimes with special equipment.



Figure 17.3 Bioarchaeologists and forensic anthropologists use archaeological excavation techniques to recover remains.



datum point

A permanent, fixed point relative to which the location of items of interest are recorded during archaeological mapping and excavation.

chain of custody

In forensic cases, the detailed notes that establish what was collected at the scene, the whereabouts of these remains, and the access to them after retrieval from the scene.

In the field, any surface discoveries are mapped and photographed. A permanent **datum point** for the site is established that represents a fixed position from which everything is measured so that the precise “find spot” of each object can be relocated in the future. The feature chosen as the datum point could be a piece of metal pipe cemented into the ground by the scientist, or in urban forensic investigations it is often a particular location on a building. Temporary structures, fence posts, and trees are poor datum choices as they are liable to be gone in the future, thwarting attempts to relocate a site.

If the remains are buried, the anthropologist will excavate using archaeological techniques. Forensic investigations and some archaeological sites require speedy recovery so teams may also use heavy equipment such as backhoes to skim off overlying soil and rocks. The archaeologist sets up a grid system, usually with 1×1 -meter squares, and plots these relative to the datum.

The excavator begins by skimming off shallow layers of dirt using a hand trowel. Objects are revealed in place and their coordinates, including their depth, are recorded relative to the grid system (Figure 17.3), and photographs are taken. Soil and rock samples may be collected to assist in dating of prehistoric remains (see Chapter 8) or the identification of insects and plants in forensic cases. All the dirt that is removed is sieved through fine mesh to ensure even the smallest pieces of bone are recovered (Figure 17.4). In the field, the anthropologist makes a preliminary determination of whether the remains are human or nonhuman (they could be those of a dog or deer, for instance) and, based on the bones, whether more than one individual is present. Once exposed and mapped, individual bones are tagged, bagged, and listed on a preliminary catalog for removal to the laboratory.

Laboratory Processing, Curation, and Chain of Custody

17.3 Describe what is involved in laboratory processing, curation, and chain of custody including how these differ in bioarchaeology and forensic work.

In the lab more detailed curation and examination can begin. Both bioarchaeologists and forensic anthropologists will start a detailed catalog in order to retain the important contextual pieces of information gained during the field recovery. However, for the forensic anthropologist this log becomes part of an evidence file, and a strict **chain of custody** must be established to ensure that the remains cannot be tampered with,

Figure 17.4 After excavation, recovered remains are screened to ensure that even tiny fragments are retrieved and saved. (a) Screening sediment at a forensic site. (b) Screening sediment from an ancient site.



(a)



(b)

Figure 17.5 After skeletal remains are cleaned, they are laid out in anatomical position for inventory.



in case they should become evidence in a court of law. Detailed notes are taken to demonstrate that the remains in question are those from the scene and that they have not been contaminated or modified since their removal from the scene. This chain may consist of catalogs and inventories of remains, signed transfers of evidence, and details concerning those who participated in recovery efforts and who had access to the area where remains are stored.

After the remains are cataloged, they are cleaned of any adhering soft tissue and dirt and then laid out in anatomical position, the way they would have looked in the skeleton in life (Figure 17.5). An inventory is made of each bone present and its condition. Most adult humans have 206 bones, many of which are extremely small (see Appendix B). Because most bones develop as several bony centers that fuse together only later in life, fetuses and children contain many more bones than do adults. Decay of a long-buried body may leave no more than a few bone fragments. The bioarchaeologist and forensic anthropologist therefore must be skilled osteologists who are very familiar with patterns of human variation. Once the initial inventory has been completed, the scientist sets about evaluating the clues that the skeleton reveals about the life and death of the individual. The first step in this process is constructing the biological profile of the individual—including determining age, sex, height, and disease status.

The Biological Profile

17.4 Understand what the biological profile is and how it is used by forensic anthropologists and bioarchaeologists.

Bioarchaeologists and forensic anthropologists both construct **biological profiles**—but for slightly different reasons. The bioarchaeologist is interested in the life of the individual, of course, but also wants to evaluate population-wide response to natural and cultural selective pressures (Larsen, 1999). And except in rare circumstances, the bioarchaeologist cannot make a positive individual identification. On the other hand, the forensic anthropologist seeks to aid in the positive identification of the victim and to provide any clues

biological profile

The biological particulars of an individual as estimated from their skeletal remains. These include estimates of sex, age at death, height, ancestry, and disease status.

Figure 17.6 Bones change radically in size and shape from newborn to adult, as these cervical vertebrae demonstrate.



that may assist a medical examiner in discerning the cause and manner of death (Snow, 1982). To meet both their goals, the bioarchaeologist and forensic anthropologist seek information about several features that may be clues to life history and identity.

Age at Death

As the human body develops, from fetus to old age, dramatic changes occur throughout the skeleton (Figure 17.6). Scientists use the more systematic of these changes to estimate the age at death of an individual. However, whenever scientists determine age, they always report it as a range (such as 35–45 years) rather than as a single definitive number. This range reflects the variation in growth and aging seen in individuals and across human populations and denotes the person's biological rather than chronological age (age in years). The goal is that the range also encompasses the person's actual age at the time of their death.

Because the skeleton grows rapidly during childhood, assessing the age of a subadult younger than about 18 years of age is easier and often more precise than estimating the age of an adult skeleton. Virtually all skeletal systems except the small bones of the ear (the ear ossicles) change from newborn to adult. For example, in small children the degree of closure of the cranial bones (covering the fontanelles, or "soft spots" of the skull) changes with age, as does the development of the temporal bone, the size and shape of the wrist bones, and virtually every other bone (Figure 17.7). However, dental eruption and the growth of long bones are the most frequently used means of assessing subadult age.

Humans have two sets of teeth of different sizes that erupt at fairly predictable intervals. Which teeth are present can help distinguish between children of different ages and between older subadults and adults of the same size (Figure 17.8). For more precise ages, the relative development of the tooth roots can also be used. However, once most of the adult teeth have erupted, by about the age of 12 years in humans, the teeth are no longer as good a guide to predicting age.

In these older children, growth of the limb bones can also be used to assess age. The long bones of the arms and legs have characteristic bony growths at each end—the

Figure 17.7 The cranium of a young infant changes dramatically in shape with age. Initially the child has several "soft spots" that allow for bones to ride over one another during birth and allow growth. And the face is proportionately very small compared to the size of the braincase.



Figure 17.8 Tooth development and eruption are commonly used to assess age in the subadult skeleton. Deciduous (baby) teeth are indicated by hatching and shades of brown.

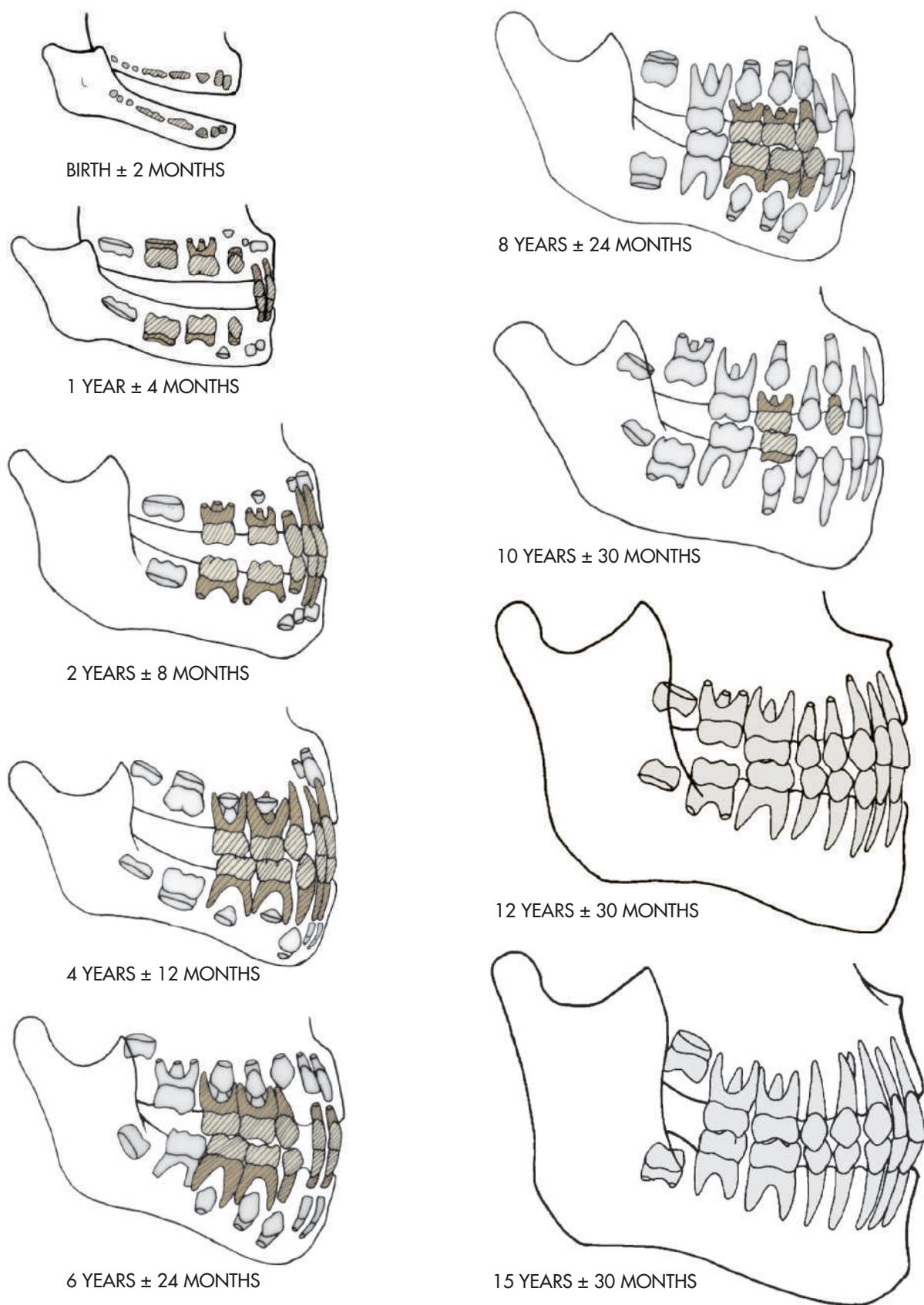
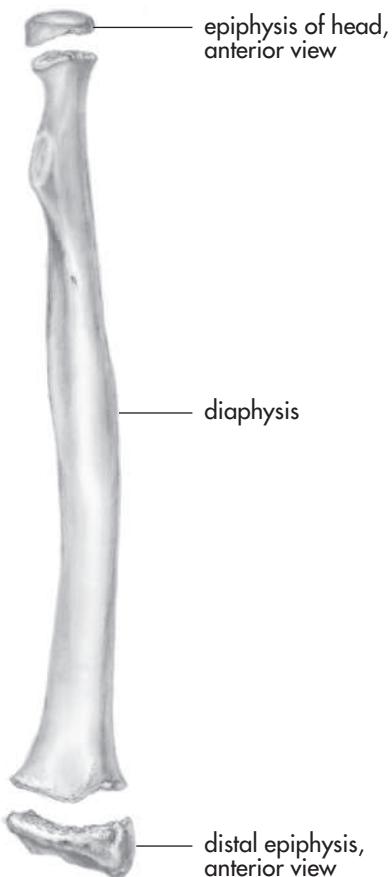


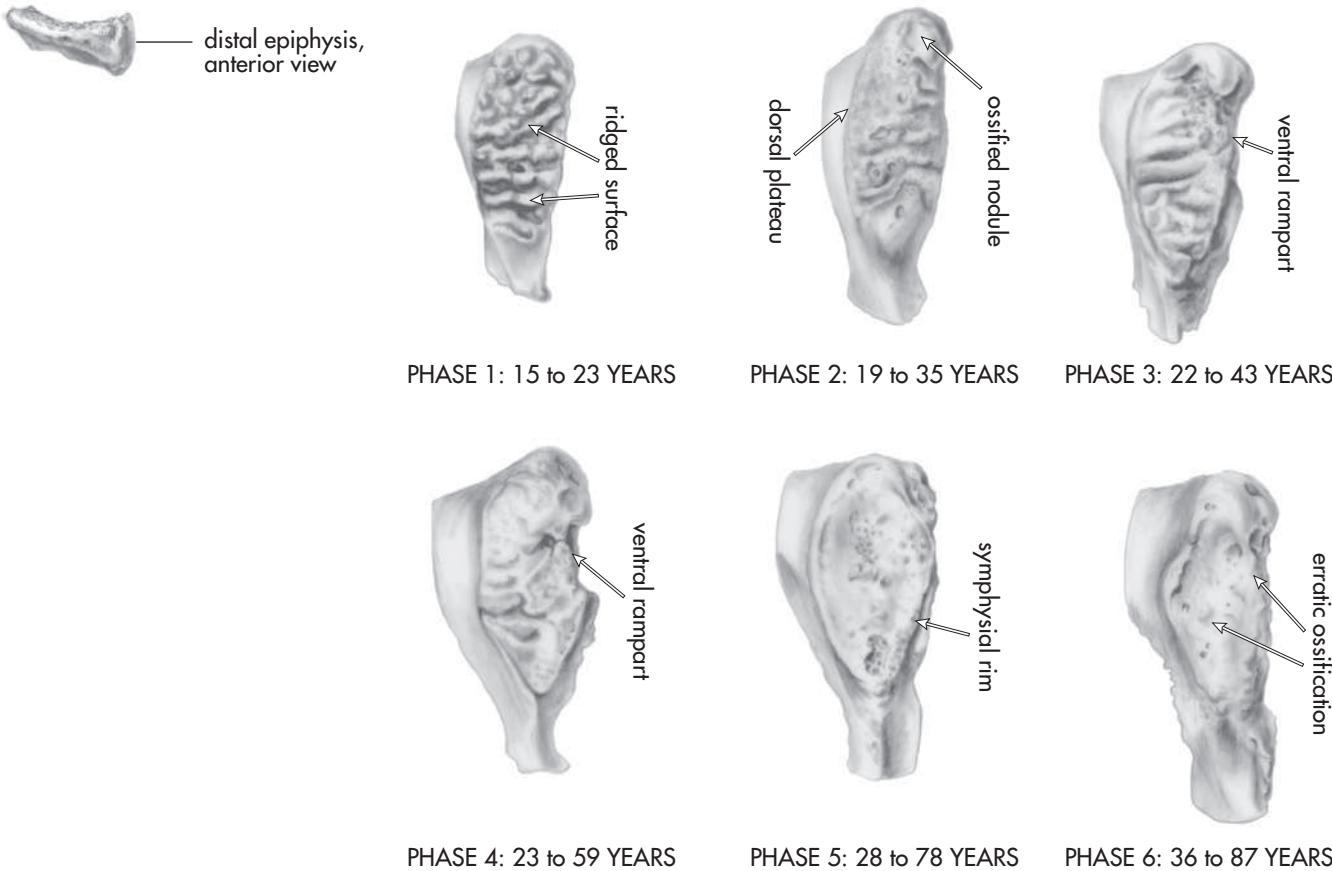
Figure 17.9 Long bones develop from several bony centers—one for the shaft and at least one for each end. The end caps are known as epiphyses.



epiphyses—which are present as separate bones while the person is still growing rapidly (Figure 17.9). Most epiphyses are not present at birth—which helps to separate fetuses from newborns—but appear during infancy and childhood. The lengths and proportions of bones change in predictable ways as children grow and are especially good indicators for assessing fetal age (Sherwood et al., 2000). In older children, the epiphyses start to fuse to the shafts of the limb bones around the age of 10 in some bones, and fusion of most epiphyses is completed in the late teenage years. However, the process of fusion may occur as late as the early 20s in a few bones (such as the clavicle). Depending upon which bones and which parts of those bones are fused, a reasonably good estimate of subadult age can be made.

In adults, age is harder to determine because growth is essentially complete. Some of the last epiphyses to fuse, such as the clavicle and top of the ilium, can be used to estimate age in young adults in their early 20s. But estimating the age of the older adult skeleton relies mostly on degeneration of parts of the skeleton. For example, the pubic symphysis and auricular surface of the innominate, and the end of the fourth rib near the sternum all show predictable changes with age (Todd, 1920, 1921; McKern & Stewart, 1957; Iscan et al., 1984; Lovejoy et al., 1985). Examination of as many of these bones as possible helps to increase age accuracy (Bedford et al., 1993). The pubic symphysis is a particularly useful indicator of adult age, and age standards have been developed separately for males and females (Gilbert & McKern, 1973; Katz & Suchey, 1986; Brooks & Suchey, 1990). The standards show how the symphysis develops from cleanly furrowed to more granular and degenerated over time (Figure 17.10). These changes tend to occur

Figure 17.10 The pubic symphysis of the pelvis is useful for estimating age in the adult skeleton.



more quickly in females than in males due to the trauma the symphysis experiences during childbirth.

The degree of obliteration of cranial sutures (the junction of the different skull bones) can also give a relative sense of age—obliteration tends to occur in older individuals (Lovejoy & Meindl, 1985). The antero-lateral sutures of the skull are the best for these purposes. However, the correlation between degree of obliteration and age is not very close, and the age ranges that can be estimated are wide.

Sex

If certain parts of the skeleton are preserved, identifying biological sex is easier than estimating age at death, at least for adults. The two parts of the skeleton that most readily reveal sex are the pelvis and the skull, and sex characteristics are more prominent in an adult skeleton than in a child. Humans are moderately sexually dimorphic, with males being larger on average than females. But their ranges of variation overlap so that size alone cannot separate male and female humans (Figure 17.11).

The best skeletal indicator of sex is the pelvis. Because of selective pressures for bipedality and childbirth, human females have evolved pelves that provide a relatively large birth canal (see Chapters 10 and 15). This affects the shape of the innominate and sacrum in females; the pubis is longer, the sacrum is broader and shorter, and the sciatic notch of the ilium is broader in females than in males (Figure 17.12 on page 536). The method is highly accurate (Rogers & Saunders, 1993) because the pelvis reflects directly the different selective pressures that act on male versus female bipeds. Thus the pelvis is considered a primary indicator of the sex of the individual. And because the femur has to angle inward from this wider female pelvis to the knee (to keep the biped's foot under its center of gravity; see Chapter 10), the size and shape of the femur also differentiate males and females fairly well (Porter, 1995).

Figure 17.11 Although males tend to be larger than females, the two overlap significantly in size. The size of a bone alone cannot be used to assess sex.

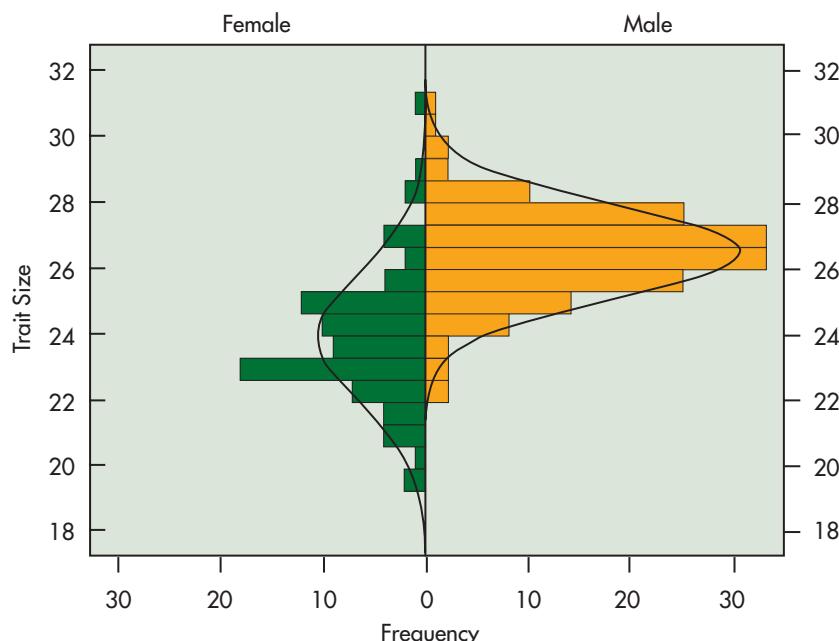
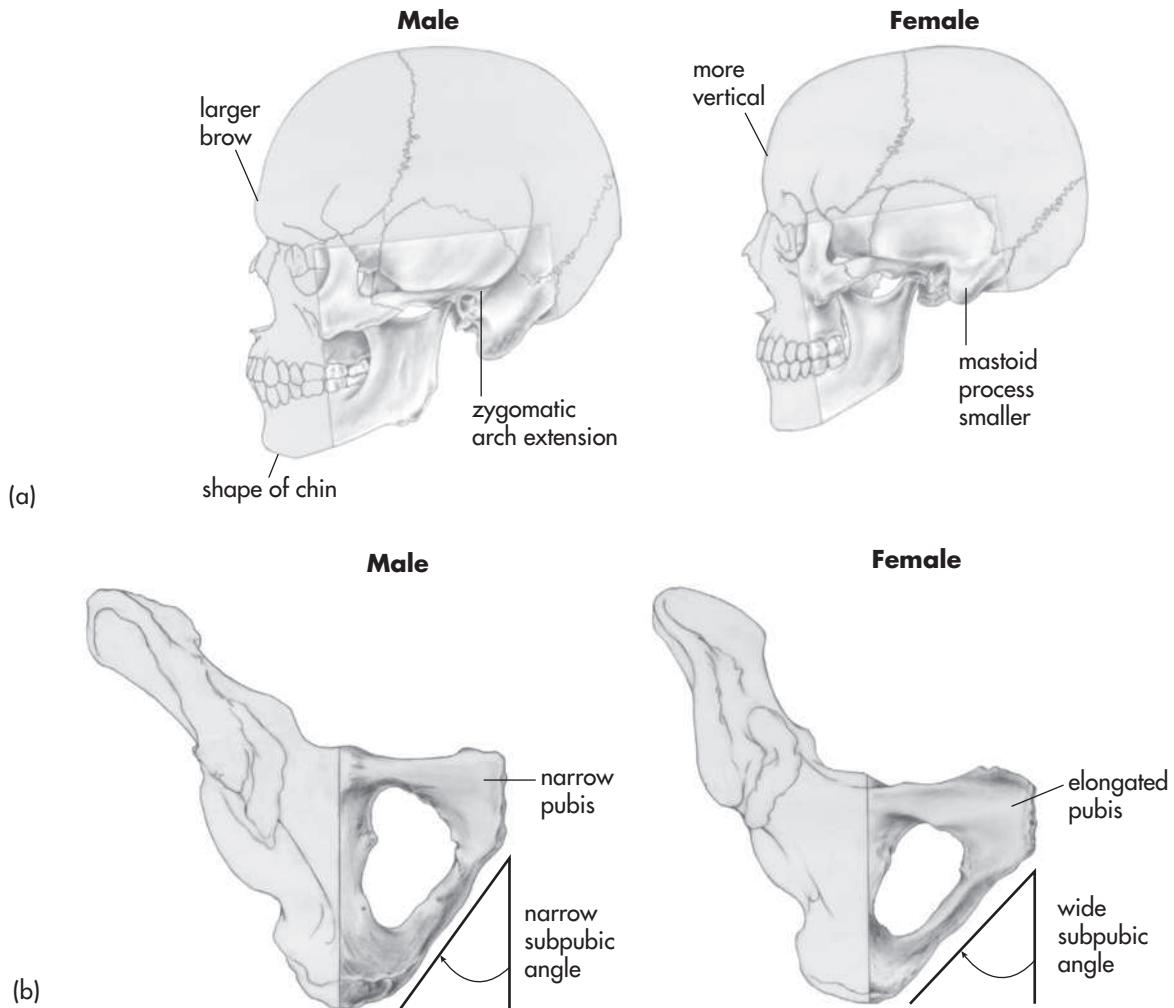


Figure 17.12 Comparison of (a) male and female skulls and (b) male and female pelves.

