The Human Origins Progam
Resource Guide to Paleoanthropology

Human Evolution

Human evolution is the lengthy process of change by which people originated from apelike ancestors. Scientific evidence shows that the physical and behavioral traits shared by all people originated from apelike ancestors and evolved over a period of at least 5 million years.

One of the earliest defining human traits, bipedalism -- the ability to walk on two legs -- evolved over 4 million years ago. Other important human characteristics -- such as a large and complex brain, the ability to make and use tools, and the capacity for language -- developed more recently. Many advanced traits -- including complex symbolic expression, art, and elaborate cultural diversity -- emerged mainly during the past 100,000 years.

Humans are primates. Physical and genetic similarities show that the modern human species, *Homo sapiens*, has a very close relationship to another group of primate species, the apes. Humans and the great apes (large apes) of Africa -- chimpanzees (including bonobos, or so-called “pygmy chimpanzees”) and gorillas -- share a common ancestor that lived between 5 and 8 million years ago. Humans first evolved in Africa, and much of human evolution occurred on that continent. The fossils of early humans who lived between 2 and 5 million years ago come entirely from Africa.

Most scientists currently recognize some 10 to 15 different species of early humans. Scientists do not all agree, however, about how these species are related or which ones simply died out. Many early human species -- certainly the majority of them -- left no living descendants. Scientists also debate over how to identify and classify particular species of early humans, and about what factors influenced the evolution and extinction of each species.

Early humans first migrated out of Africa into Asia probably between 1.6 million and 2 million years ago. They entered Europe somewhat later, generally within the past million years. Species of modern humans populated many parts of the world much later. For instance, people first came to Australia probably within the past 60,000 years and to the Americas within the past 30,000 years or so. The beginnings of agriculture and the rise of the first civilizations occurred within the past 10,000 years.

Paleoanthropology

Paleoanthropology is the scientific study of human evolution. Paleoanthropology is a subfield of anthropology, the study of human culture, society, and biology. The field involves an understanding of the similarities and differences between humans and other species in their genes, body form, physiology, and behavior. Paleoanthropologists search for the roots of human physical traits and behavior. They seek to discover how evolution has shaped the potentials, tendencies, and limitations of all people. For many people, paleoanthropology is an exciting scientific field because it investigates the origin, over millions of years, of the universal and defining traits of our species. However, some people find the concept of human evolution troubling because it can seem not to fit with religious and other traditional beliefs about how people, other living things, and the world came to be. Nevertheless, many people have come to reconcile their beliefs with the scientific evidence.

Early human fossils and archeological remains offer the most important clues about this ancient past. These remains include bones, tools and any other evidence (such as footprints or butchery marks on animal bones) left by earlier people. Usually, the remains were buried and preserved naturally. They are then found either on the surface (exposed by rain, rivers, and wind erosion) or by digging in the ground. By studying fossilized bones, scientists learn about the physical appearance of earlier humans and how it changed. Bone size, shape, and markings left by muscles tell us how those predecessors moved around, held tools, and how the size of their brains changed over a long time. Archeological evidence refers to the things earlier people made and the places where scientists find them. By studying this type of evidence, archeologists can understand how early humans made and used tools and lived in their environments

The Process of Evolution

The process of evolution involves a series of natural changes that cause species (populations of different organisms) to arise, adapt to the environment, and become extinct. All species or organisms have originated through the process of biological evolution. In animals that reproduce sexually, including humans, the term species refers to a group whose adult members regularly interbreed, resulting in fertile offspring -- that is, offspring themselves capable of reproducing. Scientists classify each species with a unique, two-part scientific name. In this system, modern humans are classified as Homo sapiens.

Evolution occurs when there is change in the genes (the chemical molecule, DNA) inherited from the parents and especially in the proportions of different genes in a population. The information contained in genes can change by a process known as mutation. The way particular genes are expressed – that is, how they influence the body or behavior of an organism -- can also change. Genes affect how the body and behavior of an organism develop during its life, and this is why genetically inherited characteristics can influence the likelihood of an organism's survival and reproduction. Evolution does not change any single individual. Instead, it changes the inherited means of growth and development that typify a population (a group of individuals of the same species living in a particular habitat). Parents pass adaptive genetic changes to their offspring, and ultimately these changes become common throughout a population. As a result, the offspring inherit those genetic characteristics that enhance their chances of survival and ability to give birth, which may work well until the environment changes. Over time, genetic change can alter a species' overall way of life, such as what it eats, how it grows, and where it can live. Human evolution took place as new genetic variations in early ancestor populations favored new abilities to adapt to environmental change and so altered the human way of life.

Primates

Human beings belong to the mammalian group known as Primates -- the scientific category that contains over 230 species of lemurs, lorises, tarsiers, monkeys of the

Old and New World, and apes. Modern humans, early humans, and other primate species all share many similarities and have some important differences. Knowledge of these similarities and differences helps scientists to understand the roots of many human traits and the significance of each development in human evolution.

All primates, including humans, share at least part of a set of common characteristics that distinguish them from other mammals. Many of these characteristics evolved as adaptations for life in the trees, an environment in which the earliest primates evolved. These characteristics include more reliance on sight than smell; overlapping fields of vision, allowing stereoscopic (three-dimensional) sight; limbs and hands adapted for clinging on, leaping from and swinging in the trees; the ability to grasp and manipulate small objects (using fingers with nails instead of claws); large brains in relation to body size; and complex social lives.

The scientific classification of primates reflects evolutionary relationships among individual species and groups of species. Strepsirhine (meaning "wet nosed") primates -- of which the living representatives include lemurs, lorises, and other groups of species -- are all commonly known as prosimians. Strepsirhines are the most primitive of living primates. They share all of the basic characteristics of primates, although their brains are neither particularly large nor complex and they have a more elaborate and sensitive olfactory system (involved in the sense of smell) then do other primates.

The earliest monkeys and apes evolved from ancestral haplorhine (meaning "dry nosed") primates, of which the most primitive living representative is the tarsier. Tarsiers were previously grouped with prosimians, but many scientists now recognize that tarsiers, monkeys, and apes share some distinctive traits, and group the three together. Monkeys, apes, and humans -- who share many traits not found in other primates -- together make up the suborder Anthropoidea. Anthropoid primates are divided into New World (South America, Central America, and the Caribbean Islands) and Old World (Africa and Eurasia) groups. The platyrrhine (broad-nosed) monkeys represent the first, and the second is the catarrhine (downward-nosed) monkeys and apes. Humans belong to this second group.

Apes and humans together make up the superfamily Hominoidea, a grouping that emphasizes the close relationship among these species. Scientists do not all agree about the appropriate classification of the families within this superfamily. Living hominoids are grouped into either two or three families: Hylobatidae, Hominidae, and sometimes Pongidae. Hylobatidae consists of the small or so-called lesser apes of Southeast Asia, commonly known as gibbons and siamangs. The Hominidae (hominids) include humans and, according to some scientists, the great apes. For those who include only humans among the Hominidae, all of the great apes, including the orangutans of Southeast Asia, belong to the family Pongidae.

Traditionally, the term "hominid" has referred to species of humans that evolved after the split between early humans and other ape lineages. But genetic evidence, which shows chimps and humans to be more closely related genetically (and evolutionarily) to each other than to any other ape, supports placing all of the great apes and humans together in the family Hominidae. According to this reasoning, the evolutionary branch of Asian apes leading to orangutans, which separated from the other hominid branches by about 13 million years ago, belongs to the subfamily Ponginae. The African apes (gorillas, chimpanzees, and humans) are then classified in the subfamily called Homininae (or hominines). And finally, the line of early and modern humans belongs to the tribe (classificatory level above genus) Hominini, or hominins.

This classification would be true to the genetic evidence. But it tends to be confusing when learning about the subject, as many similar names (hominoid, hominid, hominine, and hominin) would apply to the different aspects of ape and human evolution. In this article the term "early human" refers to all species of the human family tree since the divergence from a common ancestor with the African apes. Popular writing often still uses the word "hominid" to mean the same thing.

Humans as Primates

About 98 percent of the genes in people and chimpanzees are identical, making chimps the closest living biological relatives of humans. This does not mean that humans evolved from chimpanzees, but it does indicate that both species evolved from a common ape ancestor. Orangutans, the great apes of Southeast Asia, differ genetically from humans to a greater extent, indicating a more distant evolutionary relationship.

Modern humans have a number of physical characteristics indicative of an ape ancestry. For instance, people have shoulders with a wide range of movement and fingers capable of strong grasping. In apes, these characteristics are highly developed as adaptations for brachiation (swinging from branch to branch in trees). Although humans do not brachiate, the general anatomy of that earlier adaptation still remains. Both people and apes also have larger brains and greater cognitive abilities than do most other mammals.

Human social life, too, shares similarities with that of African apes and other primates -- such as baboons and rhesus monkeys -- that live in large and complex social groups. Group behavior among chimpanzees, in particular, strongly resembles that of humans. For instance, chimps form long-lasting attachments with each other; participate in social bonding activities, such as grooming, feeding, and hunting; and form strategic coalitions with each other in order to increase their status and power. Early humans also probably had this kind of elaborate social life.

However, modern humans fundamentally differ from apes in many significant ways. For example, as intelligent as apes are, people's brains are much larger and more complex, and people have a unique intellectual capacity and elaborate forms of culture and communication. In addition, only people habitually walk upright, can precisely manipulate very small objects, and have a throat structure that makes speech possible.

The Fossil Primates

The origin of the mammalian group primates is traced back to Plesiadapiformes, the last common ancestors of strepsirhines and other mammals. Plesiadapiformes evolved at least 65 million years ago. They were creatures similar to the modern tree shrews. The earliest primates evolved by about 55 million years ago. The first strepsirhine primates, fossil species similar to lemurs and tarsiers, evolved during the Eocene epoch (about 56 to 34 million years ago). The oldest lineages of catarrhine primates, from which monkeys and apes evolved, are known between 50 and 33 million years ago. A primate known as Propliopithecus (one lineage sometimes called *Aegyptopithecus*), from the Fayum fossil sites of Egypt, is an archaic-looking catarrhine, and is thought to be what the common ancestor of all later Old World monkeys and apes looked like. So Propliopithecus may be considered an ancestor, or closely related to a direct ancestor, of humans.

Hominoids, or members of the superfamily Hominoidea, evolved during the Miocene epoch (24 million to 5 million years ago). Large ape species had originated in Africa by 23 or 22 million years ago. Among the oldest known hominoids is a group of apes known by its genus name, *Proconsul*. Species of *Proconsul* had features that suggest a close link to the common ancestor of apes and humans. The ape species *Proconsul heseloni* lived in dense forests of eastern Africa about 20 million years ago. It was agile in the trees, with a flexible backbone and narrow chest of a monkey, yet capable of wide movement of the hip and thumb as in apes.

Early in their evolution, the large apes underwent several radiations, periods when species originated and became more diverse. After *Proconsul* had thrived for several million years, a group of apes from Africa and Arabia known as the afropithecines evolved around 18 million years ago and diversified into several species. By 15 million years ago, apes had migrated to Asia and Europe over a land bridge formed between the Africa-Arabian and Eurasian continents, which had previously been separated. Around this time, two other groups of apes had evolved – namely, the kenyapithecines of Africa and western Asia (first known about 15 million years ago) and the dryopithecines of Europe (first known about 12 million years ago). It is not yet clear, however, which of these groups of ape species may have given rise to the common ancestor of African apes and humans.

The First Humans: The Early Australopiths

By at least 4.4 million years ago in Africa, an apelike species had evolved that had two important traits, which distinguished it from other apes: (1) small canine (eye) teeth (next to the incisors, or front teeth) and (2) bipedalism--that is the ability to walk on two legs. Scientists commonly refer to these earliest human species as australopithecines, or australopiths for short. The earliest australopith species known today belongs to the genus *Ardipithecus*. Other species belong to the genus *Australopithecus* and, by some classifications, *Paranthropus*. The name australopithecine translates literally as "southern ape," in reference to South Africa, where the first known australopith fossils were found.

Countries in which scientists have found australopith fossils include Ethiopia, Tanzania, Kenya, South Africa, and Chad. Thus, australopiths ranged widely over the African continent. The Great Rift Valley of eastern Africa, in particular has become famous for its australopith finds because past movements in Earth's crust in this region were favorable to environments in which bones are easily preserved and, later, to exposure of ancient deposits of fossilized bones.

There are many ideas about why the early australopiths split off from the apes, initiating the course of human evolution. Virtually all hypotheses invoke environmental change as an important factor, specifically in influencing the evolution of bipedalism. Some well-established ideas about why humans first evolved include (1) the savanna hypothesis, (2) the woodland-mosaic hypothesis, and (3) the variability hypothesis.

The savanna hypothesis argues that the Miocene forests of Africa became sparse and broken up between 5 and 8 million years ago due to a cooler and drier global climate. This drying trend led to the separation of an ape population in eastern Africa from other populations of apes in the more heavily forested areas of western Africa. The eastern population had to adapt to drier, open savanna environments, which favored the evolution of terrestrial living. Terrestrial apes might have formed large social groups in order to improve their ability to find and collect food and to fend off predators. The challenges of savanna life might also have promoted the rise of tool use, for purposes such as scavenging meat from the kills of predators. These important evolutionary changes would have depended on increased mental abilities and, therefore, may have correlated with the development of larger brains in early humans.

Critics of the savanna hypothesis argue against it on several grounds, but particularly for two reasons. First, an early australopith jaw similar to A. afarensis has been found in Chad in west-central Africa, 2500 kilometers west of the African rift valley. This find suggests that australopiths ranged widely over the African continent and that East Africa may not have been fully separated from environments further west. Second, there is growing evidence that open savannas were not prominent in Africa until sometime after 2 million years ago.

Criticism of the savanna hypothesis has spawned alternative ideas about early human evolution. The woodland-mosaic hypothesis proposes that the early australopiths evolved in a mosaic of woodland and grassland that offered opportunities for feeding both on the ground and in the trees. Ground feeding then favored regular bipedal activity and, eventually, the evolution of anatomical features of the hip, leg, and foot that assisted this form of locomotion.

The variability hypothesis suggests that early australopiths experienced many changes in environment and ended up living in a range of habitats, including forests, open-canopy woodlands, and savannas. In response, their populations became adapted to a variety of surroundings. Evidence from early australopith sites, in fact, shows this range of habitats. So the unique appearance of their skeletons may have allowed them the versatility of living in habitats with many or few trees.

From Ape to Human

Fossils from several different early australopith species that lived between 4 million and 2 million years ago show a variety of adaptations that mark the transition from ape to human. The very early period of this transition, prior to 4 million years ago, remains poorly documented in the fossil record, but those fossils that do exist show the most primitive combinations of ape and human features.

Fossils reveal much about the physical build and activities of early australopiths, but little is known about surface physical features, such as the color and texture of skin and hair, or about certain behaviors, such as methods of obtaining food or patterns of social interaction. For these reasons, scientists study the living great apes -- particularly the African apes -- to better understand how early australopiths might have looked and behaved. The study of living apes, therefore, sheds light on how the transition from ape to human might have occurred.

For example, australopiths probably resembled the great apes in characteristics such as the shape of the face and the amount of hair on the body. Australopiths also had brains and body sizes in the same range exhibited by the great apes, leading scientists to believe that the australopiths had similar mental capabilities and possibly even social structures.

Australopith Characteristics

Most of the distinctly human physical qualities in australopiths related to their bipedal stance. Before australopiths, no mammal had ever evolved an anatomy for habitual upright walking. African apes move around their environments in a variety of ways. They use their arms to climb and to swing through the trees (known as brachiation). They knuckle-walk when on the ground, leaning on the middle parts of their fingers. And sometimes they move on two legs, as when chimpanzees feed on low branches or when gorillas show threat displays. The australopith body was devoted especially to bipedal walking. Australopiths also had small canine teeth, as compared with long canines found in almost all other catarrhine primates.

Other characteristics of australopiths reflected their ape ancestry. Although their canine teeth were not large, their faces stuck out far in front of the braincase. Their brains were about the same size as apes' today, about 390 to 550 cubic cm (24 to 34 cubic in) but were enlarged relative to body size. Their body weight, which can be estimated from their bones, ranged from about 27 to 49 kg (60 to 108 lb.) and they stood about 1.1 to 1.5 m (3.5 to 5 ft) tall. Their weight and height compare closely to those of chimpanzees (chimp height measured standing). Some australopith species had a large degree of sexual dimorphism -- males were much larger than females -- a trait also found in gorillas, orangutans, and some other primates.

Australopiths also had curved powerful fingers and long thumbs with a wide range of movement. Apes, in comparison, have longer, very strong, even more curved fingers – which are advantageous for hanging and swinging from branches -- but their very short thumbs limit their ability to manipulate small objects. While the fingers were longer than in modern humans, the australopith finger bones were not so long and curved as to suggest arm swinging. It is not yet clear whether these changes in the hand of early australopiths enabled them to use tools in a better way than earlier apes or even modern chimpanzees today.

Bipedalism

The anatomy of australopiths shows a number of adaptations for bipedalism. Adaptations in the lower body included the following: The australopith ilium, or pelvic bone, which rises above the hip joint, was much shorter and broader than it is in apes.

This new shape enabled the hip muscles to steady the body during each bipedal step. The australopith pelvis overall had evolved a more bowl-shaped appearance, which helped support the internal organs during upright stance. The upper legs angled inward from the hip joints, which positioned the knees to better support the body during upright walking. The legs of apes, on the other hand, are positioned almost straight down from the hip, so that when an ape walks upright for a short distance, its body sways from side to side. The australopith foot was also reshaped, including shorter and less flexible toes than an ape's, which provided a more rigid lever for pushing off the ground during each step.

Other adaptations occurred above the pelvis. The australopiths' spine had an S-shaped curve, which shortened the overall length of the torso and gave rigidity and balance when standing. By contrast, apes have a relatively straight spine. The australopith skull also had an important adaptation related to bipedalism. The opening at the bottom of the skull, known as the foramen magnum, where the spinal cord attaches to the brain, was more forward than it is in apes. This position set the head in balance over the upright spine.

Australopiths clearly walked upright on the ground, but paleoanthropologists debate about whether the earliest humans also spent a lot of time in the trees. Certain physical features indicate that they spent at least some of their time in the trees. Such features include their curved and elongated fingers and elongated arms.

Explaining Bipedalism

Many different explanations have been offered to account for the evolution of upright walking. Some of the ideas include: (1) freeing the hands, which was advantageous for carrying food or tools; (2) improved vision, especially to see over tall grass; (3) reducing the body's exposure to hot sun, which allowed better cooling during the day in an open landscape; (4) hunting or weapon use, which was easier with upright posture; and (5) feeding from bushes and low branches, which was easier when standing and moving upright between closely spaced bushes.

Although none of these hypotheses has overwhelming support, recent study of chimpanzees favors the last one. Chimps move on two legs most often when feeding on the ground from bushes and low branches. Chimps today are not, however, very good at walking in this way over long distances. As the distances between trees or groves of trees became wider during drier periods bipedal behavior in pre-human populations may have become more frequent. Accordingly, a more effective bipedal gait was favored not as an adaptation to savanna living but rather as a way of crossing less favored areas of open terrain. An ability to climb trees continued to be important. This idea may currently be the best explanation for the unique adaptation of the early australopiths: a combination of long, powerful arms, slightly elongated legs, and lower limbs reshaped for upright walking over long distances on the ground.

Small Canine Teeth

Compared with apes, humans have very small canine teeth. Apes, particularly males, have thick, projecting, sharp canines that they use for displays of aggression and as weapons to defend themselves. By 4 million years ago, australopiths had developed the human characteristic of having smaller, flatter canines. Canine reduction might have related to an increase in social cooperation among humans and an accompanying decrease in the need for males to make aggressive displays.

Early Australopiths

The australopiths can be divided into an early group of species (sometimes known as gracile australopiths), which arose prior to 3 million years ago; and a later group, known as robust australopiths, which evolved after 3 million years ago. The earlier australopiths -- of which several species evolved between 4.4 million and 3 million years ago -- generally had smaller teeth and jaws. The later robusts had larger faces with large jaws and cheek teeth.

A 5-million-year-old jaw fragment with one molar tooth, found in Kenya, and another jaw with two molars, about 4.5 million years old, may be the oldest australopith fossils. But scientists have not yet agreed on the matter since these fossils are so fragmented and do not tell us about the canine teeth or bipedal walking. Several of the early australopiths are given the genus name *Australopithecus*. Yet some of the oldest finds of australopith bones, dated about 4.4 million years old, have been given a different name because of their very ancient combination of apelike and humanlike traits. These fossils, first discovered in Ethiopia in 1994, are called *Ardipithecus ramidus*.

Ardipithecus ramidus

An Ethiopian member of a research team led by paleoanthropologist Tim White discovered the earliest known australopith species in Ethiopia in 1994. These recognizably human fossils were estimated to be about 4.4 million years old. White and his colleagues gave their discovery the name *Ardipithecus ramidus*. Ramid means "root" in the Afar language of Ethiopia, and refers to the closeness of this new species to the roots of humanity. At the time of this discovery, the genus *Australopithecus* was scientifically well established. White devised the genus name *Ardipithecus* to distinguish this new species from other australopiths because it had a very ancient combination of apelike and humanlike traits.

The teeth of *Ardipithecus ramidus* have a thin outer layer of enamel--a trait also seen in chimps and gorillas, but not in other australopith species or most older fossil apes. This trait suggests a fairly close relationship with an ancestor of the African apes. In addition, the skeleton shows strong similarities to that of a chimpanzee but has slightly reduced canine teeth and adaptations for bipedalism.

Australopithecus anamensis

In 1965 a research team form Harvard University discovered a single arm bone of an early human at the site of Kanapoi in northern Kenya. The researchers estimated this bone to be 4 million years old, but could not identify the species to which it belonged. It was not until 1994 that a research team, led by paleoanthropologist Meave Leakey, found numerous teeth and fragments of bone at the site that could be linked to the previously discovered fossil. Leakey and her colleagues determined that the fossils were those of a very primitive species of australopith, which was given the name

Australopithecus anamensis. Researchers have since found other *A. anamensis* fossils at nearby sites, dating between about 4.2 million and 3.9 million years old. The skull of this species appears apelike, while its enlarged tibia or lower leg bone, indicates that it supported its full body weight on one leg at a time, as in regular bipedal walking.

Australopithecus afarensis

Australopithecus anamensis was quite similar to another, much better-known species, *A. afarensis*, a gracile australopith that thrived in eastern Africa between about 3.9 million and 3 million years ago. The most celebrated fossil of this species, known as Lucy, is a partial skeleton of a female discovered by paleoanthropologist Donald Johanson in 1974 at Hadar, Ethiopia. Lucy lived 3.2 million years ago. Several hundred fossils of this species have been described from Hadar, including a collection representing at least 13 individuals of both sexes and various ages, all from a single site that is dated 3.2 million years old.

