# INTRODUCTION

For more than 150 years now it has been widely accepted among biologists and most other scientists that humans evolved from an ape. Not one that lives today, such as the chimpanzee, our closest living relative, but one that lived millions of years ago. Let me make that perfectly clear. We did not evolve from a chimpanzee, nor did chimps evolve from us. Rather, chimps and humans evolved from an unknown ape that lived before humans and chimpanzees branched off from each other, at least 7 million years ago, to pursue their own evolutionary destinies. What was this ape like? And from what did it evolve? And further back in time, what was the common ancestor of all apes and humans like? And what might studying ancient apes tell us about what makes us human?

These are the questions that have been driving my research since I was a graduate student in the 1980s and that motivate this book. We have known, ever since the work of Charles Darwin and other researchers of the late nineteenth century, that we have a special evolutionary relationship with apes. In a real sense, we *are* bipedal apes. Darwin and his principal defender, Thomas Henry Huxley, concluded in the 1870s that humans not only share a common ancestor with apes, we share a common ancestor with African apes to the exclusion of all other primates. To put this another way, Darwin and Huxley concluded that chimpanzees and gorillas are more closely related to humans than to orangutans. Orangutans are Asian great apes, a branch of the great apes that split from the common ancestor of the African apes and humans.

Among Darwin's contemporaries and researchers well into the twentieth century, the idea that African apes could be more closely related to humans than they are to orangs was hard for most scientists to swallow. Many rejected this conclusion, favoring the hypothesis that humans branched off first, and then what we call the great apes—chimps, gorillas, bonobos, and orangs—went off in their own different directions. After all, humans are very different from the apes, physically and mentally. Great apes all look more or less the same, at least superficially. They are large, hairy beasts with long arms, short legs, big jaws and teeth, and small brains compared with humans. Still, all of these early researchers recognized the reality of human evolution and our connection with apes. As we will see, there are in fact many differences among the great apes, and as a group they are not as different from humans as they may first appear.

Today, scientists group modern humans with the great apes. Although we have bigger brains and walk upright on our hind limbs, we share an enormous amount with the apes, from an almost indistinguishable genome to more similarities in our structure and behavior than we share with any other living organism. This is the reason that scientists group us with apes, to the exclusion of all other organisms, in the superfamily Hominoidea. We are especially closely related to the great apes, and so we share with them a place within the family Hominidae. (Figure 0.1 illustrates the relationships among the apes discussed in this book.) We will learn more about how all primates, apes, and humans are related later in this chapter.

In this book, I want to tell the story of ape evolution over approximately 30 million years. In many ways, my account differs from the usual textbook account, but I think it better explains how we got to be the way we are. Indeed, it is impossible to understand and explain the course of human evolution without understanding ape evolution first. Modern human anatomy can only be understood as a direct consequence of having evolved from an ape. We did not evolve from any living ape, but the anatomy of the common ancestor we share with apes sets the stage for human evolution. Everything from the structure of our teeth to our brains, our dexterous hands, our upright posture, and even our reproductive biology all have precursors in the anatomy of our ape ancestor. Many of these attributes are still found in living great apes, which is one of the reasons we study them so thoroughly.

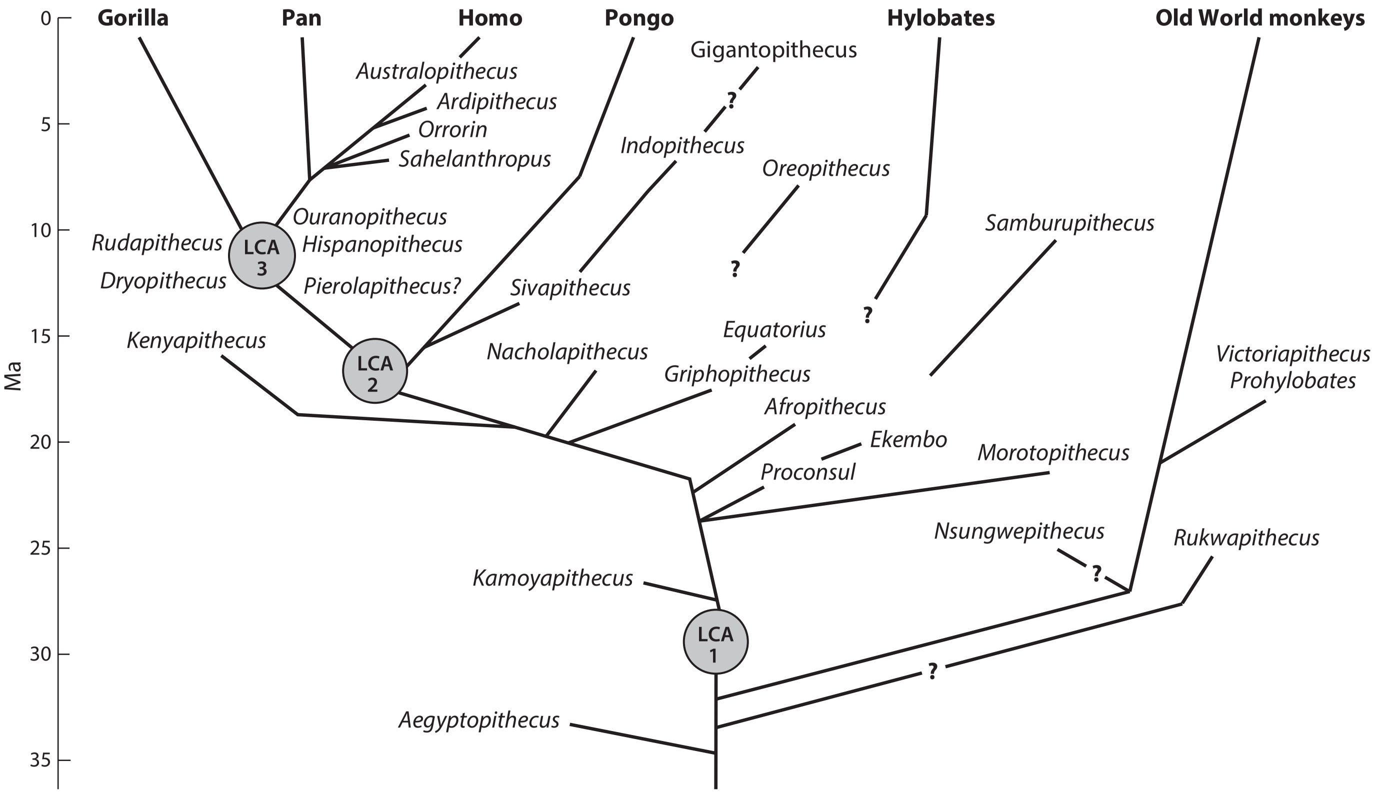


**FIGURE 0.1.** Evolutionary history of the hominoids. There are almost no direct ancestors in this diagram because it is very difficult to say if a fossil represents a direct ancestor or a side branch. LCA, last common ancestor; 1, hominoid (all apes); 2, hominid (great apes and humans); 3, hominine (African apes and humans). The fossil ape *Oreopithecus* and *Hylobates* (gibbons and siamangs) cannot be linked confidently to any known branch of the hominoid evolutionary bush. *Nsungwepithecus* may be the oldest known cercopithecoid (Old World monkey).

When I began my study of fossil apes from Europe, nearly all of them were attributed to the genus *Dryopithecus*, an animal scientists considered to be far removed from the central court of great ape and human evolution—a side branch in early ape evolution. I found no reason to challenge this conclusion at the time. However, I did come to the conclusion as I was completing my thesis that these fossil apes are great apes. In other words, they are hominids (the group that includes orangs, gorillas, chimps, bonobos, and humans.) With the discovery of more fossils, especially from Spain but also from Hungary, the view that European apes are more central to the question of hominid origins became more widely accepted. Before this, most scientists believed that European apes were just an interesting side story. Fossil apes were better known at the time in Africa, and as I said earlier, the overwhelming consensus was that great ape and human evolution was a mainly African story.

As I continued to work on European apes I had another idea. These fossil apes are not only great apes but also African apes (hominines.) This was a new idea—and it is not as widely accepted today as the conclusion that European apes are great apes. The reason this new idea is controversial is the same old story—every event of any significance in the evolutionary history of apes and humans was widely considered to have occurred in Africa. It took many new discoveries and detailed research on these new specimens to build the case for the presence of African apes in Europe.

Nevertheless, I began to wonder what African apes were doing in Europe 9 to 12.5 million years ago. At first I thought that they had dispersed into Europe from Africa, a sort of excursion by a side branch of African apes that eventually led to extinction. Finally it occurred to me that the ancestor of the African apes and humans may actually have evolved in Europe instead of Africa. While it was a radical departure from widely accepted reconstructions of ape and human evolutionary history, I was intrigued by the African ape features I found in European fossil apes and the complete lack of evidence for fossil great apes in Africa during the same time period. I found evidence that European Miocene apes were more advanced (or derived, in scientific terminology) than apes from the early Miocene of Africa and share characters with living African apes and humans. I hypothesized that African apes evolved in Europe and moved to Africa, not the other way around. Not to overdramatize the point, but I do think of this as a eureka moment that has to some extent defined the trajectory of my career afterward.

I am determined to falsify this hypothesis. That may sound strange. But we cannot really prove anything in paleontology. We can only try to find evidence inconsistent with prevailing theories. The only way to formally test my hypothesis is to seek to disprove it. To do so, I have been testing this hypothesis with new specimens. Many European fossil apes share characteristics of orangutans, which I interpret as primitive (they evolved first). But they all have features of African apes, as we shall see later. As surprising as it is, there is strong evidence, which I will reveal, to support my hypothesis. This is, to be honest, a hypothesis that goes against most opinion all the way back to Darwin, though as we shall see, Darwin was more open-minded than many persons are today (He was receptive to the idea that *Dryopithecus* might have a connection to African apes). To summarize the major conclusions of this book, my research and that of many colleagues has led me over the last thirty years to a number of conclusions. Apes evolved in Africa from ancestors of African origin (e.g., *Aegyptopithecus*). By about 20 million years ago, primitive apes, more monkey-like than apelike, began to flourish in Africa. Among these apes, one was better equipped to disperse to more seasonal climates (Eurasia). This ape, with its abilities to exploit a broader range of resources than the first apes, was poised to take on Eurasia. The ecological conditions in Eurasia selected for new adaptations in apes. The ape that dispersed into Eurasia began to evolve novel features related to diet and positional behavior, eventually splitting into the two major groups of living great apes, the pongines in Asia and the hominines in Europe. At the same time, the fossil trail in Africa went cold temporarily (there are no fossils), while in Eurasia ecological conditions favored further changes in locomotion (suspension) and increases in brain size. Large-brained and suspensory apes flourish until a progressively cooling and drying Eurasia eventually caught up with them. Many went extinct but a few were able to disperse south, tracking the forests retreating toward the equator. The ancestors of orangutans ended up in Southeast Asia while the common ancestor of the African apes and humans settled somewhere in the African tropics. By roughly 10 million years ago, gorillas separated from the common ancestor of chimps and humans, and by about 7 million years ago, chimps and humans diverged. It is at that point that the human lineage emerged. If you find the narrative confusing as you read the book, don't give up. Come back here and remind yourself of the major events in ape and early human evolution. It is a story, and I hope it will make sense to all of you. Before we embark on this grand narrative, it is important to learn more about primates and apes, and crucially what characteristics we humans share with them.

## HUMANS ARE PRIMATES

We belong to the zoological order known as the Primates. The classification of primates can be complicated, so I will make it simple here. Primates are traditionally divided into prosimians and anthropoids. Prosimians include lemurs, lorises, and galagos or bush babies, among others, and tarsiers.[1] Anthropoids include New World monkeys, Old World monkeys, apes, and humans. Nearly all anthropoids are daytime active and most are larger than prosimians. They have larger brains and rely less on insects and more on fruit and leaves. Most anthropoids are highly social and even more visually oriented than prosimians. Most anthropoids are also tree dwelling, but some spend time on the ground, especially the larger Old World monkeys (baboons) and African apes.

All primates are intelligent, dexterous, clever, vision-oriented animals, mostly tree dwelling, with grasping hands and feet (except humans; our feet have lost this ability). Brain size and eye-hand coordination is generally greater than in other mammals of similar size. It is clear that the evolution of the primates forms the foundation for the evolution of the apes and humans.

Most people use the word "monkey" to refer to those hairy, four-legged critters that kind of look like us and can be trained to do clever things. It is common to refer to chimps or gorillas as monkeys, but in fact, apes and monkeys are very different. First of all, there are two groups of animals that biologists call monkeys. One of them, the New World monkeys, live, as the name suggests, in the New World (Mexico and Central and South America but not the United States or Canada). The other kind of monkey lives in Africa and Asia, and we call them the Old World monkeys. While we refer to both groups colloquially as monkeys, New World monkeys are distinct and evolved separately from the Old World monkeys, apes, and humans. So, from now on, when I refer to monkeys, I am talking about Old World monkeys (see plate 1).

Old World monkeys, apes, and humans all fall within the zoological category of the catarrhines. New World monkeys are in a different group, having diverged before Old World monkeys and apes split. Roughly 35 million years ago, there was a population of primates that gave rise to the catarrhines to the exclusion of all other primates. In other words, we and the other catarrhines branched off from the common ancestor of the New World monkeys at that time and have since evolved in our own way. Since that initial branching event, Old World monkeys and apes have branched off from one another, as have each of the lineages of living apes and humans in turn.

Old World monkeys include baboons and macaques, which are the most common, but many other species exist. Monkeys are intelligent and very flexible in their behavior. These traits allow them to adapt to life in harsh climates, such as the snowy mountains of Japan, though most species, like the apes, live in the topics or subtropics. They generally live in social groups with complex hierarchies in which rank is important and can be inherited. The offspring of a high-ranking monkey are likely to be high ranking, too. Monkeys almost always give birth to one infant per pregnancy and invest a great deal of time raising and nurturing their young.

Compared with other mammals of similar size, monkeys generally have larger brains. They are very agile, and while some are more adapted to an arboreal (tree-living) lifestyle and others are more terrestrial (ground-dwelling), all monkeys move quickly and adeptly both on the ground and in the trees. Stay clear of them if you go on a safari or visit a place where they run free; their antics may be cute, but many have lost their fear of humans and they will not hesitate to bite. In fact, in the West we tend to think of monkeys as adorable fuzzy creatures, but where they live side by side with humans, they are often not very well liked, mainly because they steal food, destroy property, and raid crops.

So monkeys are intelligent and adaptable, traits that have allowed them to thrive alongside humