Research TOC

Australopithecus afarensis and Human Evolution

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The two-day drive from Addis Ababa, the capital of Ethiopia, to our field site near the Awash River had left me dusty and tired. The second day began well enough. Just after dawn we reached the western rim of the East African rift. The view from the edge of this massive rip in the earth is extraordinary. At the bottom, two thousand meters below, the barren badlands of the Afar depression stretch away into the haze.

It is difficult to work in the Afar depression. Because the sun always shines in the Ethiopian rift, it can get hot—very hot. Except for the sluggish Awash River, there are no permanent sources of water. We get our water from shallow wells dug in the dry river beds. Despite purification, the drinking water is usually cloudy. Unappealing, but in this treeless desert the tepid dun-colored water is refreshing. Despite these difficulties, we return to this part of the Ethiopian desert year after year because these arid deposits contain fossilized animal bones that provide direct evidence of terrestrial faunal evolution during the Pliocene (5.2 to 1.8 million years ago [mya]) and Pleistocene (1.8 mya to 10,000 ya) epochs. Entombed in the ancient clays, sands, and gravels of the Afar depression are the fossilized bones of innumerable animals. Many hours are spent each day walking across the sediments, examining the thousands of bones and teeth of extinct animals that litter the surface. The dusty landscape and glaring sunlight quickly cause a permanent squint and a bad attitude. After each long day of searching, every new fossil has to be examined and its location carefully recorded. Although most fossils are from long-extinct antelopes, elephants, pigs, monkeys, hippos, and crocodiles, the next one could be an early human ancestor. Finding an ancient hominid fossil produces immediate euphoria. The heat, frustration, bone-jarring rides, and sore feet are all instantly forgotten. Without delay, the sight of a possible human ancestor causes everyone to drop to the searingly hot ground and begin crawling around looking for more. Each little piece of fossilized bone is a rare and important link to the past—a clue that can help answer fundamental questions about our own biological evolution.

Our Family: Apes, Hominids, and Humans

The living African apes, which include humans, chimpanzees, and gorillas, are part of a common evolutionary radiation that began in the Miocene (23.5 to 5.2 mya) epoch. Hominids are upright walking, or bipedal,[1] apes that include humans and our extinct relatives. Anatomically and behaviorally, humans (*Homo sapiens*), chimpanzees (*Pan troglodytes* and *Pan paniscus*), and gorillas (*Gorilla gorilla*) share many common features, such as the absence of an external tail, a conical trunk with shoulder joints that face sideways, absolutely and relatively massive brains allowing greater behavioral complexity and plasticity, prolonged periods of development (including gestation, infancy, adolescence), and single births that are infrequent. If we compare the biochemistry of the different ape species, the similarities among them are even more striking. Modern humans and common chimpanzees, our closest relatives, share approximately 98.5 percent of their nonrepeating DNA (DeoxyriboNucleic Acid).

Even a cursory examination reveals marked morphological differences between humans and the other African apes. Modern humans are large-brained, erect-walking, small-toothed, tool-using apes. Our hair is less pronounced (although no less dense) and we communicate via symbolically-based talking and gesturing. African apes have smaller brains and larger canine teeth, are well adapted to tree climbing, and are limited in distribution to the forests and woodlands of equatorial Africa. These differences raise some extremely interesting questions. First, when did the human lineage arise, and second, when and in what sequence did the unique specializations found in modern humans occur?

Researchers use biochemical and anatomical data to answer these questions. Biochemists can study and compare the chemical composition (especially DNA) of living species. Anatomists can examine and compare the shape, function, and development of anatomical structures (bones, teeth, muscles, etc.) in living and extinct animals. Using these two approaches, we can estimate the time when two species separated and reconstruct their evolutionary history.

Despite their morphological and behavioral differences, all modern apes (which include humans) are derived from a common ancestral species, or gene pool. In other words, a now extinct species existed from which the living African apes and humans both descended. Following the separation of these chimpanzee and human lineages, each species continued to evolve and adapt to its environment. Although many of the anatomical differences that distinguish these lineages (including bipedal walking and larger brains in humans) are products of natural selection, other genetic changes have accumulated that have no apparent anatomical counterpart.

Such spontaneous changes are due to silent mutations in the DNA of both lineages. Biochemists can measure the chemical difference between species produced by such mutations. The closer the biochemical similarity between different lineages, the more recent their shared common ancestor. If we measure the degree of biochemical difference produced by mutations in the DNA between species and combine it with an estimate of the mutation rate, the time of the speciation event can be calculated. Current research suggests that hominids became a genetically distinct lineage separated from other African apes approximately five to eight mya.

Explaining why morphological changes occurred in the human lineage seems more interesting to me. Anatomical changes are not random. Bipedalism is not a historical accident. Large brains didn't just happen. These adaptations are the products of natural selection. This means that individuals who displayed brain enlargement or bipedal walking produced more offspring who survived to maturity than individuals who did not. Adaptations can allow individuals to obtain food more successfully, reduce risk from predation, gain and maintain reproductive opportunities, or somehow enhance the survivorship of their offspring. Ultimately, these anatomical changes are always an adaptive response resulting in the production of more babies that survive to adulthood.

Finding Our Ancestors: Hominid Paleontology in Africa

Primitive Hominids from South Africa

To understand changes in functional anatomy, we must learn in which order these anatomical modifications occurred and understand their ecological context. The only way paleoanthropologists can reconstruct the timing and sequence of morphological change in hominids is by analysis of the fossil record. The first primitive hominid fossil was reported by Raymond Dart in 1925.[2] A juvenile skull with associated endocast[3] was recovered from the Taung lime mine in South Africa. The Taung skull, now known to be over two million years old, allowed Dart to define a new primitive hominid genus and species named *Australopithecus africanus*.[4] Although the phylogenetic position of this small-brained, erect-walking hominid as a human relative was vigorously debated, fossil discoveries from the South African cave sites of Sterkfontein and Makapansgat during the next three decades vindicated Dart and proved the validity of the species *A. africanus*. Meanwhile, Robert Broom was discovering fossils of a different hominid species from the South African limestone cave sites of Swartkrans and Kromdraai. Unlike *A. africanus*, this new collection of fossils had larger molar and premolar teeth, smaller canines and incisors,[5] a flatter or less projecting face, and a longitudinal ridge of bone along the top of the skull known as a sagittal crest.[6] Clearly these fossils represented a species different from *A. africanus*. Although they were initially attributed to several different species, they are now included within a single taxon, *Australopithecus robustus* (although some anthropologists contend that these fossils should be named *Paranthropus robustus*). Whatever these extinct species are called, they existed during the late Pliocene and early Pleistocene in South Africa with *A. africanus* (2.8 to 2.2 mya), living earlier than and perhaps giving rise to *A. robustus* (1.8 to 1.0 mya). Anatomically, both species were small-brained (420cc to 550cc, which is slightly larger than the brain of a living chimpanzee or gorilla, but only about 40 percent the size of the brain of a modern human), and their molar and premolar teeth were unlike those of both modern humans and apes. For their body size, these species had very large postcanine teeth covered by thick enamel caps. Like the teeth of modern humans, the australopithecine canine teeth were small and very different from the large projecting canines of the other apes. Analysis of their fossilized pelves, lower limbs, and vertebrae demonstrate that both species walked upright on two legs, as do modern humans. Phylogenetically, *A. robustus* is our cousin. They apparently diverged from the lineage that includes modern humans sometime before two mya. Their unique and specialized cranial and dental anatomy makes them an unlikely human ancestor. This evolutionary experiment among hominids became extinct about one million years ago.[7]

The Hominids of East Africa

In 1959 Mary and Louis Leakey discovered a remarkable hominid fossil from early Pleistocene lake margin deposits at Olduvai Gorge in Tanzania.[8] The cranium, known as OH 5 (Olduvai

Hominid specimen #5) and dated to approximately 1.8 mya, is now attributed to the species *Australopithecus boisei* (or *Paranthropus boisei*). This specimen and others recovered from Olduvai Gorge, Peninj in Tanzania and around Lake Turkana in Kenya and Ethiopia are best described as extreme versions of the South African *A. robustus*. Similar to the southern species, *A. boisei* had a small brain, a sagittal crest, a flattened face, and large postcanine and small anterior teeth. However, the sagittal crest and molar teeth were larger than, and the canines and incisors were smaller than, those of their South African contemporaries. At approximately the same time (1.8 to 1.0 mya), the two large-toothed, flat-faced species lived thousands of miles apart yet shared many similar adaptations in their skulls and teeth.

In the early 1960s the Leakeys found other early Pleistocene hominid fossils at Olduvai Gorge that were unlike the large-toothed, crested *A. boisei*. Instead, these fossils had smaller molars and premolars and larger brains (greater than six hundred cc). Here was the first good evidence in East Africa of two very different hominid species living at the same place and time. But what was this other, more gracile hominid? Louis Leakey, along with South African anatomist Phillip Tobias and British anatomist John Napier, concluded that these fossils should be attributed to a new species, which they named *Homo habilis*, and which they suggested was ancestral to modern humans.[9] Here was the oldest evidence of the genus *Homo* and it coexisted with the larger-toothed robust australopithecines. Despite these differences, however, both were hominids, meaning they must have shared a unique common ancestor since their ancestral lineages separated from the African apes.

But what was the common stem hominid from which all subsequent hominids are derived? The only other possible candidate known was *A. africanus*. It had the advantage of being older than both of the East African lineages and it appeared to have a more generalized morphology from which both could arise. However, two problems prevented universal acceptance of *A. africanus* as the last common ancestor (LCA) of all subsequent hominids. First, paleoanthropologists were divided on the phyletic position of *A. africanus*. Some proposed that it was ancestral only to the genus *Homo*, whereas others contended that it was uniquely related to the robust australopithecines. Second, no older (>2.2 mya) fossil material had been recovered from East Africa that could unequivocally be assigned to *A. africanus*. Where was the East African hominid LCA?

Hominid Paleontology in Ethiopia: Omo and Hadar

One group that worked to resolve this problem was the Omo Research Expedition. This international cooperative effort, led by the American Clark Howell, Camille Arambourg and Yves Coppens of France, and Kenyan Richard Leakey, collected many hominid fossils from the four to one myo (million-year-old) sedimentary deposits along the Omo River in southern Ethiopia.[10] In deposits more recent than 2.5 million years of age, at least two hominid lineages were present, and these were a larger-brained *Homo* and a large-molared robust australopithecine. But in sediments older than 2.5 million years, only one type of hominid was identified. The older sediments (>2.5 mya) from the Usno and Shungura Formations at Omo yielded dozens of isolated hominid teeth but few other skeletal elements. Although these dental remains bore similarities to *Australopithecus africanus*, the unspecialized, primitive nature of these new fossils suggested to Howell and Coppens that the specimens may belong to a new species, perhaps ancestral to all later hominids.[11] Unfortunately, the fragmentary condition of the fossils prevented resolution of the problem.

In the late 1960s Maurice Taieb, a French geologist conducting research for his dissertation on the geologic history of the Awash River in the Ethiopian rift, mapped and surveyed a large basin in the north central portion of the country known as the Afar depression. This area, among the hottest and driest on earth, is a large (~two hundred thousand km^2 or ~seventy-eight thousand mi^2) triangular region where three rifting systems intersect. Three large land masses (East Africa, Africa, and Saudi Arabia) have been slowly moving away from one another for the last twenty or so million years, and the point from which they are diverging is the Afar triangle. It is a low area extending from 700 m above sea level to about 120 m below sea level. During his geological survey, Taieb noticed that in places the ground was extensively littered with fossils. Subsequently, he was introduced to Donald C. Johanson, who agreed to assist in a reconnaissance survey to evaluate the potential of the area for hominid fossils. In 1972 they explored an area along the Awash River known as Hadar. It was a hominid paleontologist's dream. There were expansive, fossiliferous deposits dated to the crucial period of 2.8 and 3.4 mya. The fossils were entombed in sands and clays deposited by the streams, rivers, and lakes present in the Ethiopian rift during the middle Pliocene.[12] This continuous deposition built a layer-cake of sediments, retaining a record of the plants and animals that lived and died along those wooded lake, swamp, and river margins.

Equally significant to our understanding of the fossils is their geologic context. The East African rift system is volcanically active. Fallout from the many volcanic eruptions becomes incorporated into the sediments. If the eruptions are large, they can form distinct layers in the sediments, known as tuffs. Such tuffs have a characteristic chemical "signature" and also contain unstable (radioactive) isotopes. The unique chemical composition of the tuffs allows geologists to match tuff layers from widely separated localities. Tuffs with the same elemental makeup must have been produced from the same eruption; therefore, the sediments surrounding them must be of similar age. If the crystals in the tuffs have not been too badly weathered, geochemists can estimate their age based on the geochemistry of isotope decay. Isotopes are elemental variants that can decay from an unstable state to a stable state at a known and constant rate. Therefore, the amount of the daughter product (the result of the decay process) depends on the age of the sample. The older the crystals, the greater the accumulation of the stable daughter isotopes. By measuring the ratio of parent to daughter elements, the age of the crystals can be calculated quite accurately.

Hadar, Laetoli, and the Discovery of *Australopithecus afarensis*

Following the initial survey of the area, Johanson and Taieb, now joined by Yves Coppens and Jon Kalb, formed the IARE (International Afar Research Expedition) and initiated a long-term multidisciplinary research project focusing on the middle Pliocene deposits at Hadar. The group was very lucky. They soon discovered the oldest hominid species, *Australopithecus afarensis*. Hadar is a rich paleontological locality, and their collections of hominid fossils were extraordinary, forcing anthropologists to rethink early hominid evolution. Remarkable hominid fossils were found in each of the first three field seasons (1973–1975). In 1973 they found a hominid knee joint. Despite its great antiquity and extremely

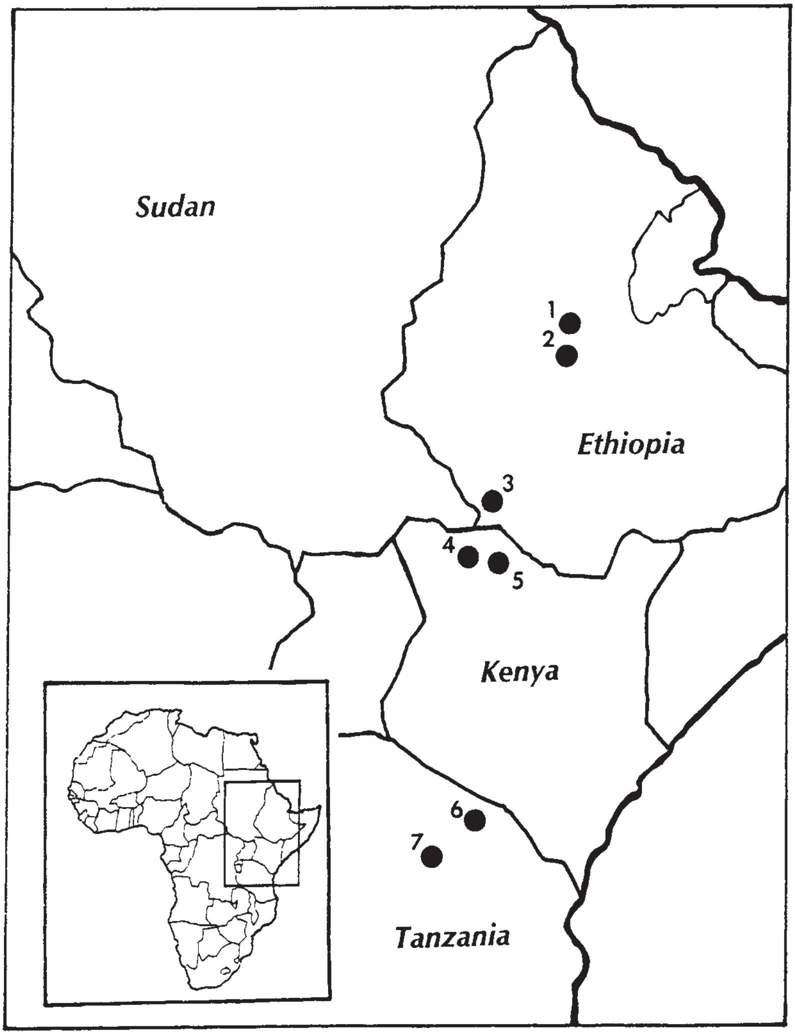

Figure 1
Location of Sites Discussed in Text
1 = Hadar; 2 = Middle Awash; 3 = Omo; 4 = East Rudolf;
5 = West Turkana; 6 = Olduvai Gorge; 7 = Laetoli

small size (smaller than that of a modern human), its bony anatomy clearly showed that it was fully adapted to bipedal walking.

During the 1974 field season at Hadar, Johanson and field assistant Tom Gray discovered what is one of the most extraordinary specimens ever found in hominid paleontology. We know the fossil as "Lucy" (named after the Beatles song "Lucy in the Sky with Diamonds"); more formally, it is known as specimen AL 288-1.[13] This number means that Lucy was the first fossil found at the 288th fossiliferous outcrop discovered in the Afar Locality (Hadar). Although other beautifully preserved hominid fossils were also found that year, the quality of Lucy overshadowed the rest. Most fossils are small, battered fragments of teeth and mandibles, with each fragment generally from a separate individual. In contrast, about 40 percent of Lucy's skeleton was found, including her left os coxa (hip bone); sacrum; left femur; portions of her lower leg and foot, including the three bones that comprise the ankle joint; some vertebral fragments; upper limb elements, including portions of the scapula, clavicle, right and left humeri, ulnae, and radii; and some hand bones. Although only a few parts of her cranium were recovered, the associated mandible (jaw bone) was nearly complete. Lucy is an important fossil because her completeness allows anthropologists to study the relationships between the size and shape of structures within a single individual. We can now estimate stature, study the functional anatomy of joints (hip, knee, ankle, shoulder, elbow, wrist), and calculate limb proportions from this 3.2 myo hominid.

In 1975 Hadar revealed its greatest treasure. Site 333, a thin clay deposit, contained over 130 hominid fossils representing at least 13 individuals. The collection includes the remains of very young to very old individuals, and it also spans a broad range of adult size from small (Lucy-sized) to large. Now we could study growth, development, and populational variation in this extinct species.

In all, the five field seasons at Hadar produced more than 250 hominid fossils representing dozens of different individuals sampling a period between 3.0 and 3.4 mya. The upright walking species at Hadar is characterized by a small brain volume (300 to 450cc), canine teeth larger than those of all other hominids but markedly smaller than those of any living ape, and a body mass between 25 and 55 kilograms (55 to 125 pounds). The Pliocene habitat at Hadar showed that these early human ancestors lived in a diverse environment that varied from open to closed woodlands near a permanent source of water.

But Hadar was not the only middle Pliocene site yielding

Figure 2
"Lucy" (AL 288-1)
Hadar, 1974. Cleveland Museum of Natural History.

hominid fossils. At the same time, Mary Leakey and colleagues were collecting hominid fossils from the 3.6 myo sediments at Laetoli in northern Tanzania. Laetoli was first surveyed in the mid-1930s by Mary and Louis Leakey and later collected by L. Kohl-Larsen. Although primitive hominid fossils were recovered during this preliminary work, they were either ignored or misidentified. Research began anew at Laetoli in the mid- through late-1970s, and approximately two dozen hominid specimens were recovered from sediments deposited in an arid upland savanna environment. The collection of primitive hominid fossils includes portions of a juvenile mandible (LH 2 [LH-Laetoli Hominid specimen #2]), an adult mandible (LH 4), and an incomplete and fragmentary juvenile skeleton (LH 21).[14]

Are the fossil collections of Laetoli and Hadar related? Fortunately, one of Mary Leakey's assistants at Laetoli was paleoanthropologist Tim White. Because of his intimate familiarity with the Laetoli hominids, when shown the Hadar fossils White recognized that the Laetoli and Hadar hominids, although separated by approximately 300,000 years and 1,500 kilometers (1,000 miles), represented the same species. Johanson, who earlier suggested that the Hadar material represented two species,[15] was soon convinced that both sites sampled a single hominid species. Following their analysis of the material from Hadar and a comparison with other early hominid fossils, Johanson, White, and Coppens announced in 1978 that these fossils represented a new hominid species named *Australopithecus afarensis*.[16] Not only was *A. afarensis* the earliest hominid species yet discovered, but also they concluded that it was ancestral to all other hominid species, including the other australopithecines (*A. africanus*, *A. robustus*, and *A. boisei*) and the *Homo* lineage. This simple conclusion has immense taxonomic and phylogenetic implications that continue to provoke intense debate (summarized in note 7).

ANALYSIS AND INTERPRETATION

Taxonomy and phylogeny aside, what did these early hominids do? What information about the biology of this extinct species can the fossils from Hadar and Laetoli tell us? What did they eat? Can their reproductive and social behaviors be reconstructed?

Although paleoanthropologists address these and other questions, we will focus on just two. First, do the fossil remains from Hadar and Laetoli represent only a single species? After all, at many other sites, multiple hominid taxa are present. Second, how did Lucy and her conspecifics walk?