Researchers working in northern Tanzania have also found fossilized bones of *A. afarensis* at Laetoli, a 3.6 million year old site best known for spectacular trails of bipedal human footprints (and the prints of other animals) preserved in a hardened volcanic ash. These footprints were discovered in 1978 by a research team led by paleoanthropologist Mary Leakey. They provide irrefutable evidence that australopiths regularly walked bipedally.

The controversy about how the australopiths moved has mainly focused on Lucy's species *A. afarensis*. While Lucy certainly walked upright, she stood only 3.5 feet tall and had longer, more powerful arms than most later human species, which suggests that she was also adept at climbing trees. And while the Laetoli footprints were made by bipedal humans, some scientists have argued that the imprints of the heel, arch, and toes are not exactly like those made by modern human feet. In addition, other fossils from Hadar and Laetoli come from individuals much larger than Lucy, up to 5 feet tall. This has caused controversy over whether the entire set of fossils represents one or two species, although most scientists accept the single-species idea since large and small adults, probably male and female, occurred together at the same site at Hadar.

Another controversy arises from the claim that *A. afarensis* was the common ancestor of both later australopiths and the modern human genus, *Homo*. While this idea remains a strong possibility, the similarity between *Australopithecus afarensis* and another australopith species -- one from southern Africa, named *Australopithecus africanus* -- makes it difficult to decide which of the two species gave rise to the genus *Homo*.

Australopithecus africanus

Australopithecus africanus thrived in what is now the Transvaal region of South Africa between about 3.5 million and 2.5 million years ago. The anatomist Raymond Dart described this species -- the first known australopith -- on the basis of a fossil discovered in 1924 at Taung, South Africa. For two decades after this discovery, almost no one in the scientific community believed Dart's claim that the skull came from an ancestral human. In the late 1930s and 1940s, teams led by paleontologist Robert Broom unearthed many more australopith skulls and other bones from the Transvaal sites of Sterkfontein and Swartkrans.

A. africanus generally had a more globular braincase and less primitive-looking face and teeth than did A. afarensis. Thus some scientists consider the southern species of early australopith to be a likely ancestor of the genus *Homo*. According to other scientists, however, A. africanus had facial features that mark it on the path to the robust australopiths found later in the same region. Some recent finds from the Transvaal site of Sterkfontein indeed have begun to blur the distinction between the early australopiths and the later robust species. In 1998 a research team led by South African paleoanthropologist Ronald Clarke unearthed an almost complete early australopith skeleton at Sterkfontein. Although it may prove to be a new species, this important find may resolve some of the questions about where *A. africanus* fits in the story of human evolution.

The Later Australopiths

By 2.7 million years ago, the robust australopiths had evolved. The robust australopiths represent an intriguing group of early humans because they survived for a long time and were quite common compared to other early human species. They had adaptations that differed from the larger-brained populations of Homo who lived at the same time, but then mysteriously became extinct by one million years ago. Although the word "robust" originally referred to the larger body once believed to exist in these australopiths, they are now known to have been roughly the same size as *A. afarensis* and *A. africanus*. Instead, "robust" accurately describes the very massive molar teeth, face, and skull muscle markings that characterized these species. The robust australopiths had megadont cheek teeth -- broad, thick-enameled molars and premolars -- which formed a flattened and worn surface. Their incisor teeth, by contrast, were small. An expanded, flattened, and more vertical face accompanied this emphasis on the back teeth. The combination of broad molars and large face was effective in absorbing the stresses of strong chewing. Along the top of the head was a sagittal crest, a raised area of bone along the skull's midline from front to back, where thick muscles that moved the jaw up and down were attached. The bars of bone along each side of the skull (the zygomatic arches) were positioned far to the side, which allowed huge openings for the chewing muscles near where they attached to the lower jaw. Altogether, these traits indicate very powerful and prolonged chewing of food. A similar expansion in the chewing structures can be seen in other groups of plant-eating animals. Microscopic wear on the teeth of *P. robustus* and *P. boisei* appear to support the idea of a vegetarian diet. It is thought that the robust australopiths had a diet consisting of tough, fibrous plant food, such as seed pods and underground tubers. However, chemical studies of fossil bones suggest that the southern species may also have eaten animals.

Because they share the features of heavy chewing, the robust australopiths appear to represent a distinct evolutionary group of early humans. Many paleoanthropologists have linked the robust species together with a unique genus name, *Paranthropus* (the name originally given to the southern robust species). This classification implies that the first robust species, *P. aethiopicus*, became separated from the other australopiths and then evolved into *P. boisei* and *P. robustus* (the other two robust species). Other researchers have kept the robust species within the genus *Australopithecus*, stating that the eastern forms (*A. aethiopicus* and *A. boisei*) evolved their massive teeth from the early australopiths of the region (perhaps *A. afarensis*), whereas the southern species (robustus) evolved independently from *A. africanus*. If this type of parallel evolution occurred, the robust species would form two separate side branches of the human family tree. Due to alternative views such as this, the robust species are often known by more than one name (such as *Australopithecus boisei* and *Paranthropus boisei*).

Paranthropus aethiopicus

The earliest known robust species, *Paranthropus aethiopicus*, had evolved in eastern Africa by 2.7 million years ago. In 1985 at West Turkana, Kenya, paleoanthropologist Alan Walker discovered the fossil skull that defined this species. It became known as the "black skull" because of the color it had absorbed from minerals in the ground. The skull, dated 2.5 million years old, had a tall sagittal crest toward the back of its cranium and a face that projected far outward from the forehead. *P. aethiopicus* shares some primitive features with *A. afarensis* -- that is, features that originated in the earlier East African australopith. This may indicate that *P. aethiopicus* evolved from *A. afarensis*.

Paranthropus boisei

Paranthropus boisei, the other well-known East African robust australopith, lived over a large geographic range between about 2.3 million and 1.2 million years ago. In 1959 Mary Leakey discovered the first fossil of this species -- a nearly complete skull at the site of Olduvai Gorge in Tanzania. Paleoanthropologist Louis Leakey, husband of Mary, named the new species *Zinjanthropus boise*i (*Zinjanthropus* translates as "East African man"). This skull, which is dated to 1.8 million years ago, has the most specialized features of all the robust species. It has a massive, wide, and dished-in face that was capable of withstanding extreme chewing forces, and its molars are four times the size of those in modern humans. Since the discovery of *Zinjanthropus*, now recognized as an australopith, scientists have found great numbers of *P. boisei* fossils in Tanzania, Kenya, and Ethiopia.

Paranthropus robustus

The southern robust species, which has the descriptive name *Paranthropus robustus*, lived between about 1.8 million and 1.3 million years ago in the Transvaal, the same region that was home to *A. africanus*. In 1938 Robert Broom, who had found many *A. africanus* fossils, bought a fossil jaw and molar that looked distinctly different from those in *A. africanus*. After finding the site of Kromdraai, from which the fossil had come, Broom collected many more bones and teeth that together convinced him to name a new species, which he called *Paranthropus robustus* (*Paranthropus* meaning "beside man").

The Fate of the Later Australopiths

The youngest fossils of robust australopiths are about 1.2 million years old, which suggests that they became extinct by around then. At about that time world climate began to fluctuate in a different pattern, and that may have reduced the food supply on which the robust species depended. Interaction with other early humans, such as Homo erectus, has been suggested as another reason for their extinction, although no compelling evidence exists of direct contact between these species. Competition with several other species of plant-eating monkeys and pigs, which thrived in Africa in the time, may have been an even more important factor. Still, the reasons why the robust australopiths became extinct, after such a successful time, are unknown.

The Origin of the Genus *Homo*

Origin of the modern human genus, *Homo*, is one of the most intriguing and controversial questions in paleoanthropology. The oldest fossils of our genus are at least 2.3 to 2.5 million years old. The evolution of the modern human genus can be divided roughly into three periods: early, middle, and late. Species of early *Homo* resembled the early australopiths in many ways. Some early *Homo* species lived until possibly 1.6 million years ago. The period of middle *Homo* began perhaps between 1.8 million and 2.0 million years ago, overlapping with the end of early *Homo*. Species of middle *Homo* evolved an anatomy much more similar to that of modern humans but had comparatively small brains. The transition from middle to late *Homo* evolved large and complex brains and eventually language. Culture also became an increasingly important part of human life during the most recent period of evolution.

The key change usually considered to signal the origin of *Homo* is an increase in brain size, measured by the volume of the inside of the brain case (cranial capacity). The average cranial capacity of modern humans (*Homo sapiens*) is 1350 cubic centimeters (cc), although the range of variation is large, around 1000 to 2000 cc. In the possible ancestors of *Homo* (*Australopithecus afarensis* and *A. africanus*) brain size was about 350 to 500 cc. What size, it may be asked, defines the difference between the brains of *Homo* and *Australopithecus*?

Louis Leakey originally argued that the origin of *Homo* related directly to the development of toolmaking--specifically, the making of stone tools. This once popular idea of "man the toolmaker" considered toolmaking to require certain mental skills and fine hand manipulation that may exist only in members of our own genus. Indeed, the species name *Homo habilis* (meaning "handy man") refers directly to the making and use of tools.

However, several species of australopiths lived at the same time as early *Homo*, making it unclear which species produced the earliest stone tools. Recent studies of australopith hand bones have suggested that at least one of the robust species, *Paranthropus robustus*, could have made tools. In addition, during the 1960s and 1970s researchers first observed that some nonhuman primates, such as chimpanzees, make and use tools, suggesting that australopiths and apes that preceded them probably also made some kinds of tools. Furthermore, several early human lineages (including early and later australopiths and possibly *Homo*) lived at the time of the oldest known stone tools, around 2.5 million years ago. So, scientists are not sure which early humans were responsible for the gradual proliferation of stone tools starting around that time.

Still, according to some scientists, early *Homo* was probably the toolmaker since handheld tools for cutting and pounding were most useful to these smaller-toothed humans, whereas intensive chewing of food inside the mouth was the hallmark of the robust australopiths. Furthermore, stone tools like the oldest known ones continued well after the early australopiths died out.

Some scientists think that a period of environmental cooling and drying in Africa set the stage for the evolution of *Homo*. According to this idea, many types of animals suited to the challenges of a drier environment originated between about 2.8 million and 2.4 million years ago, and these included the first species of *Homo*. A toolmaking human might have had an advantage in obtaining alternative food sources as vegetation became sparse. The new foods might have included underground tubers and roots and meat obtained through scavenging or hunting. However, the period in question consisted of several fluctuations between dry and wet environments, not just a change to dry. Thus brain enlargement, early stone tool use, and expansion of diet all may have been ways of adapting to unpredictable and fluctuating settings rather than just dry, cool ones. Also, the supposed pulse of species originations and extinctions is not well documented. In short, the exact causes of the origin of Homo are poorly known; future fossil discoveries in this key time period should help in understanding the earliest origin of our genus.

Early *Homo*

Paleoanthropologists generally recognize two species of early *Homo*. The two species, *Homo habilis* and *Homo rudolfensis*, overlapped in time and appear to have co-existed in the same region with other early human species. The record is unclear because most of the early fossils that scientists have identified as species of *Homo* occur as isolated fragments. In many places, only teeth, jawbones, and pieces of skull -- without any other skeletal remains -- indicate that new species of smaller-toothed humans had evolved as early as 2.5 million years ago. Scientists cannot always tell whether these fossils belong to late-surviving gracile australopiths or early representatives of *Homo*. The two groups resemble each other because *Homo* likely descended directly from an early species of australopith.

Homo habilis

In the early 1960s, at Olduvai Gorge, Tanzania, Louis Leakey, anatomist John Napier, and paleoanthropologist Philip Tobias described a newly discovered group of early human fossils that showed a cranial capacity of 590 to 690 cc. Based on this brain size, which was above the range of that known in australopiths, the scientists argued that a new species, *Homo habilis*, should be recognized. Other scientists questioned whether this amount of brain enlargement was sufficient for applying the genus name *Homo*, or even whether *H. habilis* was different from *Australopithecus africanus*, as the teeth of the two species look similar. However, scientists now widely accept both the genus and species names designated by the Olduvai team.

H. habilis lived in eastern and possibly southern Africa between about 1.9 million and 1.6 million years ago, and maybe as early as 2.4 million years ago. Although the fossils of this species somewhat resemble those of australopiths, *H. habilis* had smaller and narrower molar teeth, premolar teeth, and jaws than did its predecessors and contemporary robust species.

A fragmented skeleton of a female from Olduvai shows that she stood only about 1 m (3.3 ft) tall, and her arms were longer relative to her legs than they were the australopith Lucy (*A. afarensis*). At least in the case of this individual, therefore, *H. habilis* had very apelike body proportions. However, *H. habilis* also had more modern-looking feet and hands capable of producing tools. Many of the earliest stone tools at Olduvai have been found with *H. habilis* fossils, suggesting that this species made them.

Scientists have noticed a high degree of variability in body size as more fossils of early *Homo* were discovered. This could mean that *H. habilis* had a large amount of sexual dimorphism. For instance, the Olduvai female skeleton was dwarfed in comparison with some other fossils -- exemplified by a sizable early *Homo* cranium from East Turkana in northern Kenya. However, the differences in size actually exceeded those expected between males and females of the same species, and this finding has helped convince many researchers that another species of early *Homo* had lived in eastern Africa at around the same time.

Homo rudolfensis

This second species of early *Homo* was given the name *Homo rudolfensis*, after Lake Rudolf (now Lake Turkana), northern Kenya. The best-known fossils of *H. rudolfensis* come from the area surrounding this lake and date from about 1.9 million years ago. Paleoanthropologists have not yet determined the entire time range during which *H. rudolfensis* lived.

This species had a larger face and overall skull than did *H. habilis*. The cranial capacity of *H. rudolfensis* averaged about 750 cc. Scientists need more evidence to know whether the brain of *H. rudolfensis* in relation to its body size was larger than in *H. habilis*. A larger brain-to-body-size ratio can indicate increased mental abilities. *H. rudolfensis* also had fairly large teeth, approaching the size of those in robust australopiths. The discovery of even a partial fossil skeleton would reveal whether this larger form of early *Homo* had apelike or more modern body proportions. Scientists have found several modern-looking thighbones that date from between 1.8 million and 2 million years ago and may belong to *H. rudolfensis*. These bones suggest a body size of 1.5 m (5 ft) and 52 kg (114 lb.).

Middle *Homo*

By about 1.9 million years ago, the period of middle Homo had begun in Africa. Until recently, paleoanthropologists recognized one species in this period, Homo erectus. Many now recognize three species of middle *Homo*: *H. ergaster*, *H. erectus*, and *H. heidelbergensis*. However, some still think *H. ergaster* is an early African form of *H. erectus*, or that *H. heidelbergensis* is a late form of *H. erectus*.

The skulls and teeth of early African Homo ergaster populations differed subtly from those of later *H. erectus* populations from China and the island of Java in Indonesia. These subtle differences seem to parallel the differences that occurred between later humans, including our own species, and *H. erectus*. Since this appears to be the case, the early African species may be more closely related to modern humans. *Homo heidelbergensis* has similarities to both *H. erectus* and the later species *H. neanderthalensis*, and many paleoanthropologists refer to it as a transitional species between middle *Homo* and the line to which modern humans belong.

Homo ergaster

The oldest known appearance of *Homo ergaster* is in Africa around 1.9 million years ago. This species had a rounded cranium, prominent brow ridge (bony, protruding ridge across the brow above the eyes), small teeth, and other features that it shared with the later *H. erectus*. Many paleoanthropologists consider *H. ergaster* a good candidate for an ancestor of modern humans because it also had certain modern skull features, including relatively thin cranial bones. Specimens of *H. ergaster* are especially well known in the time range 1.6 to 1.7 million years ago.

The most important fossil find of this species is a nearly complete skeleton of a young male, dated 1.6 million years old, from West Turkana, Kenya. The sex of the skeleton is determined from the shape of the pelvis and by its brow ridges, and an age of 9 to 12 years at death is known by the pattern of tooth eruption and bone growth. It is not known how the boy died. The "Turkana boy" had long leg bones adapted for long distance walking. The length of his arms, legs, and trunk were proportioned as in modern humans, in contrast with the apelike short legs (and long arms) of *H. habilis* and *A. afarensis*. This skeleton is remarkable for the evidence it offers of an early human fully committed to bipedality, with no signs of significant tree climbing. *H. ergaster* had an elongated body, indicating that it was adapted to hot, tropical climates, just as modern humans from the tropics also tend to have long, slender bodies. An adult height of about 6-ft and a body weight of 150 lbs. is estimated from the Turkana skeleton, assuming that the body underwent an adolescent growth spurt as modern human teenagers usually do.

Homo ergaster, *H. rudolfensis*, and *H. habilis* add significantly to the known diversity of early human species nearly 2 million years ago. Most paleoanthropologists used to believe that human evolution consisted of a single line that evolved progressively over time, an australopith species followed by *Homo erectus*, then Neanderthals, and finally modern *Homo sapiens*. But now it is thought that as many as five different species of early human, including robust australopiths, inhabited Africa about 1.9 million years ago. Since hybridization rarely succeeds between species with significant skeletal differences, only one of these species could have been the ancestor of modern humans. *H. ergaster* is widely accepted as an ancestor, although it arose from earlier populations of *Homo*, possibly *H. habilis* or *H. rudolfensis*. It appears that periods of species diversity and extinction have been common during human evolution, a similarity to the evolutionary histories of other organisms. Modern *H. sapiens* has the distinction of being the only living human species today.

Homo erectus

Paleoanthropologists now know that humans first evolved in Africa and lived only on that continent for at least the first two million years of our evolutionary history. But this finding was not clear to scientists until quite recently. In fact, the first discoveries of early human fossils in the 1800s were in Europe. Later discoveries came from Asia and included fossils from the Indonesian island of Java. The first finds from Java were in 1891 by Dutch physician Eugene Dubois. Dubois named this early human *Pithecanthropus erectus,* or "erect ape-man". Today paleoanthropologists refer to this species as *Homo erectus*. *H. erectus* was the first human species known to have spread in large numbers beyond the African continent.

H. erectus appears to have evolved in Africa from earlier populations of *Homo ergaster*, and then spread to Asia between 1.8 million and 1.5 million years ago. The youngest known fossils of this species, from the Solo River in Java, have been dated to about 50,000 years old. So this species was very successful, both widespread (Africa and Asia) and long-lived, having survived for more than 1.5 million years.

H. erectus had a low and rounded braincase that was elongated from front to back, a prominent brow ridge, and an adult cranial capacity of 800 to 1,250 cc, an average twice that of the australopiths. Its bones, including the cranium, were thicker than those of earlier species. Prominent muscle markings and thick, reinforced areas on the bones of *H. erectus* indicate that its body could withstand powerful movements and stresses. Its body was well adapted for bipedal walking. Although its teeth were much reduced in size from *Australopithecus*, its lower jaw was still quite thick and rugged looking.

In the 1920s and 1930s, the most famous collection of *H. erectus* fossils was excavated from a cave at the site Zhoukoudian (Chou-k'ou-tien), China, near Beijing (Peking). Scientists dubbed these fossil humans *Sinanthropus pekinensis*, or Peking Man, but others later reclassified them as H. erectus. The Zhoukoudian cave yielded the fragmentary remains of over 30 individuals, ranging from about 500,000 to 250,000 years old. These fossils were lost near the outbreak of World War II, but anatomist Franz Weidenreich had made excellent casts and descriptions of the finds. Further studies at the cave site have yielded more *H. erectus* remains.

Other important fossil sites of *H. erectus* in China include Lantian, Yuanmou, Yunxian, and Hexian. Researchers have also recovered many tools made by *H. erectus* in China at sites such as Nihewan and Bose, and other sites of similar age (at least 1 million to 250,000 years old).

Ever since the discovery of *H. erectus*, scientists have debated whether this species was a direct ancestor of later humans, including *H. sapiens*. The last populations of *H. erectus* -- such as those from the Solo River in Java -- may have lived as recently as 50,000 years ago, at the same time as populations of *H. sapiens*. Although modern humans could not have evolved in that amount of time from these late populations of *H. erectus*, it is possible that earlier East Asian populations could have given rise to *H. sapiens*.

Homo heidelbergensis

Many paleoanthropologists believe that early humans migrated into Europe by 800,000 years ago, and that these populations were not *Homo erectus*. A growing number of scientists refer to these early migrants to Europe -- who predated both

Neanderthals and *H. sapiens* in the region -- as *H. heidelbergensis*. The species name comes from a 500,000-year-old jaw found near Heidelberg, Germany.

Scientists have found few human fossils in Africa for the period between 1.2 million and 600,000 years ago, during which *H. heidelbergensis* or their ancestors first migrated into Europe. Populations of *Homo ergaster* (or possibly *H. erectus*) appear to have lived until at least 800,000 years ago in Africa, and possibly until 500,000 years ago in northern Africa. When these populations disappeared, other massive-boned and larger-brained humans -- possibly *H. heidelbergensis* -- appear to have replaced them. Scientists have found fossils of these stockier humans at sites in Bodo, Ethiopia; Saldanha (also known as Elandsfontein), South Africa; Ndutu, Tanzania; and Kabwe, Zimbabwe.

There are at least three different ideas about these fossils. Some scientists place the African fossils in the species *H. heidelbergensis*, and think that this species gave rise to both Neanderthals (in Europe) and *H. sapiens* (in Africa). Others think that the European and African fossils are distinct, and that the African fossils belong in their own species (not *H. heidelbergensis*), which gave rise to *H. sapiens*. Still others prefer the long-held view that *H. erectus* and *H. sapiens* form a single evolving lineage, and that the African fossils should be placed in the category of archaic *H. sapiens*. According this last view, *H. erectus* was the direct ancestor of modern humans, but the first two views give that role either to *H. heidelbergensis*, saying that the species spread through Europe and Africa, or to a separate African species. The main point is this: There is a growing number of fossils from Asia, Africa, and Europe that are intermediate between early *H. ergaster* and *H. sapiens*, and this makes it hard to decide how to divide up the variation in the bones and to determine which group of fossils represents the most likely ancestor of later humans.

Why Did Humans Spread Out of Africa?

Humans evolved in Africa and lived only there for as long as 2, or possibly 3, million years. So scientists wonder what finally triggered the first human migration out of Africa (a movement that coincided with the spread of early human populations throughout the African continent). The answer to this question depends, in part, on knowing exactly when that first migration occurred. Some studies claim that sites in Asia and Europe contain crude stone tools and fossilized fragments of humanlike teeth that date from more than1.8 million years ago. Although these claims remain unconfirmed, small populations of humans may have entered Asia prior to 1.7 million years ago, followed by a more substantial spread between 1.7 million and 1 million years ago. The first major habitation of central and western Europe, on the other hand, does not appear to have occurred until between 1 million and 500,000 years ago.

By the time of the earliest humans, the world’s continents were in essentially the same positions they now occupy, so continental drift had no impact at all on human dispersal or the origin of races. Migrations were the result of several factors. First, the fall and subsequent rise in sea level occurred repeatedly, especially over the past 2.8 million years, coinciding with the expansion and melting of glaciers. When sea level fell, coastal land area expanded, which included the development of land bridges between continents and islands. Land expansion allowed new areas to be colonized.

Second, climate change led to the movement, expansion, and contraction of habitats that were favorable to early humans and other organisms. Migration from one region to another may have simply occurred as early humans tracked climate conditions or habitats to which they were already adapted. Finally, the origin of new adaptive behaviors, such as the ability to control fire or improvement in language communication, may have also resulted in the ability of populations to expand into new types of habitat.

Scientists once thought that advances in stone technology could be correlated with the earliest human spread beyond Africa. However, these advances do not seem to be related. By 1.6 million years ago early humans began to make new kinds of tools commonly known as handaxes and cleavers. But this new technology (called Acheulean) was apparently not responsible for the spread, as the earliest human presence in Asia is older than the first handaxes. Also, most of the tool kits from East Asian sites more than 200,000 years old are made up of simply shaped cores and flakes rather than symmetrical handaxes.

It's been suggested that the early Pleistocene spread of humans was part of a wider colonization of new regions by meat-eating animals, like lions and hyenas. The dispersal of these African carnivores to Eurasia also occurred during the early Pleistocene, between 1.6 million and 780,000 years ago. Meat-eating may have allowed H. erectus to move through many different environments without having to learn the diverse poisonous plants in different regions. The long dispersal to eastern Asia, however, may have been gradual and occurred through the lower latitudes and environments similar to Africa's. Even a very minor expansion of populations each generation (such as 1 mile every 20 years) would have allowed East African H. erectus to reach Southeast Asia in only 150,000 years. Careful comparison of fossil animals, stone tools, and early human fossils unearthed from African, Asian, and European sites will help to test these ideas.

Late *Homo*

The origin of our own species, *Homo sapiens*, is one of the most hotly debated topics in paleoanthropology. One distinctive group of fossil humans, the Neanderthals, and their relationship to modern humans has been at the center of the debate. Traditionally, paleoanthropologists have classified as *Homo sapiens* any fossil human younger than 500,000 years old with a braincase larger than that of *H. erectus*. Many scientists who believe that modern humans descend from a single line dating back to *H. erectus* use the term "archaic *Homo sapiens*" to cover a wide variety of fossil humans that predate anatomically modern H. sapiens. Therefore, Neanderthals are sometimes classified as a subspecies of archaic *H. sapiens* -- *H. sapiens neanderthalensis*. Other scientists think that the variation in archaic *H. sapiens* actually falls into clearly identifiable sets of traits, and that any type of human fossil exhibiting a unique set of traits should have a new species name. According to this view, the Neanderthals belong to their own species, *H. neanderthalensis*.

Neanderthals and Other Archaic Humans

The Neanderthals lived in areas ranging from western Europe through central Asia between about 200,000 and 36,000 years ago, although recently discovered fossil and stone-tool evidence suggests that Neanderthals may have persisted until 28-24,000 years ago. The name Neanderthal (sometimes spelled Neandertal) comes from fossils in 1856 in the Feldhofer Cave of the Neander Valley in Germany (thal is the old spelling of the word meaning "valley" in German). Scientists realized several years later that prior discoveries -- at Engis, Belgium, in 1829 and at Forbes Quarry, Gibraltar, in 1848 -- also represented Neanderthals. These two earlier discoveries were the first early *Homo* fossils ever found.

The distinction between Neanderthals and modern humans was supported early on by a faulty reconstruction showing bent knees and a slouching gait. This reconstruction was responsible for the standard picture of the Neanderthals' supposedly crude caveman lifestyle. This image turned out to be mistaken. The Neanderthals walked fully upright without a slouch or bent knees. Their cranial capacity was large, around 1500 cc (slightly larger on average than the brains of modern populations, a difference probably related to their large bodies and lean muscle mass). They were also culturally sophisticated compared with earlier humans. They made finer tools and were the first humans known to bury their dead and to have symbolic ritual. The practice of intentional burial is one reason why Neanderthal fossils, including a number of skeletons, are quite common compared to earlier forms of *Homo*.

Nevertheless, Neanderthals differed from modern populations in certain ways. Their skulls showed a low forehead, large nasal area, projecting cheek region, double-arched brow ridge, weak chin, and an obvious space behind the third molar (in front of the upward turn of the mandible, or lower jaw). Their bodies were distinguished by these traits: heavily-built bones, occasional bowing of the limb bones, broad scapula (shoulder blade), hip joint rotated outward, long and thin pubic bone, short lower leg and arm bones relative to the uppers, and large joint surfaces of the toes and long bones. Together, these traits made a powerful, compact body of short stature -- males averaged 1.7 m (5ft 5 in) tall and 84 kg (185 lb.), and females averaged 1.5 m (5 ft) tall and 80 kg (176lb).

The short, stocky build of Neanderthals conserved heat and helped them withstand cold conditions that prevailed in temperate regions beginning about 70,000 years ago. The last known Neanderthal fossils in western Europe are approximately 36,000 years old, and recent dates of Neanderthals from central Europe are 28,000 to 29,000 years old. Neanderthals produced sophisticated types of stone tools known as Mousterian, which involved creating blanks (rough forms) from which several types of tools could be made.

At the same time as Neanderthal populations grew in number in Europe and parts of Asia, other populations of nearly modern humans arose in Africa and Asia. These fossils, considered to be from archaic humans, are distinct from but similar to those of Neanderthals. Fossils from the Chinese sites of Dali, Maba, and Xujiayao display the long, low cranium and large face typical of archaic humans, yet they also have features similar to those of modern people in the region. And at the cave site of Jebel Irhoud, Morocco, scientists have found fossils with the long skull typical of archaic humans but also the modern traits of a somewhat higher forehead and flatter midface. Fossils of humans from East African sites older than 100,000 years -- such as

Ngaloba in Tanzania and Eliye Springs in Kenya -- also seem to show a mixture of archaic and modern traits.

Anatomically Modern *Homo sapiens*

The oldest known fossils that possess skeletal features typical of modern humans date from between 130,000 and 90,000 years ago. Several key features distinguish the skulls of modern humans from those of archaic species. These features include a much smaller brow ridge, if any; a globe-shaped braincase; and a flat or only slightly projecting face of reduced size. Among all mammals, only humans have a face positioned directly beneath the frontal lobe (forward-most area) of the brain. As a result, modern humans tend to have a higher forehead than did Neanderthals and other archaic humans. The cranial capacity of modern humans ranges from about 1,000 to 2,000 cc, with the average being about 1,350 cc.

Scientists have found both fragmentary and nearly complete cranial fossils of early anatomically modern *Homo sapiens* from the sites of Singha, Sudan; Omo, Ethiopia; Klasies River Mouth, South Africa; and Skhãl Cave, Israel. Based on these fossils, many scientist conclude that modern *H. sapiens* had evolved in Africa by 130,000 years ago and started spreading to diverse parts of the world beginning on a route through the Near East sometime before 90,000 years ago.

Theories on Modern Human Origins and Diversity

Paleoanthropologists are engaged in an ongoing debate about where modern humans evolved and how they spread around the world. Differences in opinion rest on the question of whether modern humans originated in a small region of Africa or took place over a broad area of Africa and Eurasia. By extension, opinions differ as to whether modern human populations from Africa displaced all existing populations of earlier humans in other parts of the world.

Those who think modern humans originated only in Africa and then spread around the world support what is known as the Out of Africa hypothesis. Those who think modern humans evolved over a very broad area, with gene flow between regions, support the Multiregional hypothesis. Researchers have conducted many genetic studies and carefully assessed fossils to determine which of these hypotheses agrees more with scientific evidence. The results of this research do not entirely confirm or reject either one. Therefore, some scientists think a compromise between the two hypotheses is the best explanation.

The Out of Africa Hypothesis

According to the Out of Africa hypothesis, also known as the Replacement hypothesis, the transition to modern humanity occurred in only one area, which is consistent with the idea that new species usually arise from small, geographically isolated populations. Furthermore, modern anatomical traits evolved relatively recently, within the past 200,000 years or so. Modern-looking populations expanded and divided within Africa, and then they spread to other areas of the world. During this process, populations of migrating modern humans replaced archaic human populations, including the Neanderthals and any surviving groups of H. erectus.

The Multiregional Hypothesis

According to the Multiregional hypothesis, also known as the Continuity hypothesis, the evolution of modern humans began when Homo erectus spread throughout much of Eurasia around 1 million years ago. Regional populations retained unique anatomical features for hundreds of thousands of years, but they also mated with populations from neighboring regions, exchanging inheritable traits with each other. This exchange of inheritable traits takes place by the process known as gene flow.

Through gene flow, populations of H. erectus passed on a variety of increasingly modern characteristics, such as increases in brain size, across their geographic range. Gradually this would have resulted in the evolution of more modern looking humans throughout Africa and Eurasia. The physical differences among people today, then, would result from hundreds of thousands of years of regional evolution. This is the concept of continuity. For instance, modern East Asian populations have some skull features that scientists also see in H. erectus fossils from that region.

Some critics of the Multiregional hypothesis claim that it wrongly advocates a scientific belief in race and could be used to encourage racism. Supporters of the idea point out, however, that their position does not imply that modern races evolved in isolation from each other, or that racial differences justify racism. Instead, the idea holds that gene flow linked different populations together. These links allowed progressively more modern features, no matter where they arose, to spread from region to region and eventually become universal among humans.

Genetic Evidence

Geneticists have studied the amount of difference in the DNA (deoxyribonucleic acid) of different populations of humans. DNA is the molecule that contains the inherited genetic code. Differences in human DNA result from mutations in DNA structure. Mutations may result from human exposure to external stimuli such as solar radiation or certain chemical compounds, while others occur naturally at random.

Geneticists have calculated rates at which mutation can be expected to occur over time. Dividing the total number of genetic differences between two populations by an expected rate of mutation provides an estimate of the time when the two shared a common ancestor. Many estimates of evolutionary ancestry rely on studies of the DNA in cell structures called mitochondria. This DNA is referred to as mtDNA (mitochondrial DNA). Unlike DNA from the nucleus of a cell, which is inherited from both mother and father; mtDNA is inherited solely from the mother's egg, since sperm mitochondria are usually discarded during fertilization. The mtDNA accumulates mutations about ten times faster than nuclear DNA. As a result, mtDNA is altered so quickly that it is easy to measure the difference between one human population and another, since separate groups have accumulated different sets of mutations. Two closely related populations should have only minor differences in their mtDNA. Conversely, two very distantly related populations should have large differences in their mtDNA.

MtDNA research into modern human origins has produced two major findings. First, the entire amount of variation in mtDNA across human populations is small in comparison with that of other animal species. This means that all human mtDNA originated from a single ancestral lineage -- specifically, a single mother -- fairly recently and has been mutating ever since, producing the small diversity that exists throughout the human species. Most estimates of the mutation rate indicate an origin of about 200,000 years ago. The second major finding is that mtDNA of African populations is more diverse than of peoples of other continents. This suggests that African mtDNA has been changing for a longer time than elsewhere. Thus Africa is the likely source of the original mtDNA mother (sometimes called "Mitochondrial Eve"). Some geneticists and anthropologists have concluded, then, that modern humans originated in a small population in Africa and spread from there.