The skull is also a useful indicator of sex, at least in adults. Around puberty, circulating hormones lead to so-called secondary sex characters such as distribution of body and facial hair. During this time male and female skulls also diverge in shape. Male skulls are more robust on average than female skulls of the same population. However, these differences are relative and population dependent; some human populations are more gracile than others. The mastoid process of the temporal bone and the muscle markings of the occipital bone tend to be larger in males than in females, and the chin is squarer in males than in females (Figure 17.12). The browridge is less robust and the orbital rim is sharper in females than in males, and the female frontal (forehead) is more vertical. These differences form a continuum and provide successful sex estimates in perhaps 80 to 85% of cases when the population is known.

Ancestry

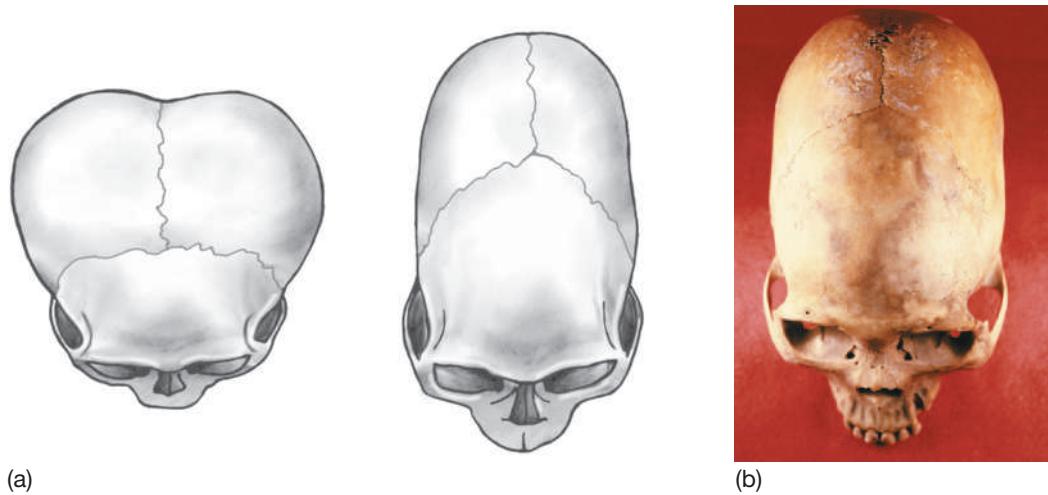
Knowing the ancestry of an individual skeleton is important for improving the accuracy of sex, age, and stature estimates. There is no biological reality to the idea of fixed biological races in humans (see Chapter 5), but we have learned that the geographic conditions in which our ancestors evolved influence the anatomy of their descendants. The term *ancestry* takes into account the place of geographic origin, which corresponds to biological realities in ways that the term *race* does not. Nonetheless, because of the

way in which variation is distributed in humans (there is more variation within than between groups, and many variation clines run in independent directions from one another) assessing ancestry from the skeleton is less accurate than assessing age or sex, and the process is also highly dependent on the comparative groups used.

Bioarchaeologists and forensic anthropologists are interested in ancestry for different reasons. A bioarchaeologist may be interested in determining the extent to which ethnic (cultural) differences in prehistoric Chile, for example, relate to actual biological relationships among groups. To do this the bioarchaeologist might look at skeletal and dental traits known to be under genetic control and compare frequencies among “populations” of skeletons to consider how closely related the groups are. She might then compare these frequencies with cultural attributions of ethnicity such as the use of particular pottery styles or the practice of artificially deforming the head (Figure 17.13). In this way, she can discern how strong the cultural differences were and whether these also reflect biological differences. However, forensic anthropologists more often need to broadly categorize a single victim’s remains in order to narrow the scope of possible missing individuals to whom the bones may belong (in much the same way that determining the sex of a skeleton narrows the search focus to only cases of that sex). So the ability to estimate even continent of origin (e.g., European American) may be useful in limiting the scope of the search. Such forensic assessments of ancestry usually are made from the skull but can also include the postcrania.

Forensic anthropologists base ancestry assessments on comparisons with skeletal populations of known ancestry. In the United States, an isolated skull can be measured and compared using multivariate statistics with the University of Tennessee Forensic Data Bank of measurements from crania of known ancestry. This process provides a likely assignment of ancestry and a range of possible error. However, human variation is such that many people exist in every population whose skulls do not match well with most other skulls of similar geographic origin. Nonetheless, the ability to even partially assign ancestry can be useful in several forensic contexts. Missing person reports often provide an identification of ancestry, and although this is not based directly on the skeleton, a skeletal determination of ancestry may suggest a match that could be confirmed by other more time-consuming means such as dental record comparisons or DNA analysis (see Innovations: Ancestry and Identity Genetics on pages 538–539 and Insights and Advances: If You Have DNA, Why Bother with Bones? on pages 544–545).

Figure 17.13 Head binding, or artificial deformation, was used by some populations as a sign of identity. (a) Two types of deformation, circumferential and anteroposterior, seen in superior view. (b) A photo of a circumferentially deformed cranium from prehistoric Peru.



Innovations

Ancestry and Identity Genetics

Genetic studies have long been used for tracing the histories of populations (Chapters 6 and 12). As geneticists have discovered an increasing variety of markers that are associated with specific geographical regions and populations, the ability to trace individual genetic histories has increased greatly, and the ability to make direct matches to DNA from a crime scene has become an important forensic technique (see Insights and Advances: If You Have DNA, Why Bother with Bones? on pages 544–545). Individuals can now obtain their genetic profile through several commercial companies in a matter of a few weeks.

There are two basic approaches to determining *personalized genetic histories* PGHs (Shriver and Kittles, 2004). The first one is the *lineage-based* approach. These are based on the maternally inherited mtDNA genomes and the paternally inherited Y chromosome DNA. The lineage-based approach has been very useful for population studies, and allows individuals to trace their ultimate maternal and paternal origins. For example, African American individuals can find out what part of Africa their founding American ancestors may have come from (<http://www.african-ancestry.com>). These are the same techniques that have been used to consider the dispersal and migration of ancient and recent peoples. For example, in a survey of more than 2,000 men from Asia using more than 32 genetic markers, Tatiana Zerjal and her colleagues (2003) found a Y chromosome lineage that exhibited an unusual pattern thought to represent the expansion of the Mongol Empire. They called this haplotype the star cluster (reflecting the emergence of these similar variants from a common source). The star cluster lineage is found in sixteen different populations, distributed across Asia from the Pacific Ocean to the Caspian Sea. The MRCA (most recent common ancestor) for this cluster was dated to about 1,000 years ago, and the distribution of populations in which the lineage is found corresponds roughly to the maximum extent of the Mongol Empire. Additionally, outside the empire the Hazaras of Pakistan (and Afghanistan), many of whom through oral tradition consider themselves to be direct male-line descendants of Genghis Khan, also have a high frequency of the star cluster. The Empire reached its peak under Genghis Khan (c. 1162–1227) and Khan and his close male relatives are said to have fathered many children (thousands, according to some historical sources). The distribution of the star cluster could have resulted from the migration of a group of Mongols carrying the haplotype or may even reflect the Y chromosome carried specifically by Genghis Khan and his relatives.

From the perspective of determining an individual's PGH, however, the lineage-based approach is limited because it traces only the origins of a very small portion of an individual's genome and does not reflect the vast bulk of a person's genetic history. In contrast to the lineage-based approach, *autosomal marker-based tests* use information from throughout the genome. *Ancestry informative markers* (AIMs) are alleles

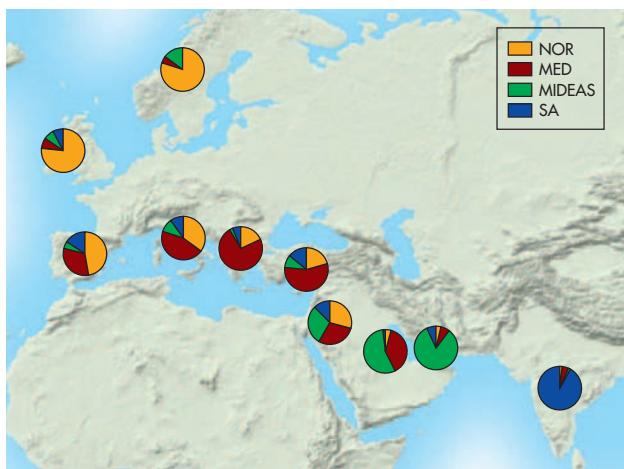
on the autosomal chromosomes that show substantial variation among different populations. The more AIMs that are examined in an individual, the



more complete the picture of that individual's *biogeographical ancestry* can be obtained (Shriver and Kittles, 2004). Combining the information from all of these AIMs requires some major statistical analysis, which has to take into account the expression of each marker and its population associations. There will be some statistical noise in the system due to factors such as the overlapping population distribution of the markers and instances of convergent evolution. In addition, even when a hundred markers are used, the tests sample only a small portion of your genome that is the product of the combined efforts of thousands of ancestors. The biogeographical ancestry of a person, expressed in terms of percentage affiliations with different populations, is a statistical statement, not a direct rendering of a person's ancestry. And both AIMs and lineage-based tests are limited by the comparative samples that form the basis of our knowledge about the distribution of DNA markers. Thus, if you submit a cheek swab to several different companies with different comparative databases, you will get somewhat different ancestry results. Nonetheless, they provide us with an intriguing snapshot of the geographic origins of a person's ancestors.

Several commercial companies are now in the ancestry genetics business. We contacted one of these companies, DNAPrint Genomics (<http://www.AncestryByDNA.com>), and obtained the biogeographical ancestry of the authors of this text. The genetic testing product used is called AncestryByDNA 2.5, which provides a breakdown of an individual's PGH in terms of affiliations with four major geographical groups: European, Native (aka Indigenous) American, Sub-Saharan African, and East Asian. As we know, there is little evidence that four distinct groups of humans ever existed. So the company makes assignments to these distinct groups by first defining the comparative groups based on sampling the DNA of living individuals from particular continents. Using information derived from about 175 AIMs and how these are distributed across the individuals in each of their preassigned groups, a statistical statement is made about how much of a client's DNA comes from one of these four groups.

John Allen's results were 46% European, 46% East Asian, 8% Native American, and 0% Sub-Saharan African. These results squared quite well with his known family history: His mother was Japanese and his father was an American of English and Scandinavian descent. The 8% Native American could have come from one or more ancestors on his father's side (some of whom arrived in the United States in the early colonial period). However, the



95% confidence intervals of the test indicate that for people of predominantly European ancestry, a threshold of 10% Native American needs to be reached before the result is statistically significant. For people of predominantly East Asian descent, the threshold is 12.5%. Therefore, in the absence of a family history of Native American ancestry, it is best to consider the 8% as statistical noise.

Craig Stanford's results were 82% European, 14% Native American, 4% Sub-Saharan African, and 0% East Asian. The Native American result, which easily exceeds the statistical threshold, was a real surprise because Craig has no family history of Native American ancestry. Following this result, his father was tested and was found to have 91% European and 9% Sub-Saharan African ancestry. Thus, all of Craig's Native American ancestry was derived from his mother's side. Although she was not tested, it is reasonable to conclude that her Native American percentage would be greater than 25%—the equivalent of a grandparent, although this does not have to represent the contribution of a single individual. Craig found this result to be somewhat ironic because earlier generations of women on his mother's side of the family had been proud members of the Daughters of the American Revolution, a lineage-based organization that was once (but is no longer) racially exclusionary. Stanford also requested a more detailed European ancestry genetic test (EuroDNA 1.0). Along with European ancestry, the tests showed 12% Middle Eastern ancestry. One of his paternal grandparents was from Italy, and the ancestry of southern Europeans often reflects population movements around the Mediterranean Sea, including Middle Eastern markers. In addition, there has been a long history of some gene flow from Sub-Saharan Africa into North Africa and the Middle East, which could explain his father's statistically significant Sub-Saharan African ancestry. Paradoxically, the result may also explain the percentage of Native American ancestry in his results as AncestrybyDNA tests are known to suggest that most people with Middle Eastern ancestry also have Native American ancestry, which likely relates to the comparative database and algorithm the company uses (Bolnick et al., 2007).

A good example of how differences in comparative samples and the types of markers used can influence results comes from the comparison of DNA results from different



companies. Susan Antón's results from AncestrybyDNA assign her to 88% European and 0% Native American. But another company, 23andMe (www.23andme.com), that uses single nucleotide polymorphisms (SNPs) from 10s of thousands of autosomal sites suggests she is 67–75% European and 10–14% Native American, with most of the European coming from Scandinavia and Northern Europe (the algorithm also suggests she is also 2.9% Neandertal). A third company, DNATribes (www.dnatribes.com), which uses the same autosomal short tandem repeat markers used in forensic identification analyses (see Insights and Advances: If You Have DNA, Why Bother with Bones? on pages 544–545), places her closest match to a Puerto Rican community in Boston and her strongest ancestral match to a population in Tunisia. And rerunning those results through a compilation of data from the National Institutes of Standards and Technology (<http://www.cstl.nist.gov/strbase/>) gave her close matches to Iberian, North African, and U.S. Hispanic populations. The 23andMe and NIST results reflect her known lineage well: her father's family is from Mexico (by way of East Los Angeles) and her mother's from Scandinavia and Northern Europe (by way of rural Minnesota). Nonetheless, the different kinds of markers assessed and different algorithms applied to the same data can yield seemingly conflicting results.

Ancestry genetics opens windows to the past, but in some cases, it raises more questions than answers about where you came from. This is not surprising because we know that the pattern of genetic variation across all humans is a complex one that does not partition well into regional or racial groups, that most of the genetic variation within humans exists within rather than between groups, and that different characteristics often follow cross-cutting clines. We can attest, however, that for anyone interested in their own biological ancestry, getting a personalized genetic history can be an exciting experience. Incidentally, humans are not the only species whose biological past can be explored:

Genetic ancestry testing for dogs is also becoming available (<http://www.whatsmydog.com>) and paternity testing is available for both cats and dogs (<http://www.catdna.org>; <http://www.akc.org/dna>).



In another context, forensic anthropologists are still working to identify the remains of soldiers killed in the Vietnam War, 30 years after that conflict ended. If a local contact leads a forensic team to a field where an American soldier was reportedly buried, the team will begin to search and excavate. Upon finding human remains, the forensic anthropologist may be able to use the skeleton to assess whether the remains are likely to be those of a local individual or of an American individual. More detailed analyses, including DNA and other means, will later be applied to test the attribution.

Height and Weight

Physical stature reflects the length of the bones that contribute to a person's height. As we know from the ecological rules described by Bergmann and Allen, different body shapes have evolved in response to different climatic environments (see Chapter 5). Thus, height and weight estimates will be more accurate if the population of the individual is known. These differences in proportions relate to differences in bone lengths; as a result, some populations will tend to have more of their stature explained by leg length and some by torso length, for example.

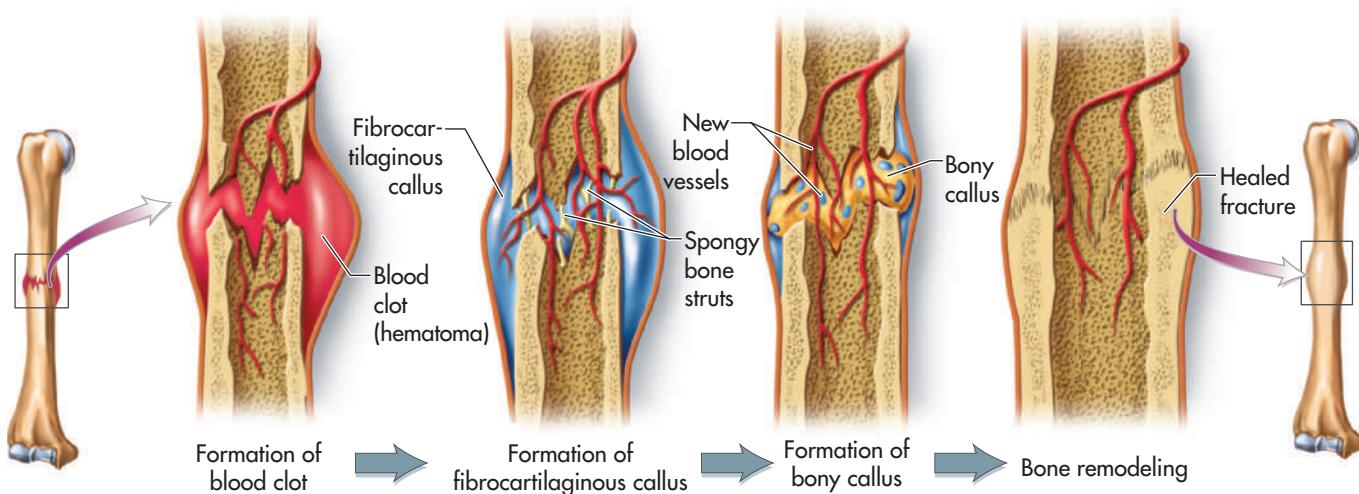
The best estimates of stature from the skeleton are based on summing the heights of all the bones in the skeleton that contribute to overall height including the cranium, vertebral column, limb, and foot bones (Fully, 1956). This so-called Fully method is fairly accurate, but requires a complete skeleton, a rarity in archaeological or forensic contexts. Biological anthropologists have developed formulas, which vary by population, for estimating stature based on the length of a single or several long bones, so that the femur, tibia, or even humerus can be used to predict stature. These methods use the relationship between the limb bones and the height in skeletal remains of individuals of known stature to predict stature for an unknown individual (e.g., Trotter, 1970). For even more incomplete remains, there are formulas for estimating total length of a long bone from a fragment of that bone (e.g., Steele & McKern, 1969). The estimated length can then be used to estimate height—although the error margin increases with each estimate. Like age, stature is estimated as a range (for example, 5'10" to 6'0") that hopefully captures the person's true height at the time of death.

As you might expect, weight is more difficult to predict since it can vary quite a lot over an individual's life time. Nonetheless, formulas exist for predicting the approximate weight of an individual from his or her weight-bearing joints, such as the head of the femur. Using the entire skeleton, scientists can estimate body weight based on formulas that relate height and body breadth to weight in populations of different build (Ruff, 2000). Some of these estimates also form the basis for inferring body size and weight in earlier hominins (see Chapters 11 and 12).

Premortem Injury and Disease

Injuries and sickness suffered during life are also an important part of the biological profile and critical for understanding an individual's life and, perhaps, identity. Not all diseases or injuries leave marks on bone. However, we can distinguish the ones that do as having occurred while the person was alive because the bones show evidence of healing and remodeling (Figure 17.14). Arthritis and infections of bone show up clearly in skeletal remains. Old healed injuries, such as broken limbs and even gunshot wounds that a person survived for several weeks, also leave their mark.

Figure 17.14 Bone fractures that occur before death show signs of healing. The process of fracture healing starts with soft callus formation and proceeds to bone fusion.



Premortem fractures can be key evidence of lifeways (Figure 17.15). In forensic anthropology, multiple healed fractures—especially of the ribs and those typical of defensive wounds—can establish a series of episodes of violence, as is often the case in child abuse (Walker et al., 1997). Old injuries can also be matched to premortem X-rays taken when a victim sought medical attention and thereby help to establish identity (see the section on Identification and Forensic Anthropology on page 546). Bioarchaeologists also use patterns of trauma and other disease in skeletal series to infer behavior, to understand the implications of important transitions such as the change to agriculture from hunting and gathering, and to assess the influence of migrations and colonizations (see Insights and Advances: The Bony Record of Health and Disease on pages 550–551). For example, ritualized warfare is suggested by the high incidence of healed nose fractures in a population from the Atacama Desert, Chile (Lessa et al., 2006). Such ritualized warfare is one means by which groups can resolve serious conflicts without the risk of actual deaths, just a few bloody noses.

In addition to injury and disease, lifestyle may leave an indelible mark on the skeleton; an athlete who uses one side of the body for intense activity (such as a baseball pitcher or tennis player) will have a more robustly developed arm on that side—especially if he or she began the activity during childhood and continued through adulthood. Other repetitive activities also cause bone deposition to differ systematically between individuals. In either a forensic or archaeological context, such hypertrophy suggests several possible types of repetitive activity. When compared in many individuals across populations such differences can tell about increases or decreases in general activity level through time. Other markers provide clues to a sexual division of labor, for example. Repetitive exposure of the ear canal to cold water can stimulate bone growth, and in coastal populations in ancient Peru, such small nodules grow almost exclusively in the ear canals of males. This distribution, along with archaeological clues, helps to establish a sexual division of labor in which males dove into cold water to retrieve marine foods, while females worked onshore.

Figure 17.15 Healed bone fractures can provide clues about activities and fresh fractures can yield information about cause of death. Note the foreshortened tibia (left bone) due to a massive healed fracture, and the less severe fracture on one end (top) of the right bone.



Injury, disease, and lifestyle all leave clues on the skeleton that tell the story of an individual's life. The skeleton may also be modified by events that occur well after or around the time of death. These changes can be critically important for understanding the context of death, but to be of use the scientist must be able to distinguish premortem bone changes from those that happened later in time.

Taphonomy

17.5 Discuss how taphonomy is used to understand events that happened around the time of death.

Taphonomy is the study of the ways in which various processes affect the skeleton after death (Chapter 8). Both forensic anthropologists and bioarchaeologists use taphonomic analysis to distinguish naturally caused bone damage from damage caused by human activity. And for forensic anthropologists, who are particularly keen to determine the length of time a victim has been dead and what contributed to this death, it is critical to distinguish events that occur well after death, or postmortem events, from perimortem events, those that occur right around the time of death. Neither perimortem nor postmortem trauma shows healing, distinguishing them from pre- or antemortem injuries and disease. To be of use in understanding the context of death, however, perimortem and postmortem trauma must be differentiated from one another since postmortem events do not suggest cause or manner of death.

Perimortem Trauma

For anthropologists, perimortem trauma is the physical evidence of activity that happened slightly before, during, or slightly after the time of death. We can differentiate it from premortem injury because in perimortem trauma no healing is evident. We can distinguish perimortem from postmortem trauma that happened well after death, because bones retain a large percentage of their organic component during the perimortem interval. As a result, they are more pliable and break differently than those that are well dried-out after death; think of the difference between how a small branch that has just been plucked from a tree bends when you try to break it, whereas a long-dead, dried-out stick is brittle and snaps in two. It is important to remember, however, that perimortem trauma isn't necessarily related to the cause of death. Such trauma can, and often does, happen after the individual is dead.

Bioarchaeologists are less concerned with perimortem trauma than are forensic anthropologists. The older age of archaeological sites means fewer clues remain to distinguish perimortem changes from those that are definitely postmortem changes. So, except in particular instances in which an interpretation hinges on determining whether the individual was recently dead when his or her skeleton was damaged, bioarchaeologists often focus on postmortem trauma. Cases in which bioarchaeologists might focus on perimortem trauma include trying to make a case for ritual sacrifice or cannibalism. At archaeological sites in the southwest United States, some human remains were broken during the perimortem interval, when the bones were fresh. These findings, along with many other lines of evidence, suggest the remains were the result of cannibalism (White, 1992).

Distinguishing perimortem trauma is one of the most routine tasks a forensic anthropologist undertakes. This type of evidence helps investigators understand what happened right around the time of death. This information also helps the medical examiner or coroner determine the cause and manner of death (whether homicide, suicide, or accident) and may help to establish intent in murder cases. For example, the presence of telltale fractures of the hyoid, a small bone in the neck, suggests strangulation. Perimortem trauma may also indicate a perpetrator's intent to hide or dispose of

a body, implying that death was not accidental. Circular saws and reciprocating saws are often used to dismember bodies after a murder. These tools leave different marks on bone and sometimes leave traces of metal fragments embedded in bone. Experts can identify types of blades used and can indicate whether they are in the same class of tools as those owned by a suspect. Being able to show, based on anatomical knowledge, that a body was fleshed when dismembered rather than skeletonized has important implications for inferring a crime or interpreting mortuary ritual in past societies.

Postmortem Trauma

Definitively postmortem events are not related to establishing cause and manner of death and are often of greater interest to bioarchaeologists than they are to forensic anthropologists. Analyses of postmortem events can be critical for establishing how bones arrived at a site: Were they deliberately placed in a burial cave, or did the individual unceremoniously fall through a chasm in the rock? Despite their greater importance for bioarchaeologists, postmortem events may rule out a crime if they suggest that marks on bone are made by natural causes, rather than knives, guns, or chain-saws, or if they show that the skeleton is of ancient rather than forensic interest. For instance, Willey and Leach (2003) cite a case in which forensic anthropologists sought to identify a human skull found in a suburban home. The skull was discolored in a variety of ways that most closely resembled the way in which skulls are sometimes treated when collected as trophies of war. As it turned out, the skull in question was a "souvenir" brought home from the Vietnam War by a man who had since moved away, leaving the skull in his garage. Many clues about both peri- and postmortem events can be gleaned from the visual examination of skeletal remains. This differentiation can have important implications for how burial rituals are reconstructed for past societies, for example. However, bones also yield clues at a molecular level that can help to identify individuals or their relatives.

DNA, Kinship, and Identity

17.6 Explain the role that DNA, kinship, and identity play in archaeological and forensic investigations.

The rise of technologies able to establish kinship using DNA analysis has given bioarchaeologists and forensic scientists a powerful new tool for investigating relationships among groups, identifying victims, and establishing the presence of an alleged perpetrator at a crime scene. However, there are also limitations to each of these uses. DNA testing can use tiny samples of hair, skin, blood, other body fluids, and even bone. However, the older the bone sample and the more hot and humid the environment in which it was buried, the less likely that DNA can be extracted from bone. Forensic scientists use a variety of tests, including examining gene sequences that only kin would be likely to share, isolating particular segments of the genetic sequence for analysis, and DNA fingerprinting (the original DNA test, in which the same segments of DNA are lined up to examine the degree of similarity between two samples perhaps one from a crime scene and one from a possible perpetrator) (Nafte, 2000; Insights and Advances: If You Have DNA, Why Bother with Bones?). Bioarchaeologists use ancient DNA techniques to look at relationships among groups, migration patterns, and such.

When skeletal material has been fragmented during a disaster (as in the World Trade Center crime scene in 2001), the identification process can be extraordinarily difficult, a biological profile may be impossible, and in such cases forensic scientists may rely heavily on comparisons with DNA reference samples, typically obtained from relatives of the victims, to make positive identifications. To use DNA for identification, the scientist must have some knowledge of who the victim might have been to

Insights and Advances

If You Have DNA, Why Bother with Bones?

Each person has a unique DNA sequence, some of which can tell us the individual's sex or hint at their ancestry; other parts may tell us about hair and eye color. And in nearly every TV episode of *CSI* or *NCIS*, a DNA sequence is compared to a computer database and successfully identifies a perpetrator or a victim. The process apparently takes seconds to yield results. Since the 1980s when it was first used in court cases, DNA

sequencing has revolutionized the forensic sciences. So if all this can be done with DNA from blood, semen, or saliva, why bother with bones and forensic anthropology at all?

In crime labs across the country, specific locations on nuclear DNA are used to establish a DNA profile. This profile is used to connect trace evidence such as blood, hair, skin, etc. from crime scenes to individuals; that is, to connect people to places and objects. Commonly, fifteen standardized locations on individual chromosomes are used to target known *short tandem repeats* (STRs) of nuclear DNA. STRs are short repeats of DNA sequences

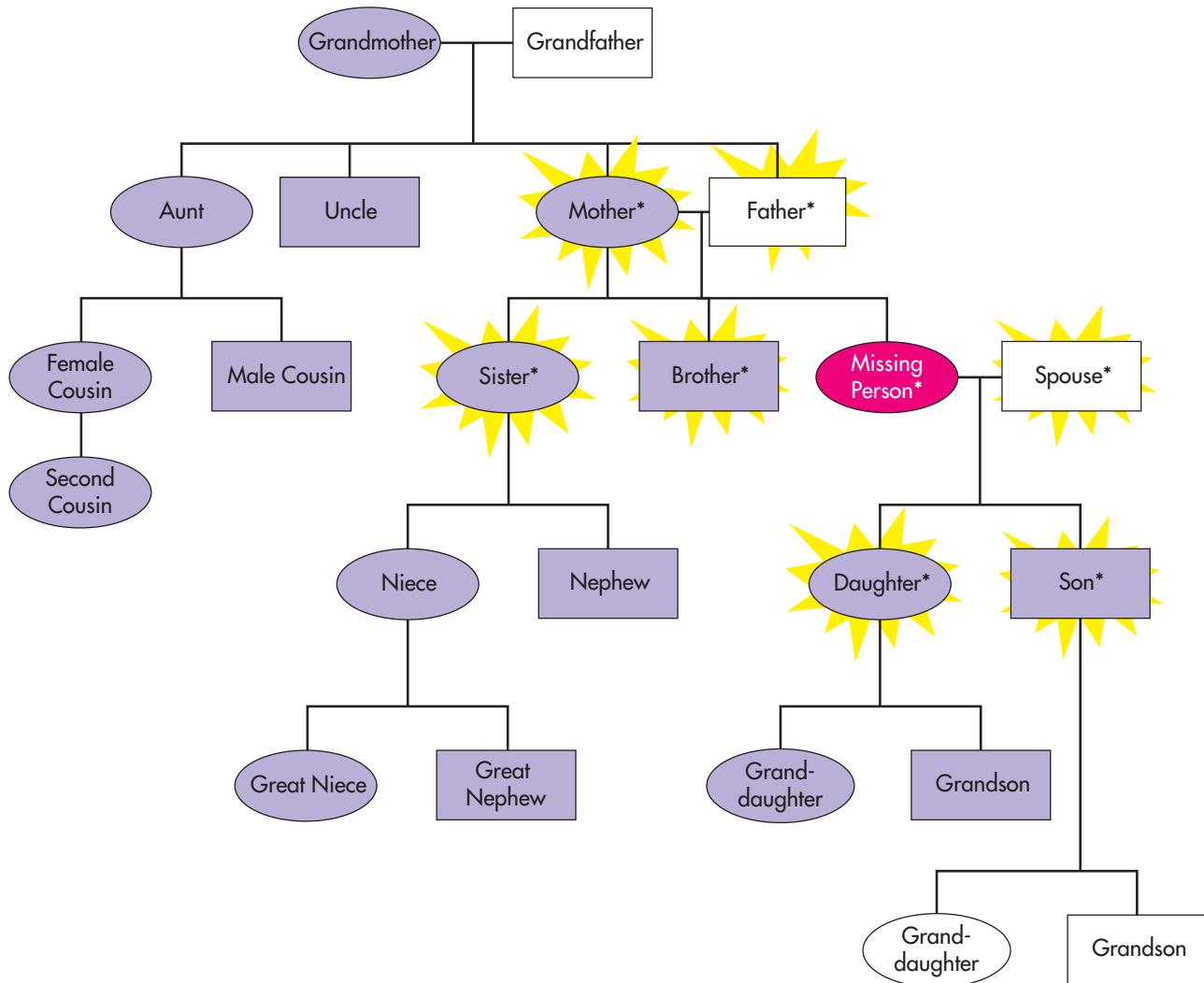


Figure A For kinship analyses, buccal swabs from close family are taken for comparison. In this chart, males are indicated by squares and females by circles. Ideal samples are marked here in starbursts and include parents and offspring of the person to be matched. In the absence of these, maternal relatives (marked here in shaded boxes) may be sampled for mtDNA analyses.

find living relatives to whom DNA can be matched, or to find personal items such as medical samples or hair brushes that might yield remnants of the victim's own DNA. Without such reference samples no identification can be made, although DNA may be able to narrow down the ancestry and identify the sex of the individual.

Unlike forensic anthropologists who are seeking individual identifications, bioarchaeologists are more interested in general kinship among groups. Ancient DNA

that come one right after the other. They do not code for anything in particular nor are they related to any particular external feature like eye or hair color. That is, they have no known function. The number of repeats varies from individual to individual, and using the number of repeats at each of these 15 locations a DNA profile unique to that individual is developed. The chance of sampling the same profile in another individual is about 1 in a trillion, or more than the number of people alive on Earth today.

Say that you are called to a crime scene where there is a dead individual of unknown identity. The preferred sources for retrieving DNA are, in order of preference, nonclotted blood (DNA is present in the white blood cells only, because only they have nuclei), deep red (fresh) muscle, compact bone (say from the shaft of a long bone like the femur or tibia), any muscle, bone, or tooth. Back in the lab, you attempt to extract DNA, which involves using the polymerase chain reaction to essentially make multiple copies of the DNA, and from these produce a DNA profile. If DNA is present, the length of each STR will be measured and translated into the number of repeats for that particular STR. Each STR will have two numbers associated with it, one each for the number of repeats on each locus of the individual's DNA (remember that each individual receives a strand from their mother and from their father).

But this DNA profile is useless for identifying the individual without something to compare it to. Ideally, an antemortem DNA sample is available from the victim—perhaps we have an idea of who they might be and we can search for medical samples taken before they died such as a Pap smear, a blood sample, a muscle biopsy, or a tooth saved for the tooth fairy. Other items, such as tooth brushes, are less desirable because we can't always be sure who they belonged to (or who used them). Any of these samples might yield a direct match. Making a direct match such as this, from a particular individual to a particular source, yields the kind of 1 in a trillion statistics mentioned earlier. Similarly, direct matches to individual DNA sequences that are in the Combined DNA Index System program (CODIS) and other databases can be powerful tools for linking individuals to trace evidence.

If no antemortem sample is available, a kinship analysis can be done by collecting DNA from the victim's direct relatives (Figure A). These are the kinds of analyses that were undertaken to confirm the death of Osama Bin Laden, for example. If both the biological mother and father are available, this is ideal. If not, the victim's children, full siblings, and maternal relatives are sought, and a

lineage analysis using mtDNA and nuclear DNA may be undertaken. Sometimes there are surprises, such as finding out that parents or siblings are not as closely related as the family thought. Even in the best circumstances though, because of how human genetic variation is distributed across populations, kinship matches have lower statistical probabilities than do direct matches.

Under the best of circumstances, the process of extracting DNA profiles is time-consuming, expensive, and destructive. A single sample can take an entire day to process, and cases can involve hundreds of samples—in some instances, DNA may not work at all. In very hot and humid environments DNA degrades quickly, and even bones that appear perfect may retain no DNA. Or, destructive sampling may not be allowed, and families may be reluctant to provide reference samples. As we have seen, making a match requires having some idea of who the individual was in order to get antemortem or kinship samples. In all of these cases a biological profile from the skeleton may be useful instead of, or in addition to, DNA extraction (Figure B). Biological profiles are relatively quick and cheap to complete, and they are nondestructive. They can also help to reduce the number of possible antemortem records that have to be considered, and positive identifications may be possible through comparisons to dental or medical records without ever having to resort to DNA. In many instances then, from individual crimes to airline crashes, the skeletal biological profile may be preferable. The DNA profile is a powerful tool for forensic scientists, but it's still not as fast or as easy as it seems on TV.



Figure B A biological profile from the bony remains of an individual may be preferable to a DNA profile for a variety of reasons.

techniques, like those used on the Neandertals (see Chapter 12, Innovations: Neandertal Genes on pages 392–393), are most frequently used to establish relationships among groups and the origins of groups. For example, population-level considerations of DNA variation have also been used to model the dispersal of historic human groups (see Innovations: Ancestry and Identity Genetics on pages 538–539). And ancient DNA has been used to establish the sex of fragmentary adult and subadult remains as well.

Identification in Forensic Anthropology

17.7 Describe the techniques used to assess identification in forensic anthropology.

Because the forensic anthropologist is concerned with making a positive identification and contributing data for understanding the cause and manner of death, there are a number of methods of inquiry unique to forensic investigations. These include techniques for estimating the time since death, which in a forensic case may be days, weeks, or months—rather than hundreds or thousands of years. They also include specific means for establishing a positive identification—which may entail obtaining antemortem medical or dental records, examining surgical implants or specific unique clothing or tattoos, or undertaking facial reconstruction.

Time since Death

One of the more difficult tasks for a forensic anthropologist is determining how long a victim has been dead. Anyone who has ever watched a police show knows that body temperature can be used to estimate time since death if the death is sufficiently recent. But over longer periods of time, other means are necessary. The research program in forensic anthropology at the University of Tennessee maintains an outdoor morgue in which bodies are left to decompose under a variety of controlled conditions so researchers can learn how natural processes affect the rate of decay (Bass & Jefferson, 2003). Many other such programs are now being developed. All the bodies used in the program are willed to the facility for this purpose, and once they are skeletonized the remains are curated in a research collection for other types of forensic research including the development of comparative databases. Additionally, other mammals, such as pig, are often used in controlled decomposition studies to understand the variables involved.

Decomposition is a continuum that includes a typical trajectory from cooling and rigidity, to bloating, skin slippage, liquefaction, deflation, and skeletonization. The rate at which decay proceeds is determined by aspects of the surrounding environment including burial depth, soil type, temperature, humidity, and so on. In general, bodies left on the surface of the ground decompose most quickly and those buried deeply in the ground most slowly. Surface remains decay more quickly because they are more likely to be interfered with by scavengers, such as rodents and carnivores, who destroy and scatter the remains. And insects also have greater access to surface remains, speeding up decomposition. The timing of insect life cycles is well known, and their preferences for certain types of tissues and extent of decay are also well studied. Forensic entomologists therefore are important members of any forensic team. Decomposition is quicker in the summer, averaging just a week or two for surface remains in the summer of the mid-Atlantic states. Although in very dry environments, such as deserts, bodies may mummify rather than skeletonize. The delay in wintertime decomposition is due almost entirely to lower temperatures and humidity, both of which reduce insect activity as well as the natural physiological rates of decay of the body itself. Corpses that are wrapped in impervious containers, like garbage bags, decompose more slowly than surface remains for many of the same reasons that buried bodies decompose more slowly. With all things being equal, single burials tend to decompose more quickly than do the more protected individuals in the middle of a mass grave—although individuals on the periphery decompose at rates similar to those of individual burials. Using all these clues and others, scientists work together to estimate time since death. This can help to narrow the focus of possible identifications and possible perpetrators by suggesting a time frame for the crime.

Antemortem Records and Positive IDs

Ideally, forensic anthropologists are trying to contribute to the positive identification of a victim. To do this they first develop the biological profile to narrow the field of focus of potential identities, and they define the time frame of the event. Once they have several possibilities, they can compare a number of different antemortem records to provide information leading to an identification. The most common are dental records, surgical implants, and the matching of antemortem and postmortem X-rays.

Your dentist keeps a chart of which teeth you have, which have been extracted, and which have been filled or crowned. All of your X-rays are also kept on file. These records can prove invaluable for making positive identifications because no two mouths are the same. However, comparing dental charts is time consuming, so the biological profile is used to limit the scope of possible identities. Forensic odontologists, specially trained dentists, work with forensic anthropologists to make identifications from dental records. Both dental X-rays and dental charts can be used for positive identifications (Adams, 2003). Exact matches of antemortem and postmortem dental X-rays can establish an identification in ways similar to antemortem medical X-rays (Stinson, 1975). But when X-rays are absent, comparing dental charts is an effective means of identification as well. A dental chart is made for the remains and this chart is compared, sometimes using the computerized program, OdontoSearch, with antemortem charts of missing individuals (Adams, 2003).

Medical X-rays taken before death can also be used for making identifications. An X-ray of a person's head after an accident may reveal the frontal sinus, an air-filled space within the frontal bone just behind the brow area (Figure 17.16). The sinus is uniquely developed in each of us, so comparison of an X-ray from a skull with an antemortem film of a known individual may lead to a positive identification. Healed wounds and infections that are caught on antemortem X-rays can also be compared to postmortem X-rays. If the healing is particularly idiosyncratic, this might lead to a positive identification or at least to a possible identification that could be confirmed by other tests.

Orthopedic implants and pins often resolve issues of identity. These implanted items often have either unique or batch serial numbers than can be traced back to an individual patient's medical records. And antemortem X-rays of a pin in place can also be compared to postmortem X-rays to lead to a positive identification. Sometimes, the biological profile doesn't match any possible identities, and so there are no antemortem records to establish a positive ID. In these cases, other more exploratory methods, such as facial reconstructions, may help the general public suggest a possible identity.

Facial Reconstruction

Facial reconstruction—the fleshing out of the skull to an approximation of what the individual looked like in life—is part art and part science. It is based on careful systematic studies of the relationship between skin thickness and bone features—and clay is used to layer on muscle, fat, and skin over a model of a victim's skull (Wilkinson, 2004). Digital technologies are also being developed to render three-dimensional virtual reconstructions. Eyes and ears are placed, although their color and shape can't be known for sure. The size of the nose is based on the height and breadth of the nasal aperture and the bony bridge. But some artistic license is required to estimate the shape of the end of the nose. Skin and hair color can't be known from the bone. For example, facial reconstructions of King Tut were commissioned by *National Geographic* magazine from two different artists. The two yielded similar facial reconstructions, much of which were dictated

Figure 17.16 The frontal sinus, an air-filled space just behind the brow, is a unique size and shape in each of us and can be used to make a positive identification if antemortem X-rays are available. The frontal and maxillary sinuses are shown here in orange.



by the king's uniquely shaped head and slightly asymmetric jaw, but inferences about weight, skin and eye color varied. Once rendered, forensic facial reconstructions may be photographed and shown to the general public in the hopes that someone might recognize something about the individual. When possible identities are proposed, antemortem records can be checked—and perhaps an ID will be made.

Bioarchaeology and Population Change

17.8 Discuss how archaeology and the skeleton are used in bioarchaeology and population change.

The field of bioarchaeology traces its origins to the 1980s with the recognition of the importance of human remains in archaeological contexts for understanding the biocultural evolution of past populations (Larsen, 1999). The population-level approach sets the field apart from earlier enterprises that focused on individual case studies. A key component to bioarchaeological study of human remains is the emphasis on understanding the cultural context of the uncovered remains. Such information helps researchers understand the biological effects of certain cultural practices. This means comparing skeletal populations across important cultural transitions—such as the transition between hunting and gathering to farming or the impact of European contact on indigenous peoples in the New World. It also means using skeletal clues to better understand the biological impact of cultural practices, such as the influence of social stratification on diet and disease. Bioarchaeologists approach a diverse number of evolutionary questions in this interdisciplinary way including looking at mortuary behavior, health and disease, and activity patterns.

Mortuary Archaeology

Ancient burial places not only preserve skeletons but are reflections of belief systems, kin structures, and social organization. Grave goods, burial position, and grouping of individuals all provide a window into past society. Using information from headstones, historians have traced cultural shifts in the outlook toward death in early American history, and they can examine the distribution within a cemetery of individuals of certain ages and sexes. In some cultures, families are buried together, but in others males and females may be separated. Both patterns tell you something about how the living society was structured. Deeper in time, archaeologists and bioarchaeologists combine their expertise to make inferences about social stratification and culture change. In the absence of headstones, the biological profiles of the buried skeletons provide critical data for these undertakings.

For example, on Mangaia, the second largest and southernmost of the Cook Islands in the South Pacific, archaeological and bioarchaeological studies document changes in burial practices through time. Prior to European contact, which occurred on Mangaia in 1823 with the arrival of Christian missionaries, individuals were buried under house floors and in burial caves, but after contact, many individuals were buried in church cemeteries (Antón & Steadman, 2003). Using the biological profiles of the skeletal remains we see that even though burial caves continued to be used after contact, the style of the burials changed. Before contact nearly equal numbers of adults and children were placed in burial caves and evidence of secondary burials, in which the skeleton had been rearranged, and of multiple burials in which several individuals were buried simultaneously was frequent (Figure 17.17). After European contact, few adults were found in burial caves and those present were buried individually. In addition, secondary burials do not seem to have been present. These changes suggest that indigenous mortuary practices, and likely religion, were influenced by Christian missionaries. Individuals were no longer buried near or among the living,

Figure 17.17 Burial caves from Mangaia, Cook Islands, document the changing patterns of mortuary ritual. Secondary burials, seen here in detail (a) and from a distance (b), are rare after contact with Christian missionaries.



(a)

(b)

and the more unusual practices (from a Christian perspective), such as secondary processing of skeletal remains, were eliminated. Although burial caves are no longer used on Mangaia today, they remain places of reverence and connection to ancestors. Only through the combined perspective of both archaeological and biological data can we see when this transition began and how it emerged.

Biocultural Evolution of Health and Disease

The combination of archaeological and biological information is also used to understand the complex interaction between cultural practices, health, and disease (see Insights and Advances: The Bony Record of Health and Disease on pages 550–551). Biological profiles and detailed analyses of health indicators in a group of skeletons of known time period, environmental context, and social status can help elucidate the evolution of disease and the role of culture change on the health of a population.

In the Channel Island's populations of prehistoric California (7200 B.C. to A.D. 1780), increased exploitation of marine foods has been linked to increases in population size and density through time; changes in health status followed. Archaeological evidence of increasing quantities of fish and shellfish, and the tools for catching and processing these fish, has been found in Channel Island sites. These very local marine resources allowed Channel Islanders to lead more sedentary lives and allowed their populations to grow in size and density. With these changes, their social organization became more complex. General health also declined; with increasing population density more individuals show bone infections and stature decreases—both indicators of general stress (Lambert & Walker, 1991). In addition, cranial fractures increased, indicating an increase in interpersonal violence perhaps due to stresses associated with increasing population size (Walker, 1989). Only the combination of these archaeological data with the biological profiles of hundreds of individuals allows the interpretations and understanding of these widespread changes in the Channel Island populations through time.

Activity Patterns and Subsistence Change

Comparisons of groups of skeletons of individuals with very different activity patterns offer further insights into the influence of, for example, subsistence change on lifestyles. Activity patterns are often assessed through CT studies of the

Insights and Advances

The Bony Record of Health and Disease

The skeleton has often been likened to a book that tells the tale of an individual's life. We've seen how evolutionary and idiosyncratic clues in the skeleton can be translated by an experienced osteologist into information about an individual's sex, age, height, and even ancestry. The skeleton also records information about some kinds of diseases and aspects of nutritional health. Bioarchaeologists use these skeletal signs of health and disease to understand the health of past populations, the evolution of disease, and the influence of differences in subsistence or social status on human health. Such clues have been used to assess the results of colonization on indigenous peoples, as well as to study the transition from hunting and gathering to agriculture and sedentism. This study of ancient diseases in skeletal remains is called paleopathology, and its practitioners use macroscopic and microscopic bone structure as well as ancient DNA from lesions.

As we saw in Chapter 15, recent human history is replete with stories of the critical influence of infectious disease such as bubonic plague and influenza on the shaping of populations, and cultural practices can either mitigate or exacerbate the spread and evolution of such diseases. So understanding which diseases were present in the deep past, how high the mortality was, and with what conditions they are associated could answer key questions in our evolutionary history and perhaps how we deal with disease today. Yet, diagnosing a particular pathological condition from a skeleton is tricky. Some diseases, including many cancers, and infectious diseases such as AIDS, hepatitis, ebola, and influenza, leave no bony signs despite the discomfort and disability they may cause the individual. Even in diseases that do affect bone, not all individuals will express the disease in their skeleton, and the bone cells of those that do can only respond to an insult in two ways—bone can be deposited or it can be resorbed. Thus a critical component of a paleopathological analysis is the construction of a *differential diagnosis*—that is, a list of the potential causes of the lesions with an assessment of which is most and least likely to be the cause.

Some infectious diseases, like syphilis, leprosy, and tuberculosis, do leave their mark on the skeleton, at least in some of the more chronically infected individuals (Figure A). In these kinds of systemic diseases a certain distribution of bone lesions is often typical of a particular disease—but diseases are also sometimes difficult to tell apart.

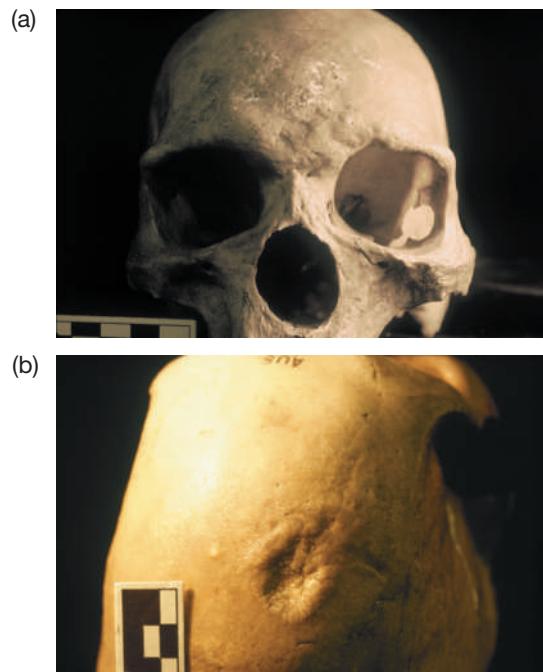


Figure A Treponemal diseases like syphilis are often accompanied by cranial and facial destruction (a) and radial lesions of the vault (b).

Syphilis, for example, is one of a group of treponematoses that also include yaws, pinta, and bejel. Except for pinta, the treponemes are caused by different subspecies of *Treponema pallidum*, and they are spread by different modes of skin contact. The most notorious forms of syphilis are venereal—yaws tends to spread by more casual contact. Not surprisingly, the treponemes exhibit patterns of bone lesions that are hard if not impossible to differentiate from each other. Their lesions leave the braincase looking moth-eaten or scarred down, some forms cause destruction of the face and nasal region, and the postcranial skeleton sees extensive bony deposition followed later by secondary erosions into the bone. Often the tibia is expanded and deformed to look like a sabre. Treponemes are indigenous to the New World, and based on skeletal evidence, a strong case can be made that they were present in the New World before it was colonized by Europeans—although whether this included venereal syphilis is unclear (Baker and Armelagos, 1988). A likely proposition seems to be that nonvenereal syphilis may have been introduced to the Old World after Columbian contact, but that the switch to a venereal transmission took place in the denser populations of the Old World—although this remains debated.

postcrania that take advantage of the fact that systematic changes in activity influence the development of the human skeleton. The distribution of bone in cross-sections of the leg bones, for example, reflects the predominant direction of force through the limb.



Figure B Linear defects in tooth enamel as seen on this canine are responses to high fevers, disease, or other insults during development.

Just as the dense urbanization of the Old World is hypothesized to have led to this shift in disease transmission, earlier shifts to agriculture led to health declines as well. Agriculture had the effect of allowing increases in population size and density, which often led to environmental degradation, increased disease loads, and interpersonal conflict. The health changes can be seen throughout the skeleton. Increased nutritional stress can be seen in the skeleton in various ways. Anemias and general nutritional stress, brought on either from too little dietary iron or from a heavy parasite load that precludes adequate absorption of nutrients, are recorded in the bone of the eye orbits (*cibra orbitalia*) and occipital (*porotic hyperostosis*) as the body attempts to produce additional red blood cells in these regions. Teeth record disruptions in growth during a high fever, infection, or other period of stress during development, which appear as linear defects in the tooth crown (Figure B). Limb bones may also show growth arrest lines resulting from the resumption of growth after either nutritional or disease stress. These lines appear on X-rays and are called Harris lines. And levels of left-right asymmetry in facial bones and other bones of the skeleton are higher in populations under greater stress. Repetitive use of various joints lead to degenerative joint disease (arthritis) that presents as lipping and degradation of the joint (Figure C). And the change in the starch and sugar content of food as well as its toughness (perhaps due to cooking) led to many cranial changes. Cranial and jaw size appear to reduce. Dental crowding follows as reduced food toughness may have led to smaller jaws and many instances of malocclusion—perhaps one of the reasons so many of us need orthodontic work today! And the increase in starch, especially in maize-based diets lowers the PH of



Figure C Repetitive use of joints can lead to lipping, pitting, and reduced function. The temporomandibular (jaw) joints in this cranium show severe arthritis (a). A close-up shows the extent of the lipping—the joint should be smooth and dense for ease of movement (b).



Figure D Changes in starch and sugar content decrease oral pH and lead to cavities and periodontal disease as seen in the holes around the tooth roots in this mandible.

the mouth's saliva leading to an increased frequency of cavities and periodontal disease—which then become a great source for infection to enter the body via the sinuses around the mouth (Figure D). Taken together, these signals suggest to bioarchaeologists that even though we think of the shifts to agriculture and urbanization as “advances” in civilization—at least initially these major transitions resulted in significantly less healthy populations.

As the activity patterns of Native American populations from the coastal region of Georgia changed with the adoption of agriculture, the strength of limb bones also changed with time (Ruff et al., 1984; Larsen & Ruff, 1994). Archaeology of the area indicates continuous occupation for thousands of years before European contact up

until about A.D. 1550. Around A.D. 1150, the hunter-gatherers incorporated maize agriculture into their economy and became more sedentary. Comparisons of the strength of the femora (thigh bones) of Native Americans from before and after the switch to sedentary agriculture show a decrease in strength in the agricultural population. The results suggest a decrease in activity level and in the types of activities once the shift to agriculture was made. Interestingly, comparison of the leg strength of these agriculturalists with early contact period (A.D. 1565–1680) groups of sedentary Native Americans living in missions in what would become the state of Georgia found the later groups to be stronger. Scientists interpret this to mean that the Native Americans living in missions, although also sedentary, were working harder than their precontact forebears (Larsen & Ruff, 1994). These bioarchaeological studies use the same techniques that forensic anthropologists apply, although in very different settings.

Forensic Anthropology of Mass Disasters, War Crimes, and Human Rights

17.9 Describe the approaches used in forensic anthropology of mass disasters, war crimes, and human rights.

The field of forensic anthropology has achieved recent popularity due in part to television shows such as *CSI* and *Bones*. But like most popularizations, the fantasy is more glamorous than the reality. The field traces its professional origins to the 1970s, when the physical anthropology section of the American Academy of Forensic Sciences (AAFS) was formed, although U.S. anatomists and biological anthropologists have been assisting in human skeletal identification since the late 1800s. Each state has medical examiners or coroners who are legally responsible for signing death certificates and determining the cause and manner of death of people not in the care of a doctor. They also have the authority to consult other experts in their investigations, including forensic anthropologists. Usually a forensic anthropologist is involved when soft tissue remains are absent or badly decomposed. Forensic anthropologists must work in accordance with the rules of science but also of the courts. They must be able to convince their colleagues of their findings, and their findings must withstand the scrutiny of lawyers, juries, and judges. Although forensic anthropologists most often work on cases of lone victims of homicide, suicide, or accidental death, they are also called to the scene of mass fatalities, to search for soldiers killed in combat, and to investigate human rights abuses that result in hidden or mass graves.

Mass Fatalities

In the days after the attack on the World Trade Center in New York on September 11, 2001, forensic anthropologists from around the country were called in to help identify the victims. The Oklahoma City bombing case 7 years earlier had brought in a similar influx of anthropologists as did the later devastation wrought by Hurricane Katrina and the Great Floods of 1993. Forensic anthropologists play key roles in the attempt to identify victims of earthquakes, plane crashes, floods, and other natural and human-wrought disasters. The United States has regional emergency response teams called Disaster Mortuary Operational Response Teams (D-MORT) that include pathologists, forensic anthropologists, and forensic odontologists who are mobilized by local or federal authorities in response to national mass disasters such as Hurricane Katrina. The National Transportation Safety Board, including their own forensic

anthropologists, investigate transportation incidents including air accidents such as United flight 93, which crashed in Pennsylvania as part of the World Trade Center plot in 2001. And military forensic experts and sometimes D-MORT respond when U.S. citizens or military are involved in mass fatalities abroad, such as the earthquake in Haiti for which D-MORT was deployed to recover American citizens.

Although we often think of mass disasters as involving hundreds or thousands of individual deaths, mass fatality incidents (MFIs) are defined as those in which the number of deaths overwhelms local resources—there is thus no minimum number and depending on the size of the municipality this might be fewer than 5 or 10 deaths. In such incidents, a main goal is to provide speedy and accurate disaster victim identification (DVI), which requires three big operational areas—search and recovery, morgue operations, and family assistance centers. Forensic anthropologists are critical participants in all three of these areas.

In 1994, a D-MORT team responded to an unusual mass disaster. Flooding of historic proportions caused the remains from a cemetery in Albany, Georgia, to surface. The lids of the concrete vaults in which coffins were placed during burial were removed by the floodwaters, and coffins floated to the surface and into town. Some remains were separated entirely from their coffins. As in Hardin, Missouri the previous year, the D-MORT team recovered the remains and established a morgue. D-MORT scientists, including forensic anthropologists, studied the remains to construct biological profiles. They then worked with antemortem dental and medical records and information collected from relatives to establish positive identifications with the goal of reconnecting the remains to their place of interment (Figure 17.18). No DNA analyses were used in this case. Of the 415 disinterred individuals, the D-MORT team was able to positively identify 320 people using the various techniques we have discussed.

In 2005, D-MORT was deployed to assist in DVI in the aftermath of Hurricane Katrina (Figure 17.19 on page 554). Hurricane Katrina was a category 3 storm that devastated the Gulf Coast of the United States in August of 2005. Up to that time it was the most costly storm in U.S. history, and major damage was caused by the breaching of the levees that protected the city of New Orleans, which sits below sea level. More

Figure 17.18 Forensic anthropologists working at a temporary morgue following the recovery of remains from a flooded cemetery in Georgia.



Figure 17.19 D-MORT teams responded to the mass fatalities incurred by Hurricane Katrina, a category 3 storm shown here approaching the Gulf Coast of the United States.



than 1,800 deaths ensued, with flooding being the main cause of death and destruction. Because of widespread flooding, victim recovery was also delayed, requiring the assistance of forensic anthropologists in identifications. The identifications were made more difficult by the flooding, which also destroyed or damaged much of the antemortem medical and dental records that are normally used in identification. D-MORT teams were rotated in for 2-week assignments, and forensic anthropologist were utilized in recovery, morgue operations, and family record collection.

War Dead

U.S. forensic anthropologists first became involved in the identification of those who died in war when the Central Identification Laboratory (CIL) now in Hawaii was formed to aid in the identification of those missing in action during World War II. Since then the skeletal remains of U.S. soldiers and civilians from World War II, the Korean War, the Vietnam War, and other military actions have been recovered and identified by this group of anthropologists. The CIL, now the laboratory of the newly formed Defense POW/MIA Accounting Agency (DPAA), sends teams around the world to identify and recover U.S. soldiers lost in the wars of the twentieth century. The remains are brought back to the DPAA Laboratory, thoroughly examined, and identified. In addition to standard forensic anthropological techniques, DPAA teams also extensively use forensic DNA techniques to reach a positive identification so that remains may be returned to the next of kin.

Not only does this group of forensic anthropologists help in identifying missing personnel, but they have also undertaken some of the most important systematic research used in forensic anthropology and bioarchaeology. For example, Dr. Mildred Trotter, an early director of the laboratory, developed regression analyses for determining stature from long bone lengths based on the skeletal remains of soldiers who died in the Korean War. This large body of work remains a standard in forensic and bioarchaeological analyses today and would not have been possible without the detailed medical histories of these military personnel.

War Crimes and Genocide

Finally, forensic anthropologists may play a key role in uncovering mass graves and identifying bodies in them, and these scientists may be important witnesses in the investigation of war crimes. Whether in Cambodia, Rwanda, Argentina, Bosnia, or Iraq, when repressive regimes crack down on their citizens, they often attempt to intimidate the population through mass murder. The mass graves that are left contain the bodies of hundreds or even thousands of victims, whose loved ones spend lifetimes attempting to locate them and determine their fate. Forensic anthropologists help to identify the victims for the sake of surviving family members and may provide key evidence in reconstructing a mass crime scene in an effort to bring those responsible to justice. Forensic anthropologists in these areas work for both government and private groups such as Physicians for Human Rights, the International Commission for Missing Persons, and the United Nations (UN). Such teams often start work before the conflicts end; for example, U.S. forensic archaeologists and anthropologists are currently at work in Iraq.

One example of such work is the effort to exhume mass graves in the former Yugoslavia that began in 1996 under the auspices of the United Nations, and in particular the International Criminal Tribunal for the former Yugoslavia (ICTY), in partnership with Physicians for Human Rights. Some of these exhumations concentrated in eastern Croatia on a grave site known as Ovcara, which contained victims from a massacre in Vukovar. The Vukovar massacre occurred in November 1991, and the mass grave site was located in 1992 based on information from a survivor. Excavation waited until 1996 because of continuing hostilities in the region (although the site was guarded by the UN for the entire time).

The forensic teams consisted of scientists from around the world and included forensic anthropologists and archaeologists, pathologists, evidence technicians, radiologists, odontologists, autopsy technicians, and computer scientists (Figure 17.20). The teams exhumed about 200 bodies from Ovcara, nearly all of them males. Mapping the grave site took more than a month. The remains were autopsied in Zagreb with the goals of constructing a biological profile that would help in identification and

Figure 17.20 A team of forensic experts working on remains recovered from Ovcara in the former Yugoslavia.



interpreting perimortem trauma to understand the cause of death. Many of the victims had multiple gunshot wounds and other forms of perimortem trauma. Biological profiles were compared with the medical and dental records of missing people, a task hampered by the destruction of hospitals and other medical facilities during the war, and lists of identifying characteristics (including tattoos) provided by family members of missing people. Through these comparisons about half of the 200 were positively identified. This evidence has been used in the prosecution of war crimes by the UN-ICTY, including the case against the region's former leader, Slobodan Milošević.

Bioarchaeologists and forensic anthropologists use the changes wrought in the human skeleton by natural selection and an individual's life experiences to read the clues of recent human history and prehistory. They apply the same principles, theory, and method to recent humans that primate paleoanthropologists applied to understanding our 65-million-year-old fossil ancestors, all in a struggle to understand what makes us universally and uniquely human.

Epilogue

The place of humans in the natural world has been the major theme of this book. We have explored this topic from a wide variety of perspectives, including the fossil record, the behavior of living nonhuman primates, the lives of people in traditional societies, the workings of the brain, and the biology of modern people. However, our explorations of these diverse topics have been linked by a single common thread: evolutionary theory.

You've now completed a comprehensive look at your own evolutionary past, and at the place of humankind in the history of the world. As you have seen, the evidence of our past is present in us today. It's visible in our DNA, our hominin anatomy, our physiological adaptations, and even in aspects of our behavior. Many people live in denial or in ignorance of this evolutionary past. In contrast, we feel that embracing and understanding it is critical to being an enlightened citizen of the twenty-first century.

It is important to keep in mind, however, that to embrace an evolutionary perspective of humankind is not to deny the importance of culture in our lives. We have seen that culture may be the most fundamental of human traits. Many aspects of the biology of modern people are influenced in some way by culture, while at the same time our cultural nature is a direct outgrowth of our biology.

This book has been concerned with our evolutionary past, but the most pressing question for humankind in the early twenty-first century is whether our species will survive long enough to experience significant evolutionary change. Environmental degradation, overpopulation, warfare, and a host of other problems plague our species. It is safe to say that no species in Earth's history has contended with so many self-induced problems and survived. But of course, no other species has had the capability to solve problems and change its world for the better the way that we humans have.

Summary

LIFE, DEATH, AND THE SKELETON

17.1 Describe how bioarchaeologists and forensic anthropologists relate aspects of Life, Death, and the Skeleton.

- Bioarchaeologists and forensic anthropologists use the theory and method of biological anthropology to glean information about individual's from their skeleton.
- Bioarchaeologists study skeletons from the Holocene using both skeletal and archaeological clues to answer population-level questions.

- Forensic anthropologists use skeletal and other information to try to help identify individuals and understand what happened around the time of death.

FIELD RECOVERY METHODS

17.2 Explain the archaeological field recovery methods used to process a site/scene.

- Remains are flagged when found and photographed.
- A datum is set up, and all remains are mapped relative to it.
- If necessary, an excavation is undertaken and remains are individually labeled.
- The sediments are screened to retain small items.

LABORATORY PROCESSING, CURATION, AND CHAIN OF CUSTODY

17.3 Describe what is involved in laboratory processing, curation, and chain of custody including how these differ in bioarchaeology and forensic work.

- In forensic anthropology, chain of custody is established in the field to keep track of evidence.
- In the lab, remains are cleaned and laid out in anatomical position.
- An inventory is taken of which bones are present and in what condition.

THE BIOLOGICAL PROFILE

17.4 Understand what the biological profile is and how it is used by forensic anthropologists and bioarchaeologists.

- Age at death can be estimated in children from dental eruption and bone development patterns and in adults from systematic degenerative changes to the pubic symphysis and other bones.
- Sex can be inferred in adults from primary sexual characteristics of the pelvis and secondary sexual characteristics of the skull and other bones.
- Ancestry is difficult to assess but may be inferred from cranial and postcranial features.
- Stature and weight are most usually estimated from the leg bones.
- Premortem trauma and disease may be evident as healed areas in the skeleton.

TAPHONOMY

17.5 Discuss how taphonomy is used to understand events that happened around the time of death.

- Taphonomy is the study of what happens to remains from death to discovery.
- Perimortem trauma tells about events that occurred around the time of death.
- Perimortem trauma shows no signs of healing but does show evidence that the bone was fresh or “green” when broken.
- Postmortem trauma tells about events well after death.
- Postmortem trauma shows no signs of healing and no evidence that the bone was fresh.

DNA, KINSHIP, AND IDENTITY

17.6 Explain the role that DNA, Kinship, and Identity play in archaeological and forensic investigations.

- DNA can be used to establish kinship, to understand relatedness across archaeological populations or to assist in identifying victims.
- DNA is costly and time-consuming to analyze, so it cannot replace a biological profile.

- For identification purposes, some idea of who the victim might have been is necessary either to provide an antemortem DNA sample or relatives from whom to gather comparative DNA.

IDENTIFICATION IN FORENSIC ANTHROPOLOGY

17.7 Describe the techniques used to assess identification in forensic anthropology.

- Forensic anthropologists provide information to the medical examiner or coroner that may assist in establishing a positive identification and cause and manner of death.
- Matches with antemortem dental or medical records often provide the basis for identifications.
- Idiosyncratic anatomy, such as the form of the frontal sinus, may also assist in making an identification.
- DNA extracted from bone or soft tissue may be used to make direct matches to antemortem samples or kinship matches to living relatives.

BIOARCHAEOLOGY AND POPULATION CHANGE

17.8 Discuss how archaeology and the skeleton are used in bioarchaeology and population change.

- Bioarchaeologists use clues from the skeleton to identify physical and behavioral changes in past human populations.
- The skeleton responds to physical stresses, and behavior can be partially read through these responses.
- The shift from hunting and gathering to farming shows a decrease in leg strength, suggesting that agriculture was less physically demanding.
- The shift to sedentism, even without a shift to farming, increases population density, which is correlated with increasing evidence of nutritional stress (e.g., rates of infection, decreased stature, developmental defects), and often interpersonal violence.
- Colonization of the New World facilitated the spread of disease between the New and Old Worlds.
- Colonization of the Pacific influenced traditional religious practices and changed, for example, how the dead were buried.

FORENSIC ANTHROPOLOGY OF MASS DISASTERS, WAR CRIMES, AND HUMAN RIGHTS

17.9 Describe the approaches used in forensic anthropology of mass disasters, war crimes, and human rights.

- In addition to individual criminal cases, forensic anthropologists also assist in victim identification in natural disasters, mass disasters, war crimes, and human rights violations.
- U.S. Disaster Mortuary Teams respond to mass fatalities from natural disasters such as Hurricane Katrina and man-made disasters such as the World Trade Center attacks.
- Forensic anthropologists excavate mass graves to collect evidence to prosecute war crimes.

Review Questions

- 17.1 How do bioarchaeologists and forensic anthropologists use the same basic methodology to approach different kinds of questions?
- 17.2 How are sites discovered, recorded, and excavated?
- 17.3 What is the chain of custody?
- 17.4 What determinations are included in an individual's biological profile?
- 17.5 What is the difference between peri- and postmortem trauma?
- 17.6 How is DNA evidence used differently in forensic anthropology and bioarchaeology?
- 17.7 How can forensic anthropologists contribute to making an identification?
- 17.8 How does studying the skeleton contribute to understanding how past populations lived?
- 17.9 What role can forensic anthropologists play in resolving mass fatalities and war crimes?

Key Terms

bioarchaeologist, p. 528
biological profile, p. 531

chain of custody, p. 530

datum point, p. 530

Appendix A

Overview of the Brain

The central nervous system consists of two main parts: the spinal cord and the brain. The spinal cord is a thick bundle of nerve fibers that runs through the bony canal formed by the vertebrae of the spine. It is the structure through which all the nerves of the body connect to the brain. The spinal cord passes through the foramen magnum of the skull where it connects to the brain.

The brain consists of three major parts: the *brain stem*, the *cerebellum*, and the *cerebrum* (Figure A.1). As its name suggests, the brain stem sits at the base of the brain and connects directly to the spinal cord. The brain stem is important in the regulation and control of complex motor patterns, in breathing, and in the regulation of sleep and consciousness. The cerebellum, or “little brain,” sits tucked in under the rest of the brain, behind the brain stem. It is densely packed with nerve cells, or *neurons*. The cerebellum is important in the control of balance, posture, and voluntary movements.

The cerebrum is the part of the brain that has undergone the most obvious changes over the course of human evolution. It is divided almost evenly along the sagittal midline into *left* and *right hemispheres*. The hemispheres can differ subtly in morphology and more substantially in function. The outer surface of the cerebrum is crisscrossed by a complex arrangement of grooves known as *sulci* (singular, *sulcus*), which gives the human cerebrum its characteristic wrinkled appearance. The sulci divide the surface of the brain into a series of thick bands or ridges, which are called *gyri* (singular, *gyrus*). Although there is individual variation, several basic sulci divide the brain into functional regions that are common to almost everyone.

If we look at a cross-section through the cerebrum (Figure A.2 on page xxx), we notice that its outer surface is actually formed by a rim of tissue (4–6 mm thick) that follows the surface down into the valleys formed by the sulci; this is the *cerebral cortex*. The cerebral cortex is made of *gray matter* (which looks more brown in the

Figure A.1 The human cerebrum is divided into two hemispheres, which are themselves divided by sulci into gyri.

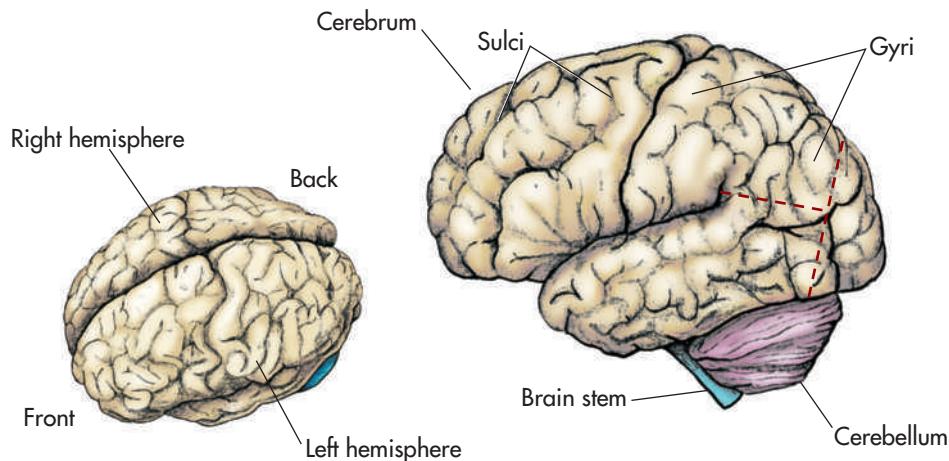
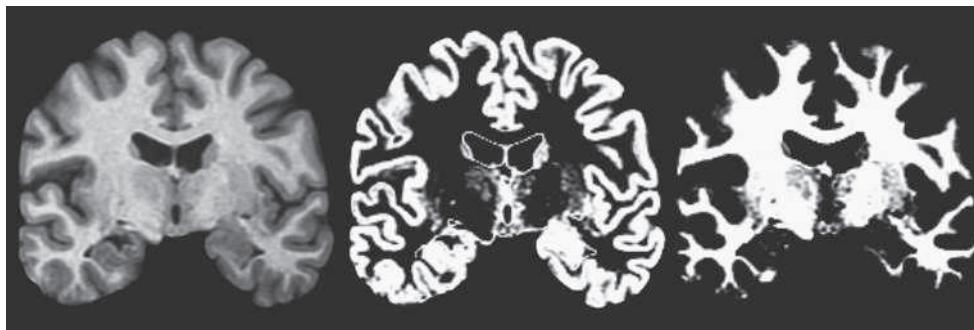


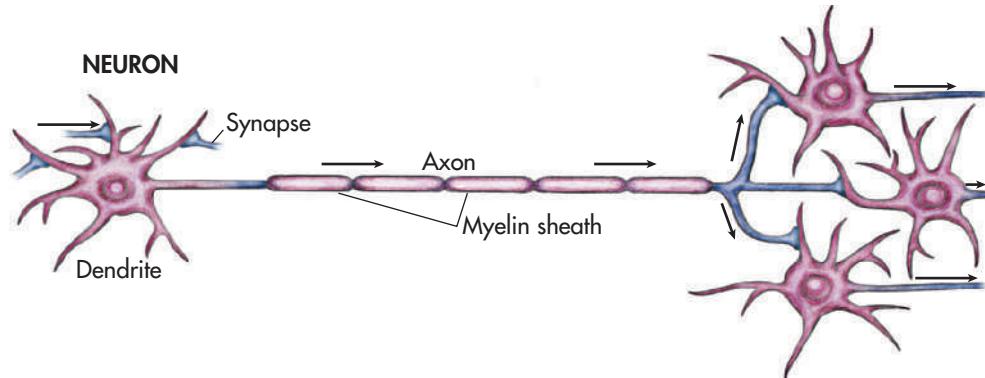
Figure A.2 The image on the left shows both gray and white matter as usually seen in MRI slices, the middle one shows gray matter, and the left one just the white matter.



living brain). Gray matter consists mostly of the cell bodies of neurons, which have a characteristic structure (Figure A.3). From the cell body, there emerge branchlike projections through which neurons communicate with one another: The *dendrites* receive inputs from other neurons, and the *axon* is the outgrowth through which one neuron sends a signal to another neuron. Neurons can have many dendrites but only one axon. The junction where the axon of one cell meets the dendrite of another cell is called a *synapse*. Communication across the synapse is facilitated by chemical agents known as *neurotransmitters*. The human nervous system consists of about 100 billion neurons. Because each neuron may form synapses with thousands or even millions of other neurons, the web of communication that forms among neurons must be of mind-boggling complexity.

Gray matter makes up about 55–60% of the cerebrum. The rest of the cerebrum is composed of *white matter*, which forms the core of the hemisphere. The white matter is made up predominantly of the axons of neurons. Axons are sheathed in a white, fatty substance known as *myelin*, which facilitates the transmission of the electrical impulse along the axon. Diseases such as *multiple sclerosis*, which results from the demyelination of axons in different parts of the nervous system, demonstrate how important myelin is for normal nerve transmission. The *corpus callosum* is a large band of white matter located in the center of the brain. It is composed of axons linking the neurons of the two cerebral hemispheres. Studies of patients who have had their corpus callosum surgically severed to prevent the recurrence of seizures have yielded many insights into how the two hemispheres work together and separately.

Figure A.3 A neuron forming synapses with three other neurons.



Major Divisions of the Cerebrum

Each of the hemispheres is divided into four major sectors, or *lobes* (Figure A.4). Two of the major boundaries of the lobes are formed by the *Sylvian fissure* and the *central sulcus*. The *frontal lobe*, which makes up about 38% of the hemisphere (Allen et al., 2002), is the part of the brain located just behind your forehead. The *parietal lobe* (about 25% of the hemisphere) is just behind the frontal lobe on the other side of the central sulcus. Below the Sylvian fissure, the *temporal lobe* (22%) forms the “thumb” of the hemisphere, as it appears in a side view. The *occipital lobe* (9–10%) forms the “knob” at the back of the hemisphere. In chimpanzees and other primates, the occipital lobe is clearly separated from the other lobes by the *lunate sulcus*, a semicircular sulcus running in an arc along the posterior (back) lateral surface of the hemisphere. In humans, the lunate sulcus often is missing or present only as a minor sulcus that does not indicate a functional boundary for the occipital lobe.

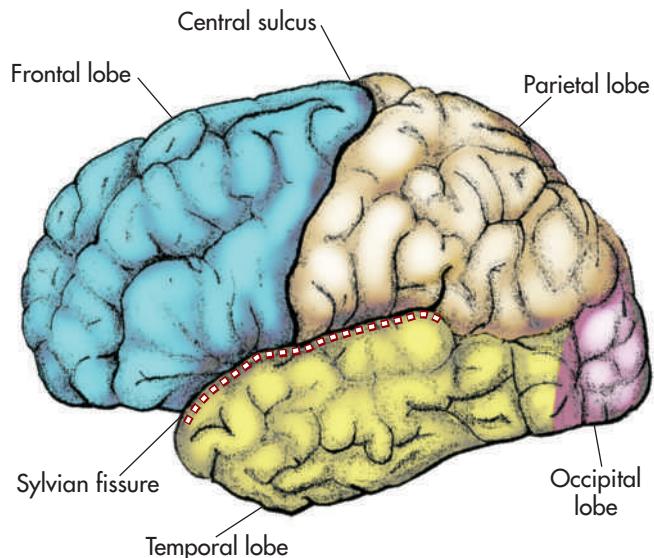
Another major part of the cerebrum—not by size but by function—is the *limbic system*. The limbic system is buried within the hemispheres in the midline region of the brain and is composed of several interrelated structures, and is most notable for being the seat of emotion (Ledoux, 1996).

Primary and Association Areas of the Cerebral Cortex

Different regions of the cerebrum have different functions. The limbic regions encompass regions of the brain important for producing emotions, and some of its regions are critically important for forming new memories. The cerebral cortex is divided into two kinds of functional areas. *Primary cortex* is involved directly with either motor control or input from the senses. *Primary motor* regions are concentrated in the frontal lobe, just in front of the central sulcus. *Primary sensory* regions are distributed throughout the cerebrum.

Most of the human cerebral cortex is not primary cortex but rather *association cortex*. Association cortex comprises the regions where the processing of primary inputs or information occurs. It is generally believed that in mammals, as brain size increases, the proportion of the brain devoted to association rather than primary regions also increases. Some association areas receive inputs from only one primary area, and other regions receive inputs from multiple primary regions. Anything that

Figure A.4 The major lobes of the cerebrum.



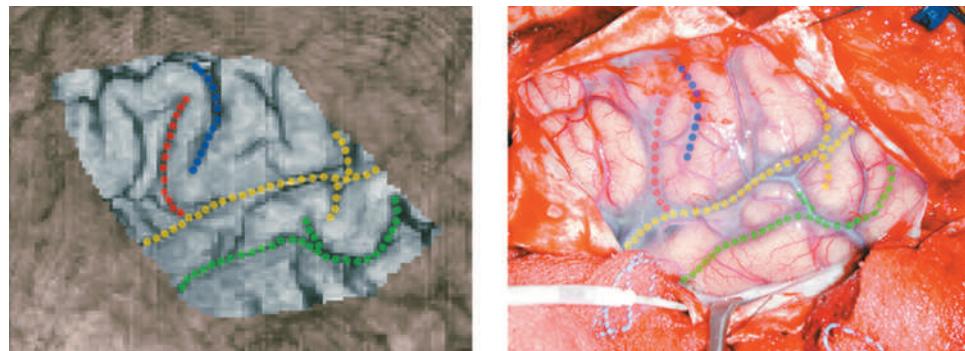
we think of as a higher-level function, such as thought, decision making, art, or music, originates in association cortices.

Methods for Studying Brain Structure and Function

Several different methods for studying brain structure and function have developed over the past 150 years. The *autopsy* was for many years the only way scientists had of studying brain structure, in which the brain is examined and described after a person's death. The *lesion method* correlates a behavioral abnormality in a living person with a brain abnormality observed at autopsy. The lesion method relies on "natural experiments": observations of people who have sustained a brain injury (for example, via stroke or infection) and who also exhibit a behavioral deficit. It has also been used widely as an experimental tool using animals as subjects; much of what we know about mammalian brain function comes from such studies.

Over the past 30 years, the development of a field called *neuroimaging* has revolutionized the study of the brain. Noninvasive methods allow us to observe the structure and function of the brain in living, healthy people under controlled experimental conditions. *Magnetic resonance imaging* (MRI) is the most commonly used method to study brain structure in living individuals (Figure A.5). A magnetic resonance image of the brain is essentially a high-resolution map of water concentration in the brain. It provides good contrast between gray and white matter and cerebrospinal fluid. For the study of brain function and activity, scientists use techniques such as *positron emission tomography* (PET) scanning and *functional MRI*. These methods show which parts of the brain are activated during a cognitive act (thinking of a word, listening to a sound, remembering an emotion) by identifying areas where metabolism or blood flow has increased.

Figure A.5 On the left, a portion of the surface of the brain as seen in an MRI reconstructed using Brainvox; on the right, the same portion of the brain shown during surgery.



Appendix B

Primate and Human

Comparative Anatomy

Figure B.1 The Axial (in pink) and Appendicular (in brown) Skeletons.

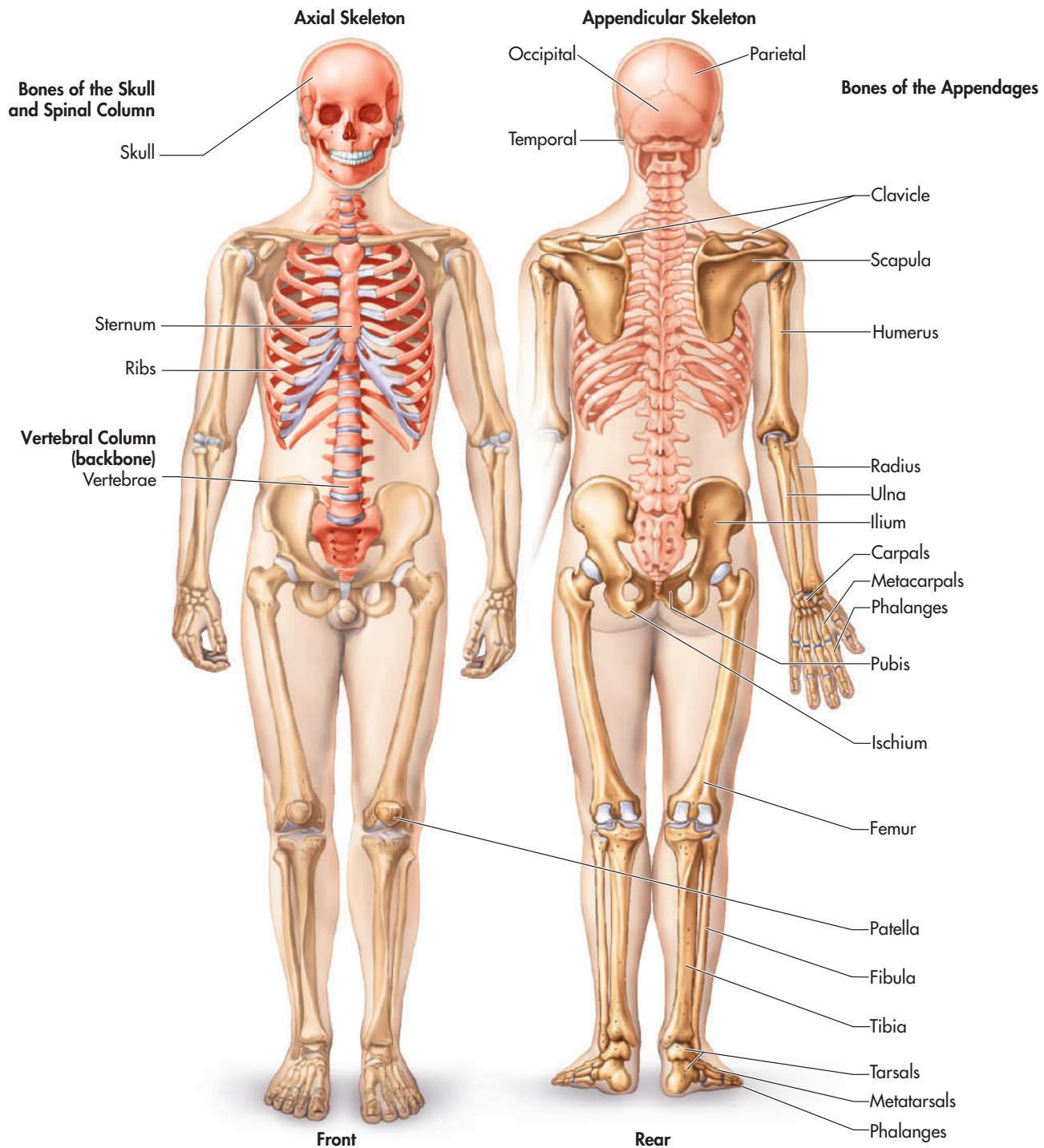


Figure B.2 Comparisons of *Gorilla*, *Homo* and *Proconsul* skeletons.

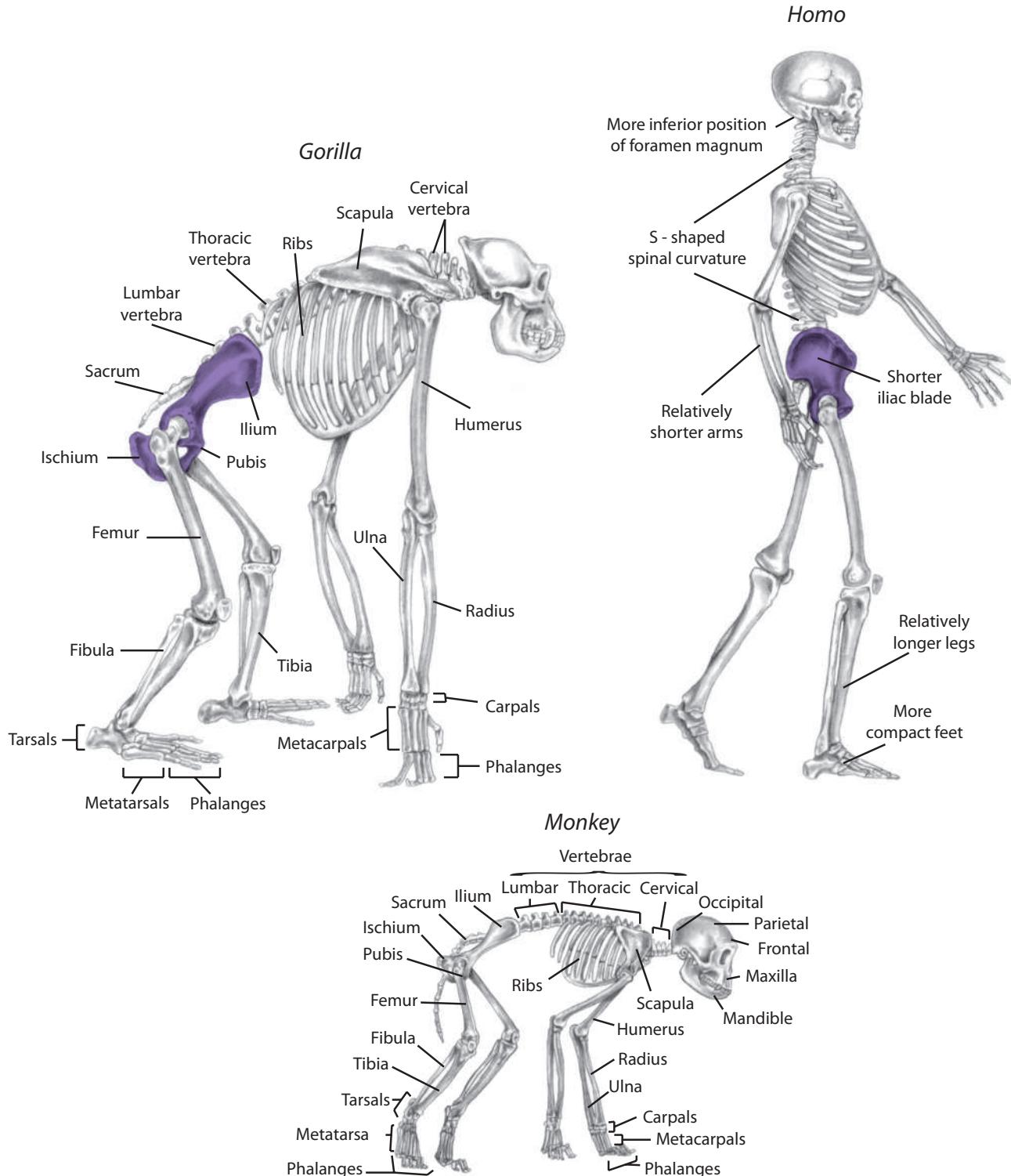
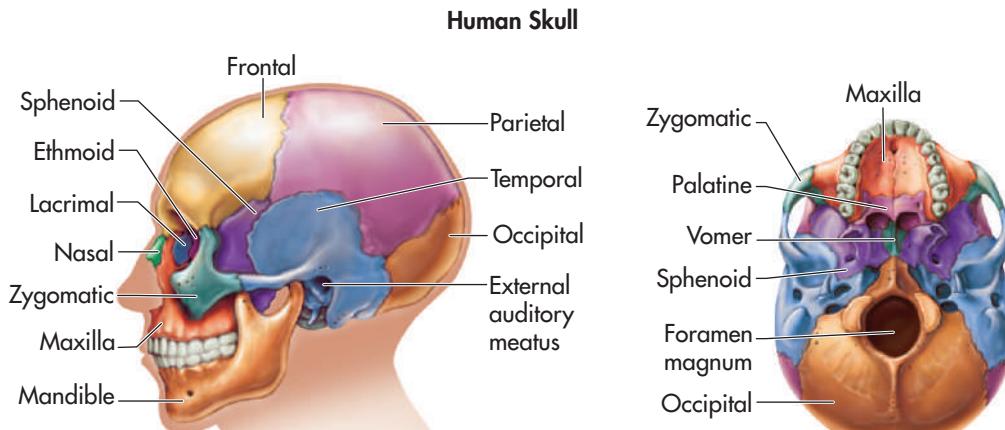
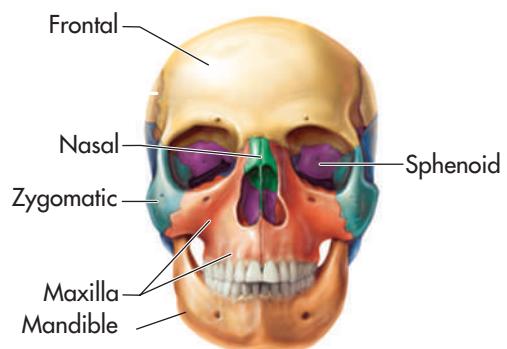
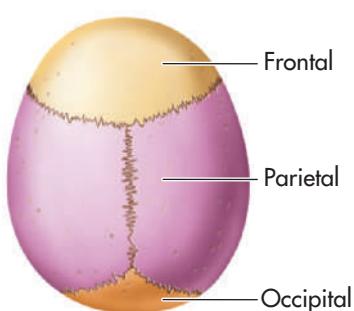


Figure B.3 (a, b, c) The major bones of the skull and face, (d) facial bones and, (e) dentition.

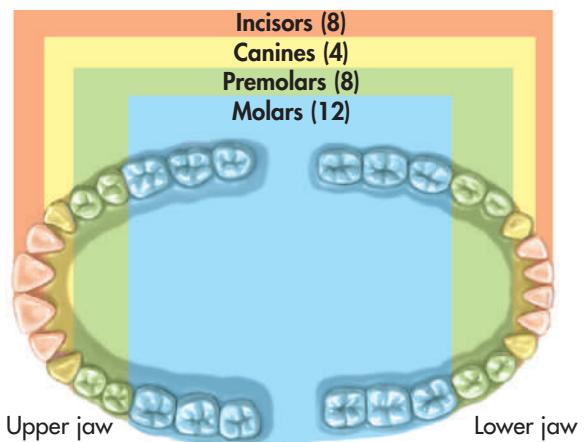
(a) The major bones of the skull and face

(b) Lower surface of skull



(c) Top view of skull

(d) Front view of skull showing facial bones



(e) Upper and lower jaws

Figure B.4 The Vertebral Column. The human vertebral column consists of 7 cervical, 12 thoracic, 5 lumbar, 5 fused sacral, and 4 or 5 diminutive coccygeal vertebrae.

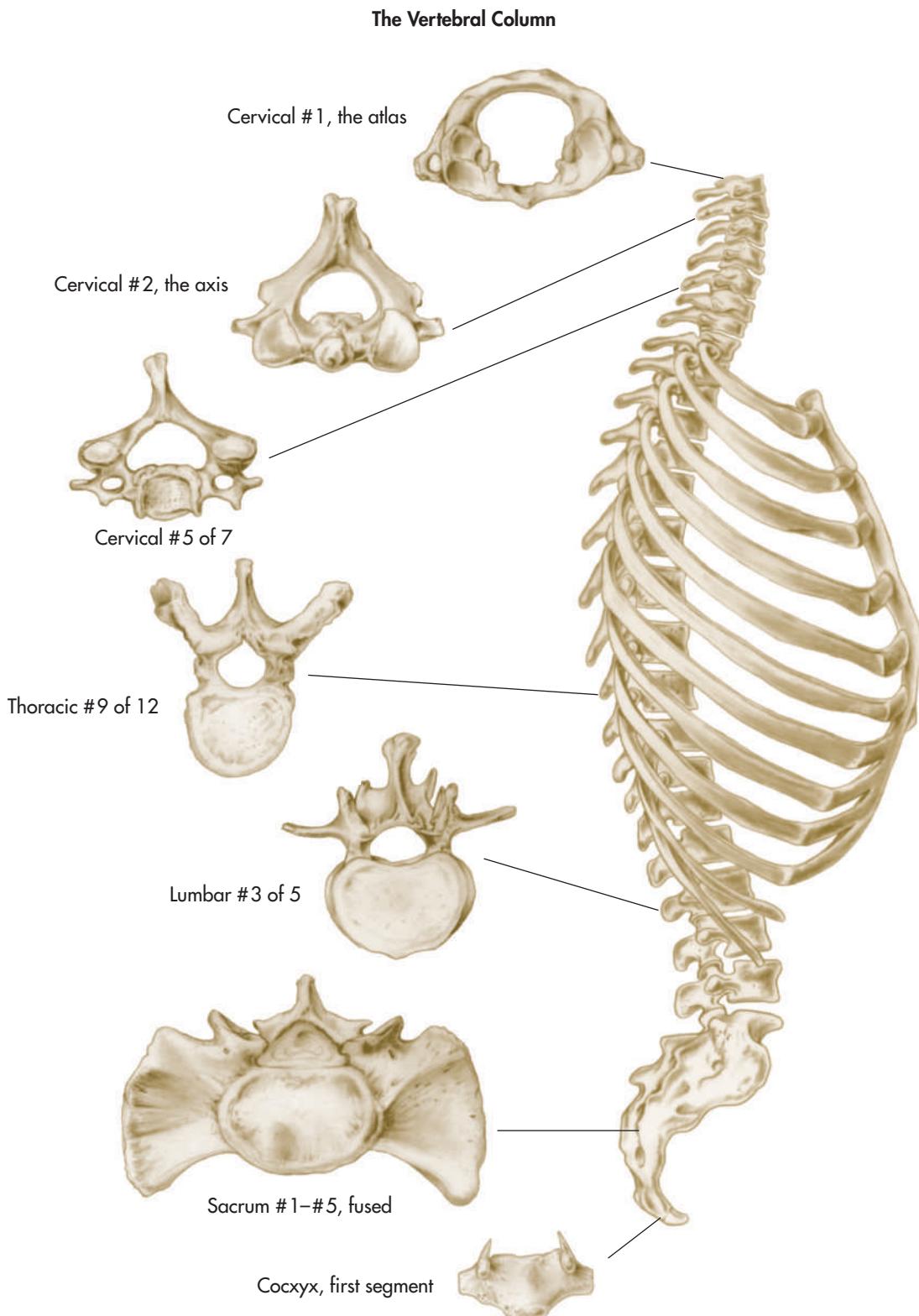
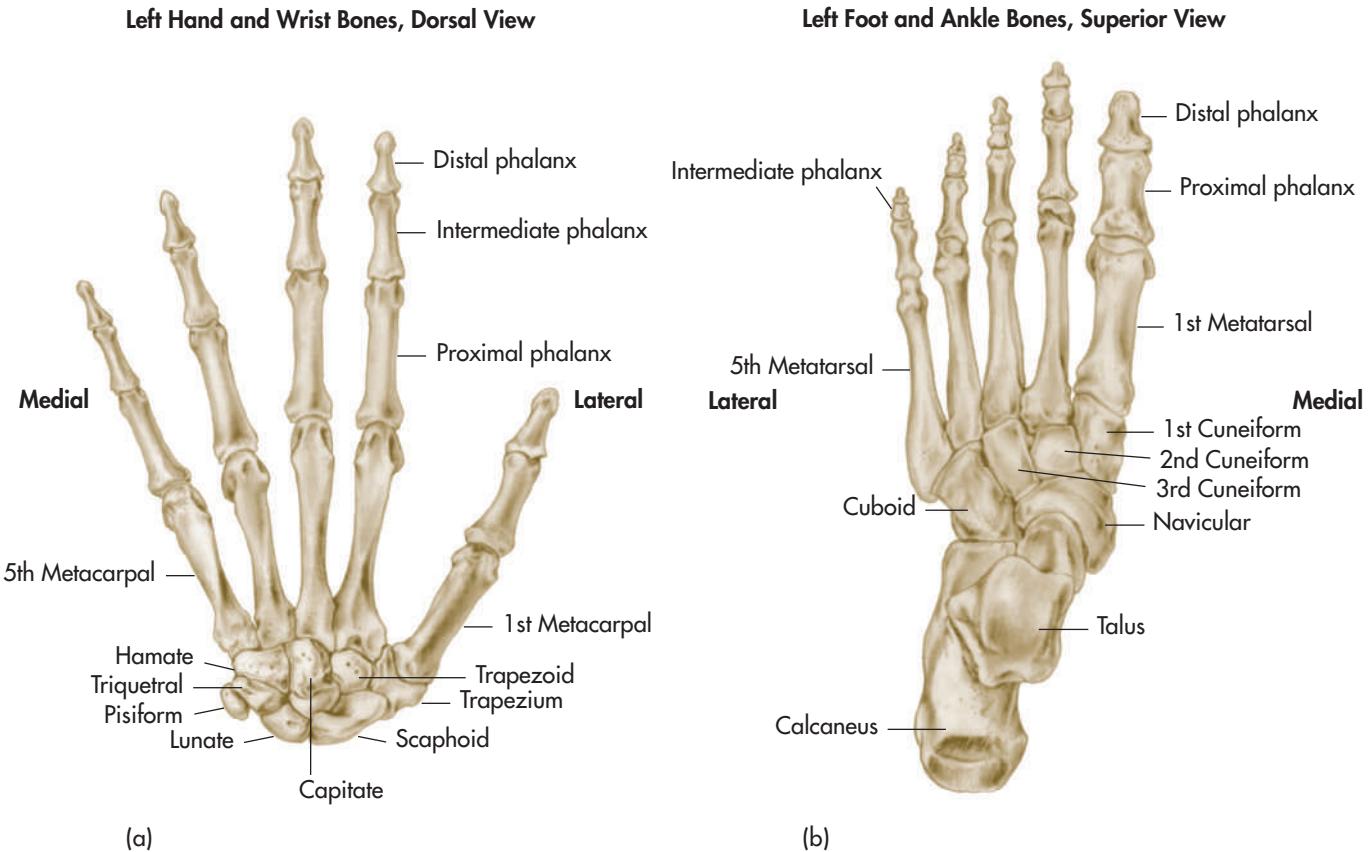


Figure B.5 (a) Left hand and wrist bones and (b) left foot and ankle bones.

Appendix C

The Hardy–Weinberg Equilibrium

In Chapter 5, we introduced the Hardy–Weinberg equilibrium in the context of our discussion of the forces of evolutionary change. Population genetics provides the mathematical underpinnings of evolutionary theory, and the Hardy–Weinberg equilibrium is at the heart of mathematical and quantitative approaches to understanding evolutionary change in diploid organisms. In this appendix, we will briefly go over a derivation of the Hardy–Weinberg equilibrium and show some applications of the equilibrium in evolutionary research.

Throughout the discussion, we will use the simplest case to illustrate our examples: a single gene (or locus) with two alleles, A and a . The frequency of A in the population is represented by p ; the frequency of a is represented by q . By definition, $p + q = 1$.

Derivation of the Hardy–Weinberg Equilibrium

The Hardy–Weinberg equilibrium states that, given known allele frequencies p and q , we can represent the genotype frequencies by $AA = p^2$, $Aa = 2pq$, and $aa = q^2$. Furthermore, these allele frequencies remain constant from generation to generation if the following conditions are met:

- Large population size (or theoretically infinite population size), which minimizes the influence of genetic drift on allele frequencies
- Random mating (no inbreeding or assortative or disassortative mating)
- No mutation
- No gene flow
- No natural selection

Let us begin by considering a specific example, where the allele frequency of A is 0.6 ($p = 0.6$) and that of a is 0.4 ($q = 0.4$). To look at this another way, the probability that any given sperm or egg will carry A is 0.6, and the probability that it will carry a is 0.4. Thus under conditions of totally random mating with, no other evolutionary forces in effect (under equilibrium conditions), the probability of producing a zygote with a homozygous AA genotype is $(0.6)(0.6) = 0.36$. We can represent the probabilities of all the genotypes occurring in a modified Punnett square:

| | | Sperm | |
|------|----------------------------|--|--|
| | | $\text{freq}(A) = p = 0.6$ | $\text{freq}(a) = q = 0.4$ |
| Eggs | $\text{freq}(A) = p = 0.6$ | $\text{freq}(AA) = p^2 =$ $(0.6)(0.6) = 0.36$ | $\text{freq}(Aa) = pq =$ $(0.6)(0.4) = 0.24$ |
| | $\text{freq}(a) = q = 0.4$ | $\text{freq}(Aa) = pq =$ $(0.6)(0.4) = 0.24$ | $\text{freq}(aa) = q^2 =$ $(0.4)(0.4) = 0.16$ |

This gives us a population with genotype frequencies of 0.36 (for AA), 0.48 (for Aa), and 0.16 (for aa). What are the allele frequencies for this population? For A , it is $0.36 + (0.5)(0.48) = 0.36 + 0.24 = 0.6$, which is what the frequency of A was originally. The allele frequency of a is $0.16 + (0.5)(0.48) = 0.16 + 0.24 = 0.40$, which is the original frequency of a . This demonstrates that allele frequencies are maintained in equilibrium under conditions of random mating and in the absence of other evolutionary forces.

The general equation for the distribution of genotypes for a population in Hardy–Weinberg equilibrium is given by the equation

$$p^2 + 2pq + q^2 = 1$$

We can derive this equation directly from the modified Punnett square.

The constancy of allele frequencies over generations is shown by the following equations. Let p' equal the allele frequency of A in the first generation. From the preceding example we see that

$$p' = (\text{frequency of } AA) + (0.5)(\text{frequency of } Aa)$$

We want to count only half the alleles for A in the heterozygotes. Substituting the allele frequency values from the Hardy–Weinberg equation, we get

$$p' = p^2 + (0.5)(2pq)$$

Because $(0.5)(2pq) = pq$, we now have

$$p' = p^2 + pq$$

Which, factoring out p , is the same thing as

$$p' = p(p + q)$$

As you recall, $p + q = 1$; therefore,

$$p' = p$$

This demonstrates that allele frequencies remain constant in a population in Hardy–Weinberg equilibrium.

One of the main uses of the Hardy–Weinberg equation is to determine if a population is *not* in equilibrium. We do this by comparing observed allele frequencies with observed genotype frequencies. If the observed genotype frequencies are significantly different from those expected based on the allele frequencies (which we usually check by using a chi-square statistical test), then we can say the population is not in equilibrium. This result indicates that one of the assumptions of the Hardy–Weinberg equilibrium is being violated and that an evolutionary force may be acting on the population or acted on the population in the past to produce the non-equilibrium distribution of alleles.

Another application of the Hardy–Weinberg equation is to estimate the frequency of heterozygotes in a population. As we discussed in Chapter 5, it is particularly useful for estimating the frequency in a population of carriers of a recessive autosomal illnesses, such as Tay–Sachs disease or cystic fibrosis. The recessive allele frequency is simply

$$q = \sqrt{\text{frequency of autosomal recessive condition}}$$

And the dominant allele frequency is

$$p = 1 - q$$

Thus the frequency of heterozygous carriers = $2pq$.

Hardy–Weinberg and Natural Selection

The Hardy–Weinberg equilibrium can help us mathematically model the effects of any of the forces of evolution (mutation, genetic drift, gene flow, and natural selection). Let us consider how to use the Hardy–Weinberg equation to understand how

natural selection may affect the distribution of allele frequencies in a population. In these equations, we assume that natural selection is the only force of evolution acting on the population.

In the simple case of one gene with two alleles, we have three possible genotypes that are subject to natural selection. To model the change in allele frequencies, we need to know not the absolute fitness of each genotype (which we could measure as its likelihood of survival) but rather the genotypes' fitness relative to each other. Relative fitness usually is represented by the letter w ; thus we have

$$w_{AA} = \text{relative fitness of } AA$$

$$w_{Aa} = \text{relative fitness of } Aa$$

$$w_{aa} = \text{relative fitness of } aa$$

Let's say that the homozygous genotype AA has the highest fitness; its relative fitness w_{AA} therefore would be equal to 1. The relative fitnesses of Aa and aa are lower, such that

$$w_{AA} = 1.0$$

$$w_{Aa} = 0.8$$

$$w_{aa} = 0.4$$

Let's also assume starting allele frequencies of $p = 0.7$ and $q = 0.3$.

If the population were in Hardy–Weinberg equilibrium, the expected genotype frequencies after one generation would be

$$p^2 = (0.7)(0.7) = 0.49 \text{ for } AA$$

$$2pq = 2(0.7)(0.3) = 0.42 \text{ for } Aa$$

$$q^2 = (0.3)(0.3) = 0.09 \text{ for } aa$$

However, natural selection is working on this population and affecting the survival of the different genotypes. So the genotype frequencies after selection are

$$w_{AA}p^2 = 1.0(0.7)(0.7) = 0.49 \text{ for } AA$$

$$w_{Aa}2pq = 0.8(2)(0.7)(0.3) = 0.336 \text{ for } Aa$$

$$w_{aa}q^2 = 0.4(0.3)(0.3) = 0.036 \text{ for } aa$$

The frequency of p after natural selection has acted on the population is

$$\begin{aligned} p' &= [(0.49) + (0.5)(0.336)] / (0.49 + 0.336 + 0.036) \\ &= 0.658 / 0.862 \\ &= 0.763 \end{aligned}$$

The frequency of q is

$$q' = 1 - p' = 1 - 0.763 = 0.237$$

So after only one generation of natural selection operating at these levels, there is a substantial change in allele frequencies, with A going from 0.7 to 0.763 and a decreasing from 0.3 to 0.237. Following this through five generations, the allele frequencies would be

| Generation | 1 | 2 | 3 | 4 | 5 |
|------------|-------|-------|-------|-------|-------|
| P | 0.763 | 0.813 | 0.852 | 0.883 | 0.907 |
| q | 0.237 | 0.187 | 0.148 | 0.117 | 0.093 |

In the case of a lethal autosomal recessive condition (such as Tay–Sachs disease), in which the relative fitness of the recessive homozygote is 0 and for the other two genotypes it is 1, we can represent the change in allele frequency of the recessive allele by a simple equation (which is derived from the Hardy–Weinberg equation):

$$q_g = q_0 / (1 + gq_0)$$

where g is the number of generations passed, q_g is the frequency of a in generation g , and q_0 is the starting frequency of a . Consider a founding population in which the allele frequency of a lethal recessive is 0.20. Over ten generations, the frequency of this allele will decrease to

$$\begin{aligned}q_{10} &= 0.2/[1 + (10)(0.2)] \\&= 0.2/3 \\&= 0.067\end{aligned}$$

Of course, a small founding population violates one of the conditions of the Hardy–Weinberg equilibrium (infinite population size), but we can ignore that for the sake of this example.

Appendix D

Metric–Imperial Conversions

| METRIC UNIT | IMPERIAL EQUIVALENT |
|-----------------------|-----------------------|
| 1 centimeter | 0.39 inches |
| 1 meter | 3.28 feet |
| 1 kilometer | 0.62 miles |
| 1 kilogram | 2.20 pounds |
| 454 grams | 1 pound |
| 1 gram | 0.035 ounces |
| 1 liter | 1.06 quarts |
| 400 cubic centimeters | 24.4 cubic inches |
| 1 square kilometer | 0.39 square miles |
| 1 square kilometer | 247 acres |
| 0 degrees Celsius | 32 degrees Fahrenheit |

Glossary

ABO blood type system Refers to the genetic system for one of the proteins found on the surface of red blood cells. Consists of one gene with three alleles: A, B, and O.

acclimatization Short-term changes in physiology that occur in an organism in response to changes in environmental conditions.

Acheulean Stone tool industry of the early and middle Pleistocene characterized by the presence of bifacial hand axes and cleavers. This industry is made by a number of *Homo* species, including *H. erectus* and early *H. sapiens*.

activity budget The pattern of waking, eating, moving, socializing, and sleeping that all nonhuman primates engage in each day.

adapoids Family of mostly Eocene primates, probably ancestral to all strepsirrhines.

adaptability The ability of an individual organism to make positive anatomical or physiological changes after short- or long-term exposure to stressful environmental conditions.

adaptation A trait that increases the reproductive success of an organism, produced by natural selection in the context of a particular environment.

adaptationism A premise that all aspects of an organism have been molded by natural selection to a form optimal for enhancing reproductive success.

adaptive radiation The diversification of one founding species into multiple species and niches.

alleles Alternative versions of a gene. Alleles are distinguished from one another by their differing effects on the phenotypic expression of the same gene.

Allen's rule Stipulates that in warmer climates, the limbs of the body are longer relative to body size to dissipate body heat.

allopatric speciation Speciation occurring via geographic isolation.

amino acids Molecules that form the basic building blocks of protein.

anagenesis Evolution of a trait or a species into another over a period of time.

analogous Having similar traits due to similar use, not due to shared ancestry.

angular torus A thickened ridge of bone at the posterior inferior angle of the parietal bone.

anthropoid Members of the primate suborder Anthropoidea that includes the monkeys, apes, and hominins.

anthropology The study of humankind in a cross-cultural context. Anthropology includes the subfields cultural anthropology, linguistic anthropology, archaeology, and biological anthropology.

anthropometry The measurement of different aspects of the body, such as stature or skin color.

antibodies Proteins (immunoglobulins) formed by the immune system that are specifically structured to bind to and neutralize invading antigens.

antigens Whole or part of an invading organism that prompts a response (such as production of antibodies) from the body's immune system.

arboreal hypothesis Hypothesis for the origin of primate adaptation that focuses on the value of grasping hands and stereoscopic vision for life in the trees.

archaeology The study of the material culture of past peoples.

argon–argon ($^{40}\text{Ar}/^{39}\text{Ar}$) dating Radiometric technique modified from K–Ar that measures ^{40}K by proxy using ^{39}Ar . Allows measurement of smaller samples with less error.

artifacts The objects, from tools to art, left by earlier generations of people.

australopithecines The common name for members of the genus *Australopithecus*.

autoimmune diseases Diseases caused by the immune system reacting against the normal, healthy tissues of the body.

autosomal dominant disease A disease that is caused by a dominant allele: Only one copy needs to be inherited from either parent for the disease to develop.

autosomal recessive disease A disease caused by a recessive allele; one copy of the allele must be inherited from each parent for the disease to develop.

autosomes Any of the chromosomes other than the sex chromosomes.

auxology The science of human growth and development.

balanced polymorphism A stable polymorphism in a population in which natural selection prevents any of the alternative phenotypes (or underlying alleles) from becoming fixed or being lost.

base Variable component of the nucleotides that form the nucleic acids DNA and RNA. In DNA, the bases are adenine, guanine, thymine, and cytosine. In RNA, uracil replaces thymine.

Bergmann's rule Stipulates that body size is larger in colder climates to conserve body temperature.

bifaces Stone tools that have been flaked on two faces or opposing sides, forming a cutting edge between the two flake scars.

binomial nomenclature Linnaean naming system for all organisms, consisting of a genus and species label.

bioarchaeologist A biological anthropologist who uses human osteology to explore the biological component of the archaeological record.

bioarchaeology The study of human remains in an archaeological context.

biocultural anthropology The study of the interaction between biology and culture, which plays a role in most human traits.

biogeography The distribution of animals and plants on Earth.

biological anthropology The study of humans as biological organisms, considered in an evolutionary framework; sometimes called physical anthropology.

biological profile The biological particulars of an individual as estimated from their skeletal remains. These include estimates of sex, age at death, height, ancestry, and disease status.

biological species concept Defines species as interbreeding populations reproductively isolated from other such populations.

biomedical anthropology The subfield of biological anthropology concerned with issues of health and illness.

biostratigraphy Relative dating technique using comparison of fossils from different stratigraphic sequences to estimate which layers are older and which are younger.

blades Flakes that are twice as long as they are wide.

blending inheritance Discredited nineteenth-century idea that genetic factors from the parents averaged-out or blended together when they were passed on to offspring.

brachiation Mode of arm-hanging and arm-swinging that uses a rotating shoulder to suspend the body of an ape or hominin beneath a branch or to travel between branches.

breccia Cement-like matrix of fossilized rock and bone. Many important South African early humans have been found in breccias.

bridewealth Payment offered by a man to the parents of a woman he wants to marry.

butchering site A place where there is archaeological evidence of the butchering of carcasses by hominins. The evidence usually consists of tool cut marks on fossilized animal bones or the presence of the stone tools themselves.

calibrated relative dating techniques Techniques that use regular or somewhat regular processes that can be correlated to an absolute chronology to estimate the age of a site.

calotte The skullcap, or the bones of the cranium exclusive of the face and the base of the cranium.

calvaria The braincase; includes the bones of the calotte and those that form the base of the cranium but excludes the bones of the face.

canine fossa An indentation on the maxilla above the root of the canine, an anatomical feature usually associated with modern humans that may be present in some archaic *Homo* species in Europe.

captive study Primate behavior study conducted in a zoo, laboratory, or other enclosed setting.

Catarrhini Infraorder of the order Primates that includes the Old World monkeys, apes, and hominins.

catastrophism Theory that there have been multiple creations interspersed by great natural disasters such as Noah's flood.

centromere Condensed and constricted region of a chromosome. During mitosis and meiosis, location where sister chromatids attach to one another.

cerebellum The "little brain" tucked under the cerebrum, and important in the control of balance, posture, and voluntary movement.

cerebral cortex The layer of gray matter that covers the surface of the cerebral hemispheres, divided into functional regions that correspond to local patterns of neuronal organization.

cerebrum The largest part of the human brain, which is split into left and right hemispheres. Seat of all "higher" brain functions.

chain of custody In forensic cases, the detailed notes that establish what was collected at the scene, the whereabouts of these remains, and the access to them after retrieval from the scene.

Châtelperronian An Upper Paleolithic tool industry that has been found in association with later Neandertals.

chromatin The diffuse form of DNA as it exists during the interphase of the cell cycle.

chromosomes Discrete structures composed of condensed DNA and supporting proteins.

chronometric dating techniques Techniques that estimate the age of an object in absolute terms through the use of a natural clock such as radioactive decay or tree ring growth.

cladistics Method of classification using ancestral and derived traits to distinguish patterns of evolution within lineages.

cladogenesis Evolution through the branching of a species or a lineage.

cladogram Branching diagram showing evolved relationships among members of a lineage.

cleaver Type of Acheulean bifacial tool, usually oblong with a broad cutting edge on one end.

cline The distribution of a trait or allele across geographical space.

co-dominant In a diploid organism, two different alleles of a gene that are both expressed in a heterozygous individual.

codon A triplet of nucleotide bases in mRNA that specifies an amino acid or the initiation or termination of a polypeptide sequence.

cognitive universals Cognitive phenomena such as sensory processing, the basic emotions, consciousness, motor control, memory, and attention that are expressed by all normal individuals.

compound temporonuchal crest Bony crest at the back of the skull formed when an enlarged temporalis muscle approaches enlarged neck (nuchal) muscles, present in apes and *A. afarensis*.

convergent evolution Similar form or function brought about by natural selection under similar environments rather than shared ancestry.

core area The part of a home range that is most intensively used.

core The raw material source (a river cobble or a large flake) from which flakes are removed.

cosmogenic radionuclide techniques Radiometric dating technique that uses ratios of rare isotopes such as ^{26}Al , ^{10}Be , and ^{3}He to estimate the time that sediments and the fossils in them have been buried.

CP₃ honing complex Combination of canine and first premolar teeth that form a self-sharpening apparatus.

cranial crests Bony ridges on the skull to which muscles attach.

creation science A creationist attempt to refute the evidence of evolution.

cross-cultural universals Behavioral phenomena, such as singing, dancing, and mental illness, that are found in almost all human cultures, but are not necessarily exhibited by each member of a cultural group.

crossing over Exchange of genetic material between homologous chromosomes during the first prophase of meiosis; mechanism for genetic recombination.

cultural anthropology The study of human societies, especially in a cross-cultural context; the subdivision of anthropology that includes ethnology, archaeology, and linguistics.

culture The sum total of learned traditions, values, and beliefs that groups of people (and a few species of highly intelligent animals) possess.

cytoplasm In a eukaryotic cell, the region within the cell membrane that surrounds the nucleus; it contains organelles, which carry out the essential functions of the cell, such as energy production, metabolism, and protein synthesis.

data The scientific evidence produced by an experiment or by observation, from which scientific conclusions are made.

datum point A permanent, fixed point relative to which the location of items of interest are recorded during archaeological mapping and excavation.

daughter isotope (product) The isotope that is produced as the result of radioactive decay of the parent isotope.

deduction A conclusion that follows logically from a set of observations.

deletion mutation A change in the base sequence of a gene that results from the loss of one or more base pairs in the DNA.

deme Local, interbreeding population that is defined in terms of its genetic composition (for example, allele frequencies).

dental apes Early apes exhibiting Y-5 molar patterns but monkey-like postcranial skeletons.

dental arcade The parabolic arc that forms the upper or lower row of teeth.

deoxyribonucleic acid (DNA) A double-stranded molecule that is the carrier of genetic information. Each strand is composed of a linear sequence of nucleotides; the two strands are held together by hydrogen bonds that form between complementary bases.

diastema Gap between anterior teeth.

diploid number Full complement of paired chromosomes in a somatic cell. In humans, the diploid number is 46 (23 pairs of different chromosomes).

directional selection Natural selection that drives evolutionary change by selecting for greater or lesser frequency of a given trait in a population.

diurnal Active during daylight hours.

dominance hierarchy Ranking of individual primates in a group that reflects their ability to displace, intimidate, or defeat group mates in contests.

dominant In a diploid organism, an allele that is expressed when present on only one of a pair of homologous chromosomes.

Duffy blood group Red blood cell system useful for studying admixture between African- and European-derived populations.

Early Stone Age (or Lower Paleolithic) The earliest stone tool industries including the Oldowan and Acheulean industries, called the ESA in Africa and the Lower Paleolithic outside Africa.

ecological species concept Defines species based on the uniqueness of their ecological niche.

ecology The study of the interrelationships of plants, animals, and the physical environment in which they live.

electron spin resonance (ESR) Electron trap technique that measures the total amount of radioactivity accumulated by a specimen such as tooth or bone since burial.

electron trap techniques Radiometric techniques that measure the accumulation of electrons in traps in the crystal lattice of a specimen.

encephalization quotient (EQ) The ratio of the actual brain size of a species to its expected brain size based on a statistical regression of brain-to-body size based on a large number of species.

endocast A replica (or cast) of the internal surface of the braincase that reflects the impressions made by the brain on the skull walls. Natural endocasts are formed by the filling of the braincase by sediments.

endoplasmic reticulum (ER) An organelle in the cytoplasm consisting of a folded membrane.

environment of evolutionary adaptedness (EEA) According to evolutionary psychologists, the critical period for understanding the selective forces that shape human behavior; exemplified by hunter-gatherer lifestyles of hominins before the advent of agriculture.

environmentalism The view that the environment has great powers to directly shape the anatomy of individual organisms.

enzyme A complex protein that is a catalyst for chemical processes in the body.

epidemiology The quantitative study of the occurrence and cause of disease in populations.

estrus Hormonally influenced period of sexual receptivity in some female mammals, which corresponds to the timing of ovulation.

ethnic group A human group defined in terms of sociological, cultural, and linguistic traits.

ethnobiology The study of how traditional cultures classify objects and organisms in the natural world.

ethnography The practice of cultural anthropology. Ethnographers study the minute-to-minute workings of human societies, especially non-Western societies.

ethnology The study of human societies, their traditions, rituals, beliefs, and the differences between societies in these traits.

eukaryotes A cell that possesses a well-organized nucleus.

eutheria Mammals that reproduce with a placenta and uterus.

evolution A change in the frequency of a gene or a trait in a population over multiple generations.

evolutionary psychology Approach to understanding the evolution of human behavior that emphasizes the selection of specific behavioral patterns in the context of the environment of evolutionary adaptedness.

evolutionary species concept Defines species as evolutionary lineages with their own unique identity.

experimentation The testing of a hypothesis.

falsifiable Able to be shown to be false.

female philopatry Primate social system in which females remain and breed in the group of their birth, whereas males emigrate.

field study Primate behavior study conducted in the habitat in which the primate naturally occurs.

fission track dating Radiometric technique for dating noncrystalline materials using the decay of ^{238}U and counting the tracks that are produced by this fission. Estimates the age of sediments in which fossils are found.

fission-fusion polygyny Type of primate polygyny in which animals travel in foraging parties of varying sizes instead of a cohesive group.

fission-fusion Form of mating system seen in chimpanzees, bonobos, and a few other primates in which there are temporary subgroups but no stable, cohesive groups.

fitness Reproductive success.

flake The stone fragment struck from a core, thought to have been the primary tools of the Oldowan.

folivores Animals who eat a diet composed mainly of leaves, or foliage.

forensic anthropology The study of human remains applied to a legal context.

fossils The preserved remnants of once-living things, often buried in the ground.

founder effect A component of genetic drift theory, stating that new populations that become isolated from the parent population carry only the genetic variation of the founders.

frequency-dependent balanced polymorphism Balanced polymorphism that is maintained because one (or more) of the alternative phenotypes has a selective advantage over the other phenotypes only when it is present in the population below a certain frequency.

frugivorous An animal that eats a diet composed mainly of fruit.

gametes The sex cells: sperm in males and eggs (or ova) in females.

gene flow Movement of genes between populations.

gene The fundamental unit of heredity. Consists of a sequence of DNA bases that carries the information for synthesizing a protein (or polypeptide) and occupies a specific chromosomal locus.

genetic bottleneck Temporary dramatic reduction in size of a population or species.

genetic code The system whereby the nucleotide triplets in DNA and RNA contain the information for synthesizing proteins from the twenty amino acids.

genetic drift Random changes in gene frequency in a population.

genome The sum total of all the genes carried by an individual.

genotype The genetic makeup of an individual. *Genotype* can refer to the entire genetic complement or more narrowly to the alleles present at a specific locus on two homologous chromosomes.

geologic time scale (GTS) The categories of time into which Earth's history is usually divided by geologists and paleontologists: eras, periods, epochs.

geology The study of Earth systems.

geomagnetic polarity time scale (GPTS) Time scale composed of the sequence of paleomagnetic orientations of strata through time.

gradualism Darwinian view of slow, incremental evolutionary change.

group selection Notion, largely discredited by the rise of Darwinian theory, proposing that animals act for the good of their social group or of their species.

half-life The time it takes for half of the original amount of an unstable isotope of an element to decay into more stable forms.

hammerstone A stone used for striking cores to produce flakes or bones to expose marrow.

hand axe Type of Acheulean bifacial tool, usually teardrop-shaped, with a long cutting edge.

haploid number The number of chromosomes found in a gamete, representing one from each pair found in a diploid somatic cell. In humans, the haploid number is 23.

haplorhine (Haplorhini) Suborder of the order Primates that includes the anthropoids and the tarsier.

haplotypes Combinations of alleles (or at the sequence level, mutations) that are found together in an individual.

hard-object feeding Chewing tough, hard-to-break food items such as nuts or fibrous vegetation.

Hardy-Weinberg equilibrium The theoretical distribution of alleles in a given population in the absence of evolution, expressed as a mathematical equation.

hemoglobin Protein found in red blood cells that transports oxygen.

heritability The proportion of total phenotypic variability observed for a given trait that can be ascribed to genetic factors.

heterodont Tooth array in which different teeth have different forms and functions.

heterozygous advantage With reference to a particular genetic system, the situation in which heterozygotes have a selective advantage over homozygotes (for example, sickle cell disease); a mechanism for maintaining a balanced polymorphism.

heterozygous Having two different alleles at the loci for a gene on a pair of homologous chromosomes (or autosomes).

home base Archaeological term for an area to which early hominins may have brought tools and carcasses and around which their activities were centered.

home range The spatial area used by a primate group.

hominin (Homininae) Member of our own human family, past or present.

hominin A member of the primate family Hominidae, distinguished by bipedal posture and, in more recently evolved species, a large brain.

homodont Having teeth that are uniform in form, shape, and function.

homologous chromosomes Members of the same pair of chromosomes (or autosomes). Homologous chromosomes undergo crossing over during meiosis.

homology Similarity of traits resulting from shared ancestry.

homozygous Having the same allele at the loci for a gene on both members of a pair of homologous chromosomes (or autosomes).

hormone A natural substance (often a protein) produced by specialized cells in one location of the body that influences the activity or physiology of cells in a different location.

human biology Subfield of biological anthropology dealing with human growth and development, adaptation to environmental extremes, and human genetics.

human evolutionary ecology Approach to understanding the evolution of human behavior that attempts to explore ecological and demographic factors important in determining individual reproductive success and fitness in a cultural context.

human leukocyte antigen (HLA) system Class of blood group markers formed by proteins expressed on the surface of white blood cells (leukocytes).

hylobatid (Hylobatidae) Member of the gibbon, or lesser ape, family.

hyoid bone A small "floating bone" in the front part of the throat, which is held in place by muscles and ligaments.

hypothesis A preliminary explanation of a phenomenon. Hypothesis formation is the first step of the scientific method.

immunoglobulins Proteins produced by B lymphocytes that function as antibodies.

immutability (or fixity) Stasis, lack of change.

inbreeding depression Lesser fitness of offspring of closely related individuals compared with the fitness of the offspring of less closely related individuals, caused largely by the expression of lethal or debilitating recessive alleles.

inbreeding Mating between close relatives.

incest A violation of cultural rules regulating mating behavior.

incidence rate The number of new occurrences of a disease over a given period of time divided by the population size.

inclusive fitness Reproductive success of an organism plus the fitness of its close kin.

infanticide The killing of infants, either by members of the infant's group or by a member of a rival group.

insertion mutation A change in the base sequence of a gene that results from the addition of one or more base pairs in the DNA.

intelligent design A creationist school of thought that proposes that natural selection cannot account for the diversity and complexity of form and function seen in nature.

isotopes Variant forms of an element that differ based on their atomic weights and numbers of neutrons in the nucleus. Both stable and unstable (radioactive) isotopes exist in nature.

juxtamastoid eminence A ridge of bone next to the mastoid process; in Neandertals, it is larger than the mastoid process itself.

karyotype The complete chromosomal complement of an individual; usually based on a photograph of the chromosomes visualized under the microscope.

kin selection Principle that animals behave preferentially toward their genetic kin; formulated by William Hamilton.

k-selected Reproductive strategy in which fewer offspring are produced per female, interbirth intervals are long, and maternal investment is high.

lactose intolerant The inability to digest lactose, the sugar found in milk; most adult mammals (including humans) are lactose intolerant as adults.

language The unique system of communication used by members of the human species.

Levallois technique A Middle Paleolithic technique that made use of prepared cores to produce uniform flakes.

linguistic anthropology The study of language, its origins, and use; also called anthropological linguistics.

linkage Genes that are found on the same chromosome are said to be linked. The closer together two genes are on a chromosome, the greater the linkage and the less likely they are to be separated during crossing over.

lithostratigraphy The study of geologic deposits and their formation, stratigraphic relationships, and relative time relationships based on their lithologic (rock) properties.

locus The location of a gene on a chromosome. The locus for a gene is identified by the number of the chromosome on which it is found and its position on the chromosome.

lunate sulcus A prominent sulcus on the lateral side of the hemisphere of most nonhuman primates, which divides the primary visual cortex of the occipital lobe from the rest of the cerebrum.

Lysenkoism Soviet-era research program that tried to apply Lamarckian thinking to agricultural production.

macroevolution Evolution of major phenotypic changes over relatively short time periods.

male philopatry Primate social system in which males remain and breed in the group of their birth, whereas females emigrate.

mastoid process A protrusion from the temporal bone of the skull located behind the ear.

material culture The objects or artifacts of past human societies.

maternal–fetal incompatibility Occurs when the mother produces antibodies against an antigen (for example, a red blood cell surface protein) expressed in the fetus that she does not possess.

matrilineal Pattern of female kinship in a primate social group.

megadontia Enlarged teeth.

meiosis Cell division that occurs in the testes and ovaries that leads to the formation of sperm and ova (gametes).

melanin A dark pigment produced by the melanocytes of the epidermis, which is the most important component of skin color.

melanocytes Cells in the epidermis that produce melanin.

menarche The onset of a girl's first menstrual period.

Mendel's law of independent assortment Genes found on different chromosomes are sorted into sex cells independently of one another.

Mendel's law of segregation The two alleles of a gene found on each of a pair of chromosomes segregate independently of one another into sex cells.

menopause The postreproductive period in the lives of women, after the cessation of ovulation and menses.

messenger RNA (mRNA) Strand of RNA synthesized in the nucleus as a complement to a specific gene (transcription). It carries the information for the sequence of amino acids to make a specific protein into the cytoplasm, where it is read at a ribosome and a protein molecule is synthesized (translation).

metatheria Mammals that reproduce without a placenta, including the marsupials.

metopic keel Longitudinal ridge or thickening of bone along the midline of the frontal bone.

microevolution The study of evolutionary phenomena that occur within a species.

microliths Small, flaked stone tools probably designed to be hafted to wood or bone; common feature of Upper Paleolithic and Later Stone Age tool industries.

Middle Paleolithic (Middle Stone Age) Stone tool industries that used prepared core technologies.

midfacial prognathism The forward projection of the middle facial region, including the nose.

mitochondria Organelles in the cytoplasm of the cell where energy production for the cell takes place. Contains its own DNA.

mitochondrial DNA (mtDNA) Small loop of DNA found in the mitochondria. It is clonally and maternally inherited.

mitosis Somatic cell division in which a single cell divides to produce two identical daughter cells.

molecular clock A systematic accumulation of genetic change that can be used to estimate the time of divergence between two groups if relative rates are constant and a calibration point from the fossil record is available.

monogamy A mating bond; primates can be socially monogamous but still mate occasionally outside the pair bond.

monogenism Ancient belief that all people are derived from a single creation.

most recent common ancestor (MRCA) In a phylogenetic tree, the MRCA is indicated by the deepest node from which all contemporary variants can be shown to have evolved.

motherese (infant-directed speech) Emotive spoken language used by mothers and other adults when addressing prelinguistic babies and children.

Movius line The separation between areas of the Old World in which Acheulean technology occurs and those in which it does not; named by archaeologist Hallam Movius.

multiregional models Phylogenetic models that suggest that modern humans evolved in the context of gene flow between middle to late Pleistocene hominin populations from different regions, so there is no single location where modern humans first evolved.

muscles of mastication The chewing muscles: masseter, temporalis, medial and lateral pterygoids.

mutation An alteration in the DNA, which may or may not alter the function of a cell. If it occurs in a gamete, it may be passed from one generation to the next.

natural selection Differential reproductive success over multiple generations.

neocortex The part of the brain that controls higher cognitive function; the cerebrum.

neurons The basic cellular units of the nervous system. A neuron consists of a cell body and specialized processes called dendrites (which receive inputs from other neurons) and axons (outgrowths through which neurons send impulses to other neurons).

nocturnal Active at night.

nondisjunction error The failure of homologous chromosomes (chromatids) to separate properly during cell division. When it occurs during meiosis, it may lead to the formation of gametes that are missing a chromosome or have an extra copy of a chromosome.

nucleotide Molecular building block of nucleic acids DNA and RNA; consists of a phosphate, sugar, and base.

nucleus In eukaryotic cells, the part of the cell in which the genetic material is separated from the rest of the cell (cytoplasm) by a plasma membrane.

null hypothesis The starting assumption for scientific inquiry, that one's research results occur by random chance. One's hypothesis must challenge this initial assumption.

observation The gathering of scientific information by watching a phenomenon.

occipital bun A backward-projecting bulge of the occipital part of the skull.

occipital torus A thickened horizontal ridge of bone on the occipital bone at the rear of the cranium.

Oldowan The tool industry characterized by simple, usually unifacial core and flake tools.

olfactory bulbs Knoblike structures, located on the underside of the frontal lobes, that form the termination of olfactory nerves running from the nasal region to the brain.

- omomyoids** Family of mostly Eocene primates probably ancestral to all haplorhines.
- ontogeny** The life cycle of an organism from conception to death.
- optically stimulated luminescence (OSL)** Electron trap technique that uses light to measure the amount of radioactivity accumulated by crystals in sediments (such as sand grains) since burial.
- osteodontokeratic culture** A bone, tooth, and horn tool kit envisioned by Raymond Dart to be made by *Australopithecus*.
- osteology** The study of the skeleton.
- paleoanthropology** The study of the fossil record of ancestral humans and their primate kin.
- paleomagnetism** The magnetic polarity recorded in ancient sediments. Reversed or normal direction is used to correlate with the geomagnetic polarity time scale to infer an age for a site.
- paleoneurology** The study of the evolution of brain structure and function.
- paleontology** The study of extinct organisms, based on their fossilized remains.
- paleopathology** The study of diseases in ancestral human populations.
- paleosol** Ancient soil.
- paradigm** A conceptual framework useful for understanding a body of evidence.
- parapatric speciation** Speciation occurring when two populations have continuous distributions and some phenotypes in that distribution are more favorable than others.
- parent isotope** The original radioactive isotope in a sample.
- particulate inheritance** The concept of heredity based on the transmission of genes (alleles) according to Mendelian principles.
- pathogens** Organisms and entities that can cause disease.
- pedigree** A diagram used in the study of human genetics that shows the transmission of a genetic trait over generations of a family.
- pedigree** A diagram used in the study of human genetics that shows the transmission of a genetic trait over several generations of a family.
- phenology** The leafing and fruiting cycles of a forest.
- phenotype** An observable or measurable feature of an organism. Phenotypes can be anatomical, biochemical, or behavioral.
- phenylketonuria (PKU)** Autosomal recessive condition that leads to the accumulation of large quantities of the amino acid phenylalanine, which causes mental retardation and other phenotypic abnormalities.
- phylogeny** An evolutionary tree indicating relatedness and divergence of taxonomic groups.
- physical anthropology** The study of humans as biological organisms, considered in an evolutionary framework.
- phytoliths** Silica bodies produced by some plants, especially grasses, that can be used to indicate the presence of certain types of vegetation at a fossil site.
- platycnemic** A bone that is flattened from side to side.
- platymeric** A bone that is flattened from front to back.
- Playtyrrhini** Infraorder of the order Primates that is synonymous with the New World monkeys or ceboids.
- pleiotropy** The phenomenon of a single gene having multiple phenotypic effects.
- plesiadiforms** Mammalian order or suborder of that may be ancestral to later Primates, characterized by some but not all of the primate trends.
- point mutation** A change in the base sequence of a gene that results from the change of a single base to a different base.
- polyandrous** Mating system in which one female mates with multiple males.
- polyandry** Mating system in which one female mates with multiple males.
- polygenic traits** Phenotypic traits that result from the combined action of more than one gene; most complex traits are polygenic.
- polygenism** Ancient belief that people are derived from multiple creations.
- polygynandrous** Primate social system consisting of multiple males and multiple females.
- polygynous** Mating system in which one man is allowed to take more than one wife.
- polygyny** Mating system consisting of at least one male and more than one female.
- polymerase chain reaction (PCR)** Method for amplifying DNA sequences using the Taq polymerase enzyme. Can potentially produce millions or billions of copies of a DNA segment starting from a very small number of target DNA.
- polymorphic** Two or more distinct phenotypes (at the genetic or anatomical levels) that exist within a population.
- polypeptide** A molecule made up of a chain of amino acids.
- polytypic species** Species that consist of a number of separate breeding populations, each varying in some genetic trait.
- pongid (Pongidae)** One of the four great apes species: gorilla, chimpanzee, bonobo, or orangutan.
- population genetics** The study of genetic variation within and between groups of organisms.
- population** An interbreeding group of organisms.
- postorbital bar** A bony ring encircling the lateral side of the eye but not forming a complete cup around the eye globe.
- postorbital constriction** The pinching-in of the cranium just behind the orbits where the temporalis muscle sits. Little constriction indicates a large brain and small muscle; great constriction indicates a large muscle, as in the robust australopithecines.
- potassium–argon (K–Ar) dating** Radiometric technique using the decay of ^{40}K to ^{40}Ar in potassium-bearing rocks; estimates the age of sediments in which fossils are found.
- prefrontal region** The association cortex of the frontal lobes, located forward of the primary motor region of the precentral gyrus and the supplemental motor areas.
- prehensile tail** Grasping tail possessed by some species of the primate families Cebidae and Atelidae.
- prevalence rate** The number of existing cases of a disease divided by the population (or the population at risk).
- primate** Member of the mammalian order primates, including prosimians, monkeys, apes, and humans, defined by a suite of anatomical and behavioral traits.
- primatology** The study of the nonhuman primates and their anatomy, genetics, behavior, and ecology.
- progesterone** A steroid hormone produced by the corpus luteum and the placenta, which prepares the uterus for pregnancy and helps maintain pregnancy once fertilization has occurred.
- prognathic face** Projection of the face well in front of the braincase.
- prokaryotes** Single-celled organisms, such as bacteria, in which the genetic material is not separated from the rest of the cell by a nucleus.
- prosimian** Member of the primate suborder Prosimii that includes the lemurs, lorises, galagos, and tarsiers.
- protein synthesis** The assembly of proteins from amino acids, which occurs at ribosomes in the cytoplasm and is based on information carried by mRNA.

proteins Complex molecules formed from chains of amino acids (polypeptide) or from a complex of polypeptides. They function as structural molecules, transport molecules, antibodies, enzymes, and hormones.

prototheria Mammals that reproduce by egg-laying, then nurse young from nipples. The Australian platypus and echidna are the only living monotremes.

provenience The origin or original source (as of a fossil).

punctuated equilibrium Model of evolution characterized by rapid bursts of change, followed by long periods of stasis.

qualitative variation Phenotypic variation that can be characterized as belonging to discrete, observable categories.

quantitative variation Phenotypic variation that is characterized by the distribution of continuous variation (expressed using a numerical measure) within a population (for example, in a bell curve).

quarrying site An archaeological site at which there is evidence that early hominins were obtaining the raw material to make stone tools.

race In biological taxonomy, same thing as a subspecies; when applied to humans, sometimes incorporates both cultural and biological factors.

racism A prejudicial belief that members of one ethnic group are superior in some way to those of another.

radiocarbon dating Radiometric technique that uses the decay of ¹⁴C in organic remains such as wood and bone to estimate the time since death of the organism.

radiometric dating Chronometric techniques that use radioactive decay of isotopes to estimate age.

recessive In a diploid organism, refers to an allele that must be present in two copies (homozygous) in order to be expressed.

recognition species concept Defines species based on unique traits or behaviors that allow members of one species to identify each other for mating.

recombination The rearrangement of genes on homologous chromosomes that occurs during crossing over in meiosis. The source of variation arising out of sexual reproduction; important for increasing rates of natural selection.

reductionism Paradigm that an organism is the sum of many evolved parts and that organisms can best be understood through an adaptationist approach.

regulatory genes Guide the expression of structural genes, without coding for a protein themselves.

relative dating techniques Dating techniques that establish the age of a fossil only in comparison to other materials found above and below it.

relative rate test A means of determining whether molecular evolution has been occurring at a constant rate in two lineages by comparing whether these lineages are equidistant from an outgroup.

replacement models Phylogenetic models that suggest that modern humans evolved in one location and then spread geographically, replacing other earlier hominin populations without or with little admixture.

reproductive isolating mechanisms (RIMs) Any factor—behavioral, ecological, or anatomical—that prevents a male and female of two different species from hybridizing.

reproductive potential The possible output of offspring by one sex.

reproductive variance A measure of variation from the mean of a population in the reproductive potential of one sex compared with the other.

rhesus (Rh) system Blood type system that can cause hemolytic anemia of the newborn through maternal–fetal incompatibility if the mother is Rh-negative and the child is Rh-positive.

ribonucleic acid (RNA) Single-stranded nucleic acid that performs critical functions during protein synthesis and comes in three forms: messenger RNA, transfer RNA, and ribosomal RNA.

ribosomes Structures composed primarily of RNA, which are found on the endoplasmic reticulum. They are the site of protein synthesis.

r-selected Reproductive strategy in which females have many offspring, interbirth intervals are short, and maternal investment per offspring is low.

sagittal crest Bony crest running lengthwise down the center of the cranium on the parietal bones; for the attachment of the temporalis muscles.

sagittal keel Longitudinal ridge or thickening of bone on the sagittal suture not associated with any muscle attachment.

scientific method Standard scientific research procedure in which a hypothesis is stated, data are collected to test it, and the hypothesis is either supported or refuted.

secondary compounds Toxic chemical compounds found in the leaves of many plants which the plants use as a defense against leaf-eating animals.

semi-free-ranging environment Primate behavior study conducted in a large area that is enclosed or isolated in some way so the population is captive.

senescence Age-related decline in physiological or behavioral function in adult organisms.

sex chromosomes In mammals, chromosomes X and Y, with XX producing females and XY producing males.

sexual dimorphism Difference in size, shape, or color between the sexes.

sexual receptivity Willingness and ability of a female to mate, also defined as fertility.

sexual selection Differential reproductive success within one sex of any species.

shovel-shaped incisors Anterior teeth which on their lingual (tongue) surface are concave with two raised edges that make them look like tiny shovels.

sickle cell disease An autosomal recessive disease caused by a point mutation in an allele that codes for one of the polypeptide chains of the hemoglobin protein.

social system The grouping pattern in which a primate species lives, including its size and composition evolved in response to natural and sexual selection pressures.

sociality Group living, a fundamental trait of haplorhine primates.

sociobiology Name popularized by E. O. Wilson for the evolutionary study of animal social behavior.

somatic cells The cells of the body that are not sex cells.

speciation Formation of one or more new species via reproductive isolation.

species An interbreeding group of animals or plants that are reproductively isolated through anatomy, ecology, behavior, or geographic distribution from all other such groups.

stabilizing selection Selection that maintains a certain phenotype by selecting against deviations from it.

stem cells Undifferentiated cells found in the developing embryo that can be induced to differentiate into a wide variety of cell types or tissues. Also found in adults, although adult stem cells are not as totipotent as embryonic stem cells.

strata Layers of rock.

stratigraphy The study of the order of rock layers and the sequence of events they reflect.

strepsirrhine (Strepsirrhini) Suborder of the order Primates that includes the prosimians, excluding the tarsier.

structural genes Genes that contain the information to make a protein.

subspecies Group of local populations that share part of the geographic range of a species and can be differentiated from other subspecies based on one or more phenotypic traits.

supraorbital torus Thickened ridge of bone above the eye orbits of the skull; a browridge.

sympatric speciation Speciation occurring in the same geographic location.

systematics Branch of biology that describes patterns of organismal variation.

taphonomy The study of what happens to the remains of an animal from the time of death to the time of discovery.

taurodontism Molar teeth with expanded pulp cavities and fused roots.

taxon A group of organisms assigned to a particular category.

taxonomy The science of biological classification.

tephrostratigraphy A form of lithostratigraphy in which the chemical fingerprint of a volcanic ash is used to correlate across regions.

teratogens Substances that cause birth defects or other abnormalities in the developing embryo or fetus during pregnancy.

territory The part of a home range that is defended against other members of the same species.

testosterone A steroid produced primarily in the testes and ovaries, and at a much higher level in men than in women. Responsible for the development of the male primary and secondary sexual characteristics. Strongly influences dominance and reproductive behavior.

theory of inheritance of acquired characteristics Discredited theory of evolutionary change proposing that changes that occur during the lifetime of an individual, through use or disuse, can be passed on to the next generation.

thermoluminescence (TL) Electron trap technique that uses heat to measure the amount of radioactivity accumulated by a specimen such as a stone tool since its last heating.

tool industry A particular style or tradition of making stone tools.

transfer RNA (tRNA) RNA molecules that bind to specific amino acids and transport them to ribosomes to be used during protein synthesis.

trinucleotide repeat diseases A family of autosomal dominant diseases that is caused by the insertion of multiple copies of a three-base pair sequence (CAG) that, which codes for the amino acid glutamine. Typically, the more copies inserted into the gene, the more serious the disease.

twin method A method for estimating the heritability of a phenotypic trait by comparing the concordance rates of identical and fraternal twins.

type specimen According to the laws of zoological nomenclature, the anatomical reference specimen for the species definition.

uniformitarianism Theory that the same gradual geological process we observe today was operating in the past.

Upper Paleolithic (Later Stone Age) Stone tool industries that are characterized by the development of blade-based technology.

uranium series (U-series) techniques Radiometric techniques using the decay of uranium to estimate an age for calcium carbonates including flowstones, shells, and teeth.

vestigial organs Body parts that seem to serve no modern purpose and have, therefore, atrophied.

visual predation hypothesis Hypothesis for the origin of primate adaptation that focuses on the value of grasping hands and stereoscopic vision for catching small prey.

X-linked disorders Genetic conditions that result from mutations to genes on the X chromosome. They are almost always expressed in males, who have only one copy of the X chromosome; in females, the second X chromosome containing the normally functioning allele protects them from developing X-linked disorders.

zygomatic arch The bony arch formed by the zygomatic (cheek) bone and the temporal bone of the skull.

zygote A fertilized egg.

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