Morphological Variation: How Many Species at Hadar?

Let's start with the number of species represented by the fossils from Hadar and Laetoli. Although Johanson and White concluded that these materials represent a single species, other researchers suggested that the amount of morphological variation found in this collection was too great for a single species and that the Hadar and Laetoli fossils sample two or more contemporaneous hominid species. How can we resolve this problem? First, we must learn why variation is a necessary prerequisite of evolution. Second, we have to be familiar with the factors that contribute to the amount of variation in living and fossil ape species.

Variety in form and behavior is a crucial element of evolution. We live with anatomical variation every day. How else do we distinguish among people? When I teach human anatomy to medical students, every group complains during dissection that the muscles, arteries, and nerves in their cadaver look different from the pictures and descriptions in anatomy texts. Why? Because no two humans are morphologically identical. We are all variations on a common theme. All humans have the same bones, muscles, nerves, organs, and so forth, but their size, shape, and relationships differ. Most variation is a natural consequence of sexually reproducing organisms. Without variation, evolution by natural selection could not occur. Because no two individuals are behaviorally or anatomically identical, not all individuals are equally adapted to their environment. Some will have a slight edge. This advantage allows them to produce more offspring who survive to maturity. What initially was a rare or uncommon anatomical advantage may, over time, become prevalent in a species. This is evolution by natural selection. Not all diversity, however, affects our fitness, and some variation may be selectively neutral. Other factors contribute to the amount of variation in a population—age composition of the sample, for instance. Obviously, you look different today than when you were a child or than you will in twenty years. A fossil collection sampling a diversity of ages will appear heterogeneous.

Sex differences in morphology (sexual dimorphism) are another source of variation. Male and female humans do not look the same. Although the sexes differ in their primary reproductive roles and this is reflected in our reproductive anatomy, sexual dimorphism generally describes those anatomical differences associated with gaining access to and retaining a mate. In African apes (including hominids), males are generally larger than females. Male gorillas can weigh twice as much (or more) than a female. Male gorillas also look different from females. As the males mature, the normally black hair on their backs becomes gray or silver colored. This does not occur in females. Males also have much larger canine teeth than do females, and develop sagittal crests. Chimpanzee males are approximately the same stature as females but they weigh about 15 percent more. Except for this difference in muscle mass and noticeably larger canine teeth, male and female chimps look pretty much the same. Humans are very sexually dimorphic. Human males are taller, weigh more, and have a different distribution of fat and hair than do females. From available fossil evidence it appears that australopithecine males also were larger than females, to a greater degree than modern humans. Therefore, when estimating size variation from fossils, researchers must consider age variation, sexual dimorphism, and natural variety as contributing factors to the morphological heterogeneity in *Australopithecus afarensis*.

As informative as one fossil can be, numerous anatomical specimens are necessary to understand the scope of normal biological variation. In paleontological studies the fossil evidence for extinct animals is usually fragmentary. It cannot provide a complete picture of the biology and behavior of the long dead animals. In historical studies we must begin with what can be observed directly and only then extrapolate to the unknown. Therefore, anthropologists must be familiar with anatomy and its variation in humans and African apes. Fortunately, Don Johanson served as curator of the Laboratory of Physical Anthropology at the Cleveland Museum of Natural History (CMNH) in Cleveland, Ohio, when he addressed the species question at Hadar. The CMNH houses the Hamann-Todd osteological collection, which contains over three thousand well-documented (age, sex, cause of death, race) human skeletons and the largest collection of chimpanzee and gorilla skeletons in the world. These extensive collections provide direct evidence of the normal range of variation in living species.

Johanson and White, with their extensive experience in human and ape musculoskeletal variation, were well aware of the amount of normal variation that could be found in temporally diverse anatomical collections. The *A. afarensis* fossils represent a population of individuals that spanned more than six hundred thousand years in an ecologically dynamic habitat. Considering the above discussion, it is not unexpected that the Hadar and Laetoli fossils, although belonging to a single species, were not morphologically homogeneous.[17]

The first time I saw the Hadar fossils at the Ethiopian National Museum in Addis Ababa, I was impressed by the great range of size and shape of the specimens. Lucy's femur is much smaller than the largest femur from Hadar. Is this too much variation for a single species? First impressions suggest it is, but scientists must always question their initial assessments. Lucy is the centerpiece of the collection. Because of her completeness, she figures prominently in any comparison. However, with a height of only 1.1 meters, she is one of the smallest hominids ever discovered. Therefore, any comparison involving Lucy must take her short stature into account. The large proximal femur (AL 333-3) is also well preserved and is among the largest individuals from Hadar. It is natural to pick up the best preserved fossils to make a comparison (i.e., Lucy and AL 333-3), while ignoring the other more fragmentary, banged-up fossils. Quite simply, our natural bias toward the nicest specimens from Hadar causes us to compare the extremes in size. Any comparison that involves the largest and smallest individuals will necessarily overestimate the degree of size variation in a species. However, when all of the proximal femora from Hadar are examined, a continuum of small to large is seen with the best preserved specimens at the extremes. Independent analyses estimating sexual dimorphism by Owen Lovejoy and his colleagues and Henry McHenry[18] concluded that skeletal sexual dimorphism at Hadar only slightly exceeded that seen in modern humans. The early australopithecines were more dimorphic than chimpanzees and humans but much less so than modern gorillas and orangutans.

How Did "Lucy" Walk?

Considerable debate surrounds the manner in which *A. afarensis* moved around. Quite simply, did they walk upright on two legs like modern humans or was their locomotor pattern unlike any living species? Fortunately, we can reconstruct with some accuracy the locomotor behavior of this extinct species from their fossilized bones. Some authors suggest that the collection of fossils attributed to *A. afarensis* may represent the missing locomotor link between modern African apes and humans. Randy Susman, Jack Stern, and Bill Jungers (all of the State University of New York at Stony Brook) proposed that Lucy was anatomically adapted to both arboreal quadrupedality and terrestrial bipedality.[19] They suggest that the bipedal locomotion of *A. afarensis* was not like modern humans; Lucy and her type walked about with bent hips and knees. Not only is this an energetically expensive and uncomfortable way to get around (try it for a couple of minutes), but also it is inconsistent with the available fossil evidence. Although *A. afarensis* looked like a chimpanzee with small canines above the neck, below the neck the locomotor anatomy had evolved away from the primitive quadrupedal condition toward human-like bipedal function.[20] This species may be phyletically intermediate between humans and the ape/human LCA, but, like modern humans, it was fully adapted to terrestrial bipedality.

How do chimpanzees move around? Modern apes are among the largest arboreal animals alive today. They spend much time climbing in the canopies of trees as they feed or escape from enemies. Clearly, climbing is a major component of their daily activities and this is reflected in their anatomy. Although male gorillas rarely climb trees, they do, nevertheless, maintain the essential climbing adaptation seen in smaller apes. As you can imagine, a fall from a tree by so large an animal has severe consequences. Because even one fall can kill a large animal, selection has favored those who minimize the risk of falling by enhancing their anatomical adaptations to climbing. They display multiple anatomical specializations for climbing, reaching, and grasping. While moving about on the ground, chimps and gorillas use a unique quadrupedal locomotor style, known as knuckle-walking. When knuckle-walking, chimps and gorillas support themselves by resting their weight on the backs of their fingers. In the wild, they only infrequently walk bipedally on the ground. Apes are capable of this behavior (watch a trained chimpanzee at the circus), but it is energetically expensive for them. They do not demonstrate any anatomical adaptations to this method of progression.

What are the anatomical specializations that allow these large mammals to climb about in the trees? If we focus on the pelvis and the lower limbs in apes, we can identify several major and important morphological adaptations to arboreality, including an elongated ilium (a part of the hip bone), a stiff, inflexible trunk, a medially directed ankle joint, a mobile and abducted great toe, a flexible mid-tarsal joint in the foot, and absence of a bicondylar angle of the knee. Together, these anatomical specializations allow a large-bodied primate to climb into the highest portions of the canopy and traverse along the canopy in adjacent trees.

Many different aspects of the musculoskeletal system must be altered to evolve a terrestrial biped from an arboreal quadruped. Owen Lovejoy of Kent State University in Ohio has devoted much time to documenting these changes.[21] Bipeds, unlike quadrupeds, must support themselves on a single leg at some point during each gait cycle. To accommodate this functional shift, the musculoskeletal anatomy of the lower limb and hip must change. The human pelvis has a much shorter and laterally directed ilium. This changes the functional relationship of the gluteal musculature (muscles acting across the hip joint) and alters their role from that of extensors or thigh straighteners (as seen in other primates and quadrupeds) to that of trunk supporters or thigh abductors. Similar modifications are seen in the pelves of Lucy and in *A. africanus*. As Lovejoy and his colleagues—Jim Ohman of Johns Hopkins University and Bruce Latimer of the Cleveland Museum of Natural History (CMNH)—have noted, evidence of this muscular shift can be identified not only in the shape and external morphology of the hip and thigh bones but also in the internal bony organization of the femoral neck. Bone is a dynamic tissue that remodels (adds or removes bone, which modifies its internal or external shape) according to the direction and magnitude of the mechanical forces acting on it. Because of differences in mode of locomotion and orientation of their locomotor muscles, the way in which humans and apes transmit forces across their hip joint differs. Consequently, their bony anatomy differs as well. The morphology of the internal bony structure and external surface topography in the proximal thigh bones of *A. afarensis* is similar to that of humans, thus suggesting that the extinct species walked bipedally like humans.

The knee of a striding biped is placed under the center of mass to support the body when walking. If you look at a standing person, you will notice that his or her hips are wider than his or her knees. Humans are knock-kneed. In contrast, the knee in quadrupeds is located directly beneath the hip joint. To verify this for yourself, notice that the thighs of a dog, cow, or gorilla, when seen from the front, are perpendicular to the ground. This angulation of the thigh in bipeds, known as the bicondylar angle, is a product of modifications in the distal end of the femur or thigh bone. Apes do not have this characteristic feature but, like all hominids, *A. afarensis* does.

The biped's foot is very different from that of a climbing ape. Bruce Latimer of the CMNH has carefully identified the many anatomical differences between apes and humans.[22] The ape foot is a grasping organ, more like our hands. In humans, the foot is best described as a propulsive lever. In apes, the big toe (hallux) is very mobile and abductable. This means that it diverges from the other toes and is not parallel to the remaining toes as in humans. Their hallux can be used for gripping and holding. To facilitate this grasping function, apes also maintain a greater amount of mobility between the ankle bones (mid-tarsal joint).

Humans propel themselves during bipedal walking by pushing against the ground. The foot, acting as a propulsive structure, is relatively rigid. This rigidity is maintained by the shapes of the tarsal (ankle) and metatarsal (foot) bones, ligaments, and muscles of the foot. When humans walk, they push off with the hallux. Apes, with the divergent, or thumb-like, position of their great toe, cannot transmit the propulsive force of walking in the same fashion as humans. Consequently, the bones of the big toe in humans, unlike those of chimpanzees but similar to those of *A. afarensis*, are large and robust. Therefore, the morphology of the bones of the foot is characteristic of and can be used to reconstruct the way animals walk. In each instance in which the function of the foot fossils from Hadar could be assessed, Latimer showed that *A. afarensis* used its foot as a propulsive lever, like humans, and not as a grasping structure like chimpanzees and gorillas.

Most quadrupedal animals use the hindlimb for propulsion or acceleration and the front limb for maneuvering and as a shock absorber. Bipeds must employ the hindlimb for all these functions. Not only must the hindlimb propel and support the body (as discussed earlier), but also the foot and leg must be adapted to absorb the repeated impacts of the foot striking the ground. Again, the anatomy reflects the function. Unlike apes, who have flat feet, humans have arched feet. Thus, not all of the sole of the foot contacts the ground during walking. This arch is maintained by both the shapes of the bones and the surrounding soft tissues. When humans walk, the arch deforms or straightens slightly. The deformations of the arches act like the shock absorbing springs in a car. They prevent the sudden jarring at impact that would ultimately lead to the deterioration of the joints and ligaments of the feet. That is why individuals with flat feet (less-developed or absent foot arches) were routinely rejected from military service. Flat-footed soldiers would soon develop painful and injured feet from the many long marches. In addition, humans and australopithecines, unlike other apes, have modified the shape and distribution of bone in their calcaneus (heel bones) to help dissipate the repeated shock of striking the ground during walking, thus preventing joint degeneration. Overall, the foot bones of *A. afarensis* show clearly that they had an arched foot, an adducted hallux, a less mobile midtarsal joint, and a human-like heel bone. The anatomy of the early hominid fossils demonstrates that *A. afarensis* walked bipedally.

But other data reinforce the anatomical conclusions. The site of Laetoli in Tanzania is famous for preserving a very rare and unusual fossil. Although an important series of fossilized bones was recovered there, the sediments include a 3.6-myo-volcanic tuff, which contains a series of footprint trails.[23] The ash from a volcanic eruption blanketed the savanna 3.6 million years ago, and many different animals walked, slithered, hopped, crawled, or ran across the ancient landscape that day and left their marks in the freshly deposited ash. The rain-moistened layer hardened and was soon covered by materials from another volcanic eruption, thus preserving the footprints. Unlike fossil bone collections that represent remains sampled over a very long period, these footprints represent a snapshot of just a few minutes of time. Significantly for anthropologists, three hominids, one larger and two smaller individuals, were walking across the savanna that day 3.6 mya. Interestingly, one of the smaller trails parallels the larger individual while the other small-footed individual carefully walked in the impressions left by the larger australopithecine. Does this represent a male and female walking side by side with their child following behind? Obviously, we can never know. But the evidence for a modern human-like foot morphology and striding bipedal gait is unequivocal.

The preserved skeletal anatomy of the hip, knee, ankle, and foot (and other aspects not discussed here, i.e., upper limb, hand, vertebral column) in *A. afarensis* demonstrates that it was undoubtedly a terrestrial biped. In the anatomical specializations associated with locomotion found in *A. afarensis*, every one shows an adaptive response to upright, bipedal walking. This assessment is reinforced when the footprints from Laetoli are considered. *A. afarensis*, like modern humans, was behaviorally and morphologically adapted to terrestrial bipedalism. This does not mean that they could not or did not use the trees as a source of food or safety, merely that they had become adapted to life on the ground. If *A. afarensis* climbed the trees, they climbed them like modern humans. Why? Because they exhibit no anatomical specializations for arboreality.

THE SEARCH CONTINUES

The search for *A. afarensis* continues throughout East Africa, especially in Ethiopia and Kenya. During the past fifteen years Hadar and two other areas in Ethiopia, known as Fejej and the Middle Awash, have produced fossils of *A. afarensis*. Fejej (pronounced Fedj-edj) is a hot, desolate area east of the Omo site in the southern part of the country. The site was originally discovered in 1989 during the Paleoanthropological Inventory organized by the Ethiopian Ministry of Culture.[24] Subsequent survey of the area by John Fleagle (SUNY at Stony Brook) and his associates yielded hominid teeth dated to about four mya.[25] Future surveys at Fejej should produce more early hominids.

The Middle Awash area, initially studied by Jon Kalb and associates during the 1970s,[26] is an extensive series of fossiliferous sediments along the Awash River about fifty kilometers (thirty-five miles) upstream (or south) of Hadar. Like Hadar, these sediments sample woodland environments associated with streams, swamps, and lakes. The Middle Awash deposits have yielded a series of cranial and postcranial remains dated to 3.4 and 3.85 mya. The first Middle Awash early hominid remains were found in 1981 by Tim White (University of California at Berkeley) and his colleagues in the adjacent dry stream drainages of Maka and Belohdelie.[27] In 1990, when fieldwork resumed, White and his fossil hunters were successful again and more 3.4 myo hominid fossils were recovered from Maka.[28] The Maka fossils, which include a mostly complete lower jaw, other mandibular fragments, isolated teeth, a proximal femur, and a humerus, are morphologically similar to the Hadar and Laetoli finds yet are temporally intermediate. Berhane Asfaw, who described the 3.85 myo cranial remains from Belohdelie, concluded that they were very similar to the cranial fragments recovered from Hadar.[29] Therefore, the earliest appearance of *A. afarensis* can now be expanded by another two hundred thousand years. The Middle Awash finds serve to strengthen the links between the Hadar and Laetoli collections, extend the earliest appearance of *A. afarensis* in Ethiopia to 3.85 mya, and reinforce the idea that *A. afarensis* was a single, bipedal, widely distributed, sexually dimorphic species.[30]

Recent paleontological research at Hadar, led by Don Johanson and Bill Kimbel of the Institute of Human Origins (IHO), has continued to add more high quality fossils to the already extensive Hadar collections. Beside the usual assortment of teeth and mandibles (fifty-three new specimens discovered between 1990 and 1993) the IHO team has also recovered a partial arm and a virtually complete skull.[31] Previously, Hadar had not yielded a complete (or near complete) adult skull (cranium and mandible), but with the recovery of three myo AL 444-2 by Yoel Rak (an Israeli anatomist), that changed. This very large, presumably male, skull is a spectacular find. We can use the AL 444-2 skull to study the size and relationship between the face and the cranial vault, giving us insight into such factors as brain size and the chewing muscles in this early hominid species. Future research at Hadar and other African sites will continue to refine our understanding of the evolution, ecology, anatomy, and behavior of this early hominid species.

In tandem with the increasing number of *A. afarensis* fossils being recovered, researchers are asking new questions, reanalyzing existing data, and using improved analytic approaches, including increasingly sophisticated biomechanical studies, computerized tomography imaging, and scanning electron microscopic studies, to examine the fossils. In addition, new techniques of aerial and satellite survey allow researchers to locate and prospect new fossiliferous areas.[32] Also, the many recent advances in geochronology give us a better understanding of the ages of the fossils we find. These new data and independent studies of previously recovered fossils and their context reinforce earlier assessments that *A. afarensis* was a single, upright-walking species that arose about four mya and lived in slightly to heavily wooded areas throughout Ethiopia,

Figure 3
AL 444-2
Hadar, 1992. Institute of Human Origins.
Photographer: Donald C. Johanson, Ph.D.

Kenya, and Tanzania for at least one million years. But so many other questions remain. What did they eat? How long did they live? What were the size and makeup of their social groups? Did they habitually make or use tools? Are bipedal locomotion and canine reduction linked together as part of an adaptive complex or did they arise independently? To date, the earliest australopithecines have been recovered only from sediments in the East African rift. Were they confined to this area or did they live outside this ecological zone? Why and when did *A. afarensis* become extinct? Did this lineage continue as the South African australopithecines, or the East African australopithecines, or as the *Homo* lineage that includes us? Clearly *A. afarensis* is an early hominid but is it the earliest hominid? Recently recovered fossils from the Aramis site in the Middle Awash suggest otherwise. With the announcement in 1994 of a new and older type of hominid, *Ardipithecus ramidus*, we have pushed back even farther the origins of our lineage to 4.4 mya and beyond.[33] Now we must search for more evidence of this newest early hominid. Unfortunately, deposits older than four mya are uncommon and only infrequently contain hominid fossils. But we will continue searching the Ethiopian badlands for our ancient relatives. Many long days of walking across the multicolored sediments still stand between us and the earliest hominids. With the hot sun and cloudy water, looking for our early ancestors isn't easy, but we, like many others, are anxious to continue. In East Africa, our past is lying at our feet. We just have to look.

NOTES

1. Hominids are bipeds, meaning they walk on two feet (*bi* = two; *ped* = foot). All other primates are quadrupeds (*quad* = four) or use all four limbs during locomotion.
2. Raymond A. Dart, "*Australopithecus africanus*: The Man-Ape of South Africa," *Nature* 115 (1925): 195–199.
3. An endocast forms when sediments accumulate and harden within an empty braincase. This fossil retains the shape, size, and markings of the inside of the skull, allowing measurement of brain size and description of brain anatomy.
4. Dart named the newly described hominid from South Africa *Australopithecus africanus*, which means "southern ape of Africa" (*Austral* = south; *pithecus* = ape; *africanus* = African).
5. Many mammals, including all apes and monkeys, have four types of teeth. From front to back they are the incisors, canines (cuspids or unicuspids), premolars (bicuspids), and molars. Each tooth type has a characteristic shape and function.
6. The sagittal crest is a ridge of bone running from the front to the back of the skull and is formed by the enlargement of the chewing muscles (Temporalis muscle). This is commonly found in male gorillas, orangutans, and robust australopithecines.
7. Fred E. Grine, "Australopithecine Taxonomy and Phylogeny: Historical Background and Recent Interpretations," in Russell L. Ciochon and John G. Fleagle, eds., *The Human Evolutionary Sourcebook* (Englewood Cliffs, NJ: Prentice Hall, 1993), pp 198–210; Fred E. Grine, ed., *Evolutionary History of the "Robust" Australopithecines* (New York: Aldine de Gruyter, 1988).
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Research TOC