The mtDNA studies have been criticized on several grounds. First, the mutation rate is not known exactly, and some estimates could mean an origin age closer to 850,000 years. If so, the original mtDNA line of all modern humans might have occurred in Homo erectus, which then spread and gradually evolved in Homo sapiens, an interpretation that favors the Multiregional idea. Second, mtDNA is a small part of the total genetic material that humans inherit. Although the diversity of mtDNA may owe its origin to a single African female 200,000 years ago, the rest of our genetic material (about 400,000 times the amount of mtDNA) was inherited from many individuals who lived at the same time as that female. Some scientists argue that these individuals may have been spread over a wide area. Third, the time at which modern mtDNA began to diversify does not necessarily coincide with the origin of modern biological and cultural traits. Finally, non-African populations may have been smaller or experienced large drops in numbers, which could explain the smaller amount of modern genetic diversity outside of Africa.

Despite these criticisms, many geneticists continue to favor the Out of Africa model. Studies of nuclear DNA also suggest an African origin for other genes besides mtDNA. Furthermore, in a remarkable study, ancient mtDNA has been recovered from the original Neanderthal fossil find in Germany, and it does not closely match modern human mtDNA. This finding suggests that at least the population of this one Neanderthal had diverged from the lineage to modern humans by about 600,000 years ago.

Fossil Evidence

As with genetic research, fossil evidence also does not entirely support or refute either of the competing hypotheses of modern human origins. However, many scientists see the balance of evidence favoring an African origin of modern H. sapiens within the past 200,000 years. The oldest known modern-looking skulls come from Africa and date from perhaps 130,000 years ago. The next oldest come from the Near East, where they date from about 90,000 years ago. Fossils of modern humans in Europe are unknown prior to about 40,000 years ago. In addition, the first modern humans in Europe -- often referred to as Cro-Magnon people -- had elongated lower leg bones, as did African populations that were adapted to warm, tropical climates. This suggests that populations from warmer regions replaced those in colder European regions, such as Neanderthals.

On the other hand, fossils of archaic and modern humans in some regions show continuity in certain physical characteristics. These similarities may indicate multiregional evolution. For example, both archaic and modern skulls from eastern Asia have flatter cheek and nasal areas than do skulls from other regions. By contrast, the same parts of the face project forward in the skulls of both archaic and modern humans of Europe. Assuming that these traits were influenced primarily by genetic inheritance rather than environmental factors, archaic humans may have given rise to modern humans in some regions or at least interbred with migrant modern-looking humans.

A Compromise Hypothesis

Each of the competing major hypotheses of modern human origins has its strengths and weaknesses. Genetic evidence appears to support the Out of Africa hypothesis. In the western half of Eurasia and in Africa, this hypothesis also seems the better explanation, particularly for the apparent replacement of Neanderthals by modern populations. At the same time, the Multiregional hypothesis appears to explain some of the regional continuity found in East Asian populations.

Therefore, many paleoanthropologists advocate a view of modern human origins that combines elements of the Out of Africa and the Multiregional hypothesis. Humans with modern features may have first emerged in Africa or come together there as a result of gene flow with populations from other regions. These African populations may then have replaced archaic humans in certain regions, such as western Europe and the Near East. Yet elsewhere -- especially in East Asia -- gene flow may have occurred among local populations of archaic and modern humans, resulting in distinct and enduring regional characteristics.

All three of these views -- the two competing positions and the compromise -- acknowledge the strong biological unity of all people. In the Multiregional hypothesis, this unity results from hundreds of thousands of years of continued gene flow among all human populations. According to the Out of Africa hypothesis, similarities among all living human populations result from a recent common origin. The compromise position accepts both of these as reasonable and compatible explanations of modern human origins.

Evolution of Cultural Behavior

The word "culture" -- the social transfer of information from one generation to the next -- is often used to distinguish human behavior from that of other animals. Yet complex social learning also occurs in apes and other organisms. Different groups of chimpanzees, for example, alter sticks and twigs in distinctive ways for use in capturing termites for food. In some regions, chimps use stones or pieces of wood for cracking open nuts, and they have a sophisticated memory of where such implements were last used. In other regions, chimpanzees do not practice this behavior even though the same nut trees and potential tool materials are present. These behaviors appear to reflect different traditions of behavior passed on within the social group across generations. Since traditions are also part of human cultural behavior, they may have also occurred in the australopiths and other early human species.

However, modern humans differ from other animals, and probably from some early human species, in that they actively teach each other and pass on unusually large amounts of knowledge. People have a uniquely long period of learning before adulthood and also the physical and mental capacity for language. Language of all forms -- spoken, signed, and written -- provides a medium for communicating vast amounts of information, much more than any other animal appears to be able to transmit through gestures and vocalizations.

Scientists have traced the evolution of human cultural behavior through the study of archeological artifacts, such as tools, and related evidence, such as the charred remains of cooked food. Artifacts show that throughout much of human evolution, culture has developed slowly. During the Paleolithic, or early Stone Age, basic techniques of making stone tools changed very little for periods well over a million years.

Human fossils also provide information about how culture has evolved and what effects it has had on human life. For example, over the past 30,000 years, the basic anatomy of humans has undergone only one prominent change: The bones of the average human skeleton have become smaller and thinner. Innovations in making and using tools and in obtaining food -- due to cultural evolution -- may have enabled a more efficient and less physically taxing way of life, and thus led to the changes in the skeleton.

Culture has played a prominent role in the evolution of Homo sapiens. Within the last 60,000 years, people have migrated to almost all previously unoccupied regions of the Earth, such as small island chains and the continents of Australia and the Americas. These migrations depended on developments in transportation, hunting and fishing tools, shelter, and clothing. Within the past 30,000 years, cultural evolution has sped up dramatically. This change shows up in the archeological record as a rapid expansion of stone tool types and toolmaking techniques, and in works of art and indications of evolving religion, such as sophisticated burials. By 10,000 years ago, people first began to harvest and cultivate grains and to domesticate animals -- a fundamental change in the ecological relationship between human beings and other forms of life. The development of agriculture provided people with larger quantities and more stable supplies of food, which set the stage for the rise of the first civilizations. Today culture -- particularly technology – is a dominant aspect of human life.

Paleoanthropologists and archeologists have studied many topics in the evolution of human cultural behavior. These have included the evolution of (1) social life; (2) subsistence (the acquisition and production of food); (3) the making and using of tools; (4) environmental adaptation; (5) symbolic thought and its expression through language, art, and religion; and (6) the development of agriculture and the rise of civilizations.

Social Life

Most primate species, including the African apes, live in social groups of varying size and complexity. Within their groups, individuals often have multifaceted roles, based on age, sex, status, social skills, and personality. The discovery in 1975 at Hadar, Ethiopia, of a group of several Australopithecus afarensis individuals who died together 3.2 million years ago appears to confirm that early humans lived in social groups. Scientists have referred to this collection of fossils as The First Family.

One of the first physical changes in the evolution of humans from apes -- a decrease in the size of male canine teeth -- also indicates a change in social relations. Male apes sometimes use their large canines to threaten (or sometimes fight with) other males of their species, usually over access to females, territory, or food. The evolution of small canines in australopiths implies that males had either developed other methods of threatening each other or become more cooperative. In addition, both male and female australopiths had small canines, indicating a reduction of sexual dimorphism from that in apes. Although sexual dimorphism in canine size decreased in australopiths, males were still much larger than females. Thus, male australopiths might have competed aggressively with each other based on sheer size and strength, and the social life of humans may not have differed much from that of apes until later times.

Scientists believe that several of the most important changes from apelike to characteristically human social life occurred in species of the genus *Homo*, whose members show even less sexual dimorphism. These changes, which may have occurred at different times, included (1) prolonged maturation of infants, including an extended period during which they required intensive care from their parents; (2) special bonds of sharing and exclusive mating between particular males and females, called pair-bonding; and (3) the focus of social activity at a home base, a safe refuge in a special location known to family or group members.

Parental Care

Humans, who have a large brain, have a prolonged period of infant development and childhood because the brain takes a long time to mature. Since the australopith brain was not much larger than that of a chimp, some scientists think that the earliest humans had a more apelike rate of growth, which is more rapid than that of modern humans. This view is supported by studies of australopith fossils that have examined tooth development, which is thought to be a good indicator of overall body development.

In addition, the human brain becomes very large as it develops, so a woman must give birth to a baby at an early stage of development in order for the infant's head to fit through her birth canal. Thus, human babies require a long period of care to reach a stage of development at which they depend less on their parents. In contrast with a modern female, a female australopith could give birth to a baby at an advanced stage of development because its brain would not be too large to pass though the birth canal. The need to give birth early -- and therefore to provide more infant care -- may have evolved around the time of the species *Homo ergaster*. This species had a brain significantly larger than that of the australopiths, but a narrow birth canal.

Pair-Bonding

Pair-bonding, usually of a fairly short duration, occurs in a variety of primate species. Some scientists speculate that prolonged bonds developed in humans along with increased sharing of food. Among primates, humans have a distinct type of food-sharing behavior. People will delay eating food until they have returned with it to the location of other members of their social group. This type of food sharing may have arisen at the same time as the need for intensive infant care, probably by the time of *H. ergaster*. By devoting himself to a particular female and sharing food with her, a male could increase the chances of survival for his own offspring.

The Home Base

Foraging peoples, or hunter-gatherers, obtain food when and where it is available in the territory surrounding a central campsite, or home base. In modern foraging societies, such as that of the San people in the Kalahari Desert of southern Africa, men and women divide work duties. Women gather readily available plant and animal foods, while men take on the often less successful task of hunting. Female and male family members and relatives bring together their food to share at their home base. Sharing of food at the home base is usually done within the family, including relatives.

Because some of the oldest archeological sites were places where food remains and stone tools were found together, they were thought to represent home bases, indicating many of the social features of modern hunter-gatherer campsites, including pair-bonded males and females. Indeed, with further study, marks on bones were detected proving that early humans cut up and bashed open animal bones at these sites. Yet tooth marks made by hyenas, cats, and jackals were also prevalent, indicating that potential predators were active at these sites. Safe home bases where social groups lived, children were active, the sick were attended, and food was brought for sharing, may have developed sometime after 1.7 million years ago. In fact, evidence of hearths and shelters, typical of modern human home bases, are not clearly evident in the archeological record until after 500,000 years ago.

Subsistence

Human subsistence refers to the types of food humans eat, the technology used in and methods of obtaining or producing food, and the ways in which social groups or societies organize themselves for getting, making, and distributing food. For millions of years, humans probably fed on-the-go, not unlike other primates. The great apes eat mostly plant foods. Many primates also eat easily obtained animal foods such as insects and bird eggs. Among the few primates that hunt, chimpanzees will prey on monkeys and even small gazelles. The first humans also had a diet based mostly on plant foods. In addition, they undoubtedly ate some animal foods and might have done some hunting. Human subsistence began to diverge from that of other primates with the production and use of the first stone tools. With this development, the meat and marrow (the inner, fat-rich tissue of bones) of large animals became a part of the human diet.

Scientists have found broken and butchered fossil bones of antelopes, zebras, and other comparably sized animals at the oldest archeological sites, which date from about 2.5 million years ago. At younger sites, about 1.8 million years old, scientists have discovered that many bones have been cut and broken by the toolmakers. With the evolution of late *Homo*, humans began to hunt even the largest animals on Earth, including mastodons and mammoths, members of the elephant family. Agriculture and the domestication of animals arose only in the recent past, with *H. sapiens*.

Views/Interpretations/Models of Subsistence in Homo

The idea that predation and meat-eating had a strong effect on early human evolution is known as the hunting hypothesis. According to this hypothesis, acquiring meat by aggressive hunting with primitive tools was the main way that the oldest human ancestors survived in the arid environments in Africa. Hunting and competition with the meat-loving carnivores, it was thought, had great impact on human social behavior, toolmaking, and the evolution of intelligence. Many advocates of the hunting hypothesis believe that toolmaking had a big influence on the evolution of human hands, brains, and social groups. Tools and hunting thus acted as powerful forces in early human evolution.

Since the 1960s, the hunting hypothesis has been called into doubt. For one thing, scientists discovered that chimpanzees hunt at least small animals, and so the evolution of the capacity to hunt itself did not set the earliest humans apart as much as we once thought. Some scientists instead argued in favor of the importance of food sharing in early human life. According to a food-sharing hypothesis, cooperation and sharing within family groups -- instead of aggressive hunting -- strongly influenced the path of human evolution. Although the food-sharing idea was also criticized, it led to a more careful study of animal bones from the early archeological sites. From this research, scientists began to think that scavenging meat and bone marrow from dead animals was more important than hunting. The scavenged body parts were carried away to special places for further cutting and bashing with stone tools; these places were the tool-and-bone sites dug up by archeologists. The scavenging idea was supported when scientists observed that antelopes and other animals often die in the dry season. So maybe early toolmakers also had an opportunity to scavenge animal fat and meat during dry times of the year. Other archeological studies -- and the occasional hunting by chimpanzees -- suggest, however, that the scavenging hypothesis is too narrow. A broader view is that early humans did a combination of scavenging and hunting. Although new evidence can change things, most paleoanthropologists agree that early human toolmakers scavenged at least the larger animals (and also ate plant foods). There is still a difference of opinion about how much hunting was done, especially of smaller animals.

The Rise of Hunting

Scientists still debate about when humans first began hunting on a regular basis. For instance, elephant fossils found with tools made by middle *Homo* once led researchers to the idea that these early humans were hunters of big game. However, the simple association of animal bones and tools at the same site does not necessarily mean that early humans had killed the animals or eaten their meat. Animals may die in many ways, and natural forces can accidentally place fossils next to tools. Recent excavations at Olorgesailie, Kenya, show that *H. erectus* cut meat from elephant carcasses but do not reveal whether these humans were hunters.

Humans who lived outside of Africa -- especially in colder temperate climates -- almost certainly needed to eat more meat than their African counterparts. Humans in temperate Eurasia would have had to learn about which plants they could safely eat, and the number of available plant foods would have dropped significantly during the winter. Although scientists have found very few fossils of edible or eaten vegetation at sites, nevertheless the early inhabitants of Europe and Asia probably did eat plant foods in addition to meat.

Sites that provide the clearest evidence of early hunting include Boxgrove, England, where about 500,000 years ago people trapped a great number of large game animals between a watering hole and the side of a cliff and then slaughtered them. At Sch`ningen, Germany, a site about 400,000 years old, scientists have found wooden spears with sharp ends that were well designed for throwing and probably used in hunting large animals.

Neanderthals and other archaic humans seem to have eaten whatever animals were available at a particular time and place. So, for example, in European Neanderthal sites, the number of bones of reindeer (a cold-weather animal) and red deer (a warm-weather animal) fluctuated depending on the ancient climate. Like earlier humans, Neanderthals probably combined hunting and scavenging to obtain animal protein and fat.

For at least the past 100,000 years, various human groups have eaten foods from the ocean or coast, such as shellfish, and some sea mammals and birds. Others began fishing in interior rivers and lakes. Between probably 60,000 and 90,000 years ago, people at the site of Katanda, Democratic Republic of Congo, caught large catfish using a set of barbed bone points, the oldest known specialized fishing implements. The oldest stone tips for arrows or spears date from about 40,000 to 50,000 years ago. These technological advances, probably first developed by early modern humans, indicate an expansion in the kinds of food humans could obtain.

Beginning 40,000 years ago humans began making even more significant advances in hunting dangerous animals and large herds, and in exploiting ocean resources. People cooperated in large hunting expeditions in which they killed great numbers of reindeer, bison, horses, and other animals of the expansive grasslands that existed at that time. In some regions, people became specialists in hunting certain kinds of animals. The familiarity these people had with the animals they hunted is manifested in sketches and paintings on cave walls, dating from as much as 32,000 years ago. Hunters also used the bones, ivory, and antlers of their prey to create art and beautiful tools. Later on, in some areas, such as the central plains of North America that once teemed with a now-extinct type of large bison, hunting may have contributed to the extinction of entire species.

Tools

The making and use of tools alone probably did not distinguish early humans from their ape predecessors. Instead, humans made the important breakthrough of using one tool to make another. Specifically, they developed the technique of precisely hitting one stone against another, known as knapping. Stone toolmaking characterized the period sometimes referred to as the Stone Age, which began at least 2.5 million years ago in Africa and lasted until the development of metal tools within the last 10,000 years (at different times in different parts of the world). Although early humans may have made stone tools before 2.5 million years ago, toolmakers may not have returned often enough to one spot to leave clusters of tools that can be easily detected.

The earliest simple form of stone toolmaking involved breaking and shaping an angular rock by hitting it with a palm-sized round rock known as a hammerstone. Scientists refer to tools made in this way as Oldowan, after Olduvai Gorge in Tanzania, a site from which many such tools have come. The Oldowan tradition lasted for about 1 million years. Oldowan tools consist of larger stones with a sharp chopping edge, and small flakes that could be used to scrape and slice. Sometimes Oldowan toolmakers used anvil stones, flatter rocks sitting or placed on the ground, on which hard fruits or nuts could be broken open. Chimpanzees today, in fact, are known to use anvils for cracking nuts.

Because of the different shapes and flake scars on Oldowan stones, scientists once believed that the toolmaker (possibly *Homo habilis*) intentionally made different "tool types" (called chopper, scraper, and so on). If so, Homo habilis must have had a culture and language in order to teach how to make the different kinds of tools. But this idea led scientists to make new observations, which showed that the different tool types were not really distinct from one another. Instead, the original rocks had different shapes (like a rounded pebble or flattened slab), and these were then struck a different number of times by the toolmakers, without trying to create any particular shape. It's now thought that making sharp-edged rocks was the main goal of early stone flaking. Learning this skill certainly required observation but not necessarily instruction or language.

Oldowan toolmakers sought out the best stones for making tools and carried them over long distances to new locations. In at least some situations, the toolmakers also gained access to large animals and carried portions of the carcasses to these same locations, thus avoiding any predators that might return to a kill. At these toolmaking and food-processing sites, the toolmakers would further butcher carcasses and eat the meat and marrow. This behavior of bringing food and tools together contrasts with an eat-as-you-go strategy of feeding commonly seen in other primates.

The oldest stone tools were simple, used for cutting, bashing, and whittling. These activities allowed the toolmakers to reach new foods—to slice meat from an animal's body, to crack open a bone for the marrow, or to sharpen a stick for digging out an underground root or tuber.

The Acheulean toolmaking tradition, which began sometime between 1.7 million and 1.5 million years ago, consisted of increasingly more symmetrical tools, most of which scientists refer to as handaxes and cleavers. Acheulean toolmakers, such as *Homo erectus*, also worked with much larger pieces of stone than did Oldowan toolmakers. Acheulean tools show increased planning and design -- and thus probably increased mental capacities -- on part of the toolmakers. The Acheulean tradition continued for over 1.3 million years.

The next significant advances in stone toolmaking were made by at least 200,000 years ago. This new method of toolmaking is known as the Levallois or "prepared core technique". This technique involves a planned removal of flakes, which produced pieces of stone from which tools of a preformed shape and thickness could be made by further flaking. Tools made using this technique are known for their thinness and regular shape. The prepared core technique is thought to have signified a cultural change among early humans. The making of a preshaped flake involves considerable cognitive ability; the maker has to be able to imagine the end product and work from that mental concept.

Though early humans have been making blades for approximately 300,000 years, it was within the past 40,000 years that the most advanced blade toolmaking techniques came about. The technique involved removing a section of a stone, leaving a flat platform, and then breaking off multiple blades perpendicular to the striking platform. A blade is a flake that is at least twice as long as it is wide. Using these blades as blanks, people made exquisitely shaped spearheads, blades, and numerous other kinds of tools. The most advanced stone tools also exhibit distinct and consistent regional differences in style, indicating a high degree of cultural diversity.

Environmental Adaptation

Early humans experienced dramatic shifts in their environments over time. Fossilized plant pollen and animal bones, along with the chemistry of soils and sediments, reveal much about the environmental conditions to which humans adapted, often through cultural behavior.

Well before 8 million years ago, the continents of the world, which move over very long periods, had come to the positions they now occupy. But the crust of the Earth has continued to move since that time. These movements have dramatically altered landscapes around the world. Important geological changes that affected the course of human evolution include those in southern Asia that continued to raise the Himalayan mountain chain and the Tibetan Plateau, and those in eastern Africa that formed the Great Rift Valley. The formation of major mountain ranges and valleys led to changes in wind and rainfall patterns. In many areas dry seasons became more pronounced, and in Africa conditions became generally cooler and drier.

By 5 million years ago, the amount of fluctuation in global climate (between cool and warm, dry and wet environments) had increased. Temperature fluctuation became quite pronounced during the Pliocene Epoch (5 million to 1.6 million years ago). During this time, especially around 2.8 million years ago, the world entered a period of intense climate fluctuation, including periods of cooling called ice ages. Ice ages cycle through colder phases known as glacials (times when glaciers form) and warmer phases known as interglacials (during which glaciers melt). During the Pliocene, each glacial and interglacial cycle lasted about 40,000 years. Cycles of this length continued during the Pleistocene Epoch (1.6 million to 10,000 years ago), but a shift to much larger and longer ice age fluctuations, repeating about every 100,000 years, began about 900,000 years ago. The causes of these ice ages are complex but include changes in Earth's orbit around the sun. For example, our planet's distance from the sun changes over time, which leads to natural fluctuations in

Earth's warming. The pattern of change in ice-age climates during the Pleistocene matches the changes in Earth's orbit. And so these orbital changes are believed to be a major factor causing ice-age cooling and warming.

All of these changes -- dramatic shifts in the landscape, changing rainfall and drying patterns, and temperature fluctuations --posed challenges to the immediate and long-term survival of early human populations. Populations in different environments evolved different adaptations, one reason why more than one species existed at the same time during much of human evolution.

Some early human adaptations to new climates involved changes in physical (anatomical) form. For example, the physical adaptation of having a tall lean body, such as that of *H. ergaster*, would have dissipated heat very well. This adaptation probably helped the species to survive in the hotter, more open environments of Africa around 1.7 million years ago. Conversely, the short, wide bodies of the Neanderthals would have conserved heat, helping them to survive in the ice age climates of Europe and western Asia.

Early humans also adapted to their environments through their behavior. In the early australopiths, the combination of moving in the trees and on the ground probably helped them survive changes between wooded and open habitats. In later humans, stone toolmaking and carrying food over long distances increased the number of different foods they could eat, which helped the toolmakers survive unexpected shifts in their environment and food supply. The largest increases in brain size occurred over the past 700,000 years, a period during which global climates and environments fluctuated dramatically. Human adaptability, which was made possible in part by complex brain functions, and cultural evolution associated with this time period most likely reflected responses to the challenges of coping with unpredictable and changing surroundings.

Between 2 and 5 million years ago, Africa was a mixture of forests, woodlands, and grassy habitats. Significant drying in eastern Africa began to occur around 1.7 million years ago. So, the early australopiths and early *Homo* lived in relatively wooded places, while *H. erectus* (and *H. ergaster*) lived in more open areas of Africa. Very early humans lived in low-lying places, next to lakes and rivers, where dirt from higher ground was deposited.

With the spread beyond Africa, early human populations met many different environments, including colder temperatures in the Near East and bamboo forests in southeast Asia. By at least 1 million years ago, populations moved into the Temperate Zone of Europe and Asia, and they encountered very cold seasons of the year. Either populations migrated away from the colder regions each winter, or they sought shelters. Some of the earliest definitive evidence of cave dwellers dates from around 800,000 years ago at the site of Atapuerca in southern Spain. This site may have been home to early *H. heidelbergensis* populations, but *H. erectus* also used caves for shelter.

Eventually, early humans learned to control fire and to use it to create warmth, cook food, and protect themselves from other animals. The oldest known fire hearths date from between 450,000 and 300,000 years ago, at sites such as Bilzingsleben, Germany; VJrtessz`ll`s, Hungary; and Zhoukoudian (Chou-k'ou-tien), China. African sites as old as 1.2 million to 1.6 million years contain burned bones and reddened sediments, but many scientists find such evidence too ambiguous to prove that humans controlled fire. Early populations in Europe and Asia may also have worn animal hides for warmth during glacial periods. The oldest known bone needles, which indicate the development of sewing and tailored clothing, date from about 30,000 to 26,000 years ago.

Humans have also evolved cultural ways of adapting to their surroundings. Culture involves passing on socially learned (rather than genetic) information from one generation to the next, and in *Homo sapiens* it also involves the accumulation of many different kinds of social knowledge concerning food preferences, language expression, and complex rituals. Compared with earlier humans and other primates, our own species accumulates social knowledge very quickly, which leads separate groups to develop widely different social behaviors and beliefs. As a result, *H. sapiens* is characterized by many different ways of living (cultures). By 40,000 years ago, greater diversity and faster changes in stone technology and other activities can be seen in the archeological record compared with earlier times. And so some paleoanthropologists think that *H. sapiens* was the first species to evolve the ability to adapt culturally in complex ways, and that this ability was an advantage over earlier species that seemed to have been less prone to change and to diversify their ways of life.

Symbolic Thought, Language, Art, and Religion

The evolution of cultural behavior relates directly to the development of the human brain, and particularly the cerebral cortex, the part of the brain that allows abstract thought, beliefs, and expression through language. Humans have evolved a form of communication – language -- that involves the use of symbols (such as words), which are creatively joined together (in sentences) according to complex mental rules (grammar). It allows an almost unlimited ability to link symbols with complex meanings and thus to create complex thoughts. It also allows an ability to talk about past and future events, things that are not visible, and complex abstractions. There are many theories and debates about language evolution.

People can also paint abstract pictures or play pieces of music that evoke emotions or ideas, even though emotions and ideas have no form or sound. In addition, people can conceive of and believe in supernatural beings and powers -- abstract concepts that symbolize real-world events such as the creation of Earth and sky, the weather, and the healing of the sick. Thus, symbolic thought lies at the heart of three hallmarks of modern human culture: language, art, and religion.

Language

Language gives people many adaptive advantages, including the ability to plan for the future, to communicate the location of food or dangers to other members of a social group, and to tell stories that unify a group, such as mythologies and histories. However, words, sentences, and languages cannot be preserved like bones or tools, so the evolution of language is one of the most difficult topics to investigate through scientific study.

It appears that modern humans have an inborn instinct for language. Under normal conditions, it is almost impossible for a person not to develop language, and people everywhere go through the same stages of increasing language skill at about the same ages. While people are born with genetic information for developing language, they learn specific languages based on the cultures from which they come and the experiences they have in life.

The ability of humans to have language depends on the complex structure of the modern brain, which has many interconnected, specific areas dedicated to the development and control of language. Given the complexity of the modern brain, language and its benefits probably took a long time to evolve. Some chimpanzees and other apes have been taught to use symbols for simple communication. So, some scientists think that even the early australopiths had some ability to understand and use symbols. Nevertheless, it appears that language, art, and religious rituals became vital aspects of human life only within the past 100,000 years, primarily in our own species.

Art

Humans also express symbolic thought through many forms of art, including painting, sculpture, and music. The oldest known object of possible symbolic artistic value dates from about 250,000 years ago and comes from the site of Berekhat Ram, Israel. Scientists have interpreted this object, a figure carved into a small piece of volcanic rock, as a representation of the outline of a female body. Only a few other possible art objects are known from between 200,000 and 50,000 years ago. These items, from western Europe and usually attributed to Neanderthals, include two simple pendants -- a tooth and a bone with bored holes -- and several grooved or polished fragments of tooth and bone.

Sites dating from at least 400,000 years ago contain fragments of red and black pigment. Humans might have used these pigments to decorate bodes or perishable items, such as wooden tools or clothing of animal hides, but this evidence would not have survived to today. The use of pigments in symbolic activities became sophisticated only after 40,000 years ago; when we find carefully made crayons used in painting and evidence of pigment burning to create a range of colors.

The complex use of symbols and art started to become very common after 50,000 years ago. There was a tremendous blossoming of these behaviors in the archeological record between 30,000 and 15,000 years ago. During this period people adorned themselves with intricate jewelry of ivory, bone, and stone. They began to carve beautiful figurines, representing animals and human forms. Many carvings, sculptures, and paintings depict stylized images of the female body. Some scientists think such female figurines represent fertility.

Early wall paintings made sophisticated use of texture and color. The area of what is now southern France contains many famous sites of such paintings. These include the caves of Chauvet, which contain art over 30,000 years old, and Lascaux, in which paintings date from as much as 18,000 years ago. In some cases, artists painted on walls that can be reached only with special effort, such as by crawling. The act of getting to these paintings gives them a sense of mystery and ritual, as it must have to the people who originally viewed them, and archeologists refer to some of the most extraordinarily painted chambers as sanctuaries. Yet no one knows for sure what meanings these early paintings and engravings had for the people who made them.

Religion

Graves from Europe and western Asia indicate that the Neanderthals were the first humans to bury their dead. At some sites, the graves were shallow and may have been dug simply to remove corpses from sight. In other cases, rituals may have been involved. Some scientists have claimed that grave goods, such as meaty animal bones or flowers, had been placed with buried bodies, which would suggest that some Neanderthal groups might have believed in an afterlife. In a larger proportion of Neanderthal burials, the corpse had its legs and arms drawn in close to its chest, which could indicate a ritual burial position.

Other researchers have challenged these interpretations, however. They suggest that perhaps the Neanderthals had practical rather than religious reasons for putting objects in burials, or adorning and positioning dead bodies. For instance, a body manipulated into a fetal position would need only a small hole for burial, making the job of digging a grave easier. The animal bones and flower pollen near the corpses could have been deposited by natural forces.

Many scientists once thought that fossilized bones of cave bears (a now-extinct species of large bear) found in Neanderthal caves indicated that these people had what has been referred to as a cave bear cult, in which they worshiped the bears as powerful spirits. However, after careful study researchers concluded that the cave bears probably died while hibernating and that Neanderthals did not collect their bones or worship them. Considering current evidence, the case for religion among Neanderthals remains controversial

Domestication, Agriculture, and the Rise of Civilizations

There has been little biological change in Homo sapiens over the past 40,000 years -- in fact, probably as far back as the beginning of our species over 100,000 years ago. But the amount of cultural change, especially in technology and subsistence (how food is obtained), has been remarkable. One of the key cultural developments is the domestication of plants and animals, and the growth of farming (agriculture). Dozens of staple crops are grown today in the temperate and tropical regions. Almost the entire world's population depends, however, on just four major crops--wheat, rice, corn, and potatoes. The growth of farming and care of herd animals (pastoralism) began one of the most remarkable changes in Earth's ecology. The change began just 10,000 years ago and has been very rapid. During this period, many of the plants and animals over large areas have come under human control. The overall number of plant and animal species has decreased, replaced by the few needed to support large human populations. In the areas dominated by people, the interaction among plants and animals is usually controlled by a single species, our own. These environments are very different from earlier ones, in which the food chain was much more complex and many different plants and animals interacted.

The transition to agriculture, starting around 10,000 years ago, took place in several regions of the world. By this time, the cool, ice-age landscapes of 18,000 years ago had given way to warmer, wetter environments. People adapted to these changes by making more intensive use of the landscape. At first they took advantage of a broad range of plants and animals within each region, but later focused on certain wild plants and animals. Among the plants they exploited were cereal grains in western Asia and maize (corn as one variety) in Central America. By carefully collecting plants and controlling wild herd animals, people could select desirable characteristics in the food species they favored. This process of selection, protection, and controlled breeding eventually created new forms of life (such as sheep, cattle, pigs, and new species of wheat, corn and other plants) and useful products (such as milk, hides, and wool). Agriculture greatly increased the food supply, which encouraged population growth and settlement. Seeds, tubers, and livestock could be stored for long periods, an impossible achievement for hunting-and-gathering people.

Effects of Food Production on Human Society

By creating a readily available supply of plant foods, meat and milk, people were given some long-term food security. In contrast, the foraging lifestyle of earlier human populations never provided them with a significant store of food. With increased food supplies, agricultural peoples could settle into villages and have more children. The new reliance on agriculture and change to settled village life also had some negative effects. The average diet became more susceptible to diseases brought on by a lack of certain nutrients. A settled lifestyle also increased contact among people and between people and their refuse and waste matter, both of which acted to increase the incidence and transmission of disease.

People responded to the increasing population density -- and a resulting overuse of farming and grazing lands -- in several ways. Some people moved to settle entirely new regions. Others devised ways of producing food in larger quantities and more quickly. The simplest way was to expand to new fields for planting and new pastures to support growing herds of livestock. Many populations also developed systems of irrigation and fertilization that allowed them to reuse cropland and to produce greater amounts of food on existing fields.

The Rise of Civilizations

The rise of civilizations -- the large and complex types of societies in which most people live today -- developed along with surplus food production. People of high status eventually used food surpluses as a way to pay for labor and to create alliances among groups, often against other groups. In this way, large villages could grow into city-states (urban centers that governed themselves) and eventually empires covering vast territories. With surplus food production, many people could work exclusively in political, religious, or military positions; in artistic and various skilled vocations; or as menial laborers or subjugated as slaves. All civilizations developed on the basis of such hierarchical divisions of status and vocation.

The earliest civilization arose over 7,000 years ago in Sumer in what is now Iraq. Sumer grew powerful and prosperous by 5,000 years ago, when it centered on the city-state of Ur. The region containing Sumer, known as Mesopotamia, was the same area in which people had first domesticated animals and plants. Other centers of early civilizations included the Nile Valley of Northeast Africa, the Indus Valley of South Asia, the Yellow River Valley of East Asia, the valleys of Oaxaca and Mexico and the Yucatn region of Central America and the Andean South America.

With the rise of civilizations, human evolution entered a vastly different phase. Before this time, humans had lived in small, family-centered groups essentially exposed to and controlled by forces of nature. Only a few thousand years after the rise of the first civilizations, most people now live in societies of millions of unrelated people, all separated from the natural environment by houses, buildings, automobiles, and numerous other inventions and technologies. Culture will continue to evolve quickly and in unforeseen directions, and these changes will, in turn, influence the physical evolution of *Homo sapiens* and any other human species to come.

http://www.mnh.si.edu/anthro/humanorigins/faq/Encarta/encarta.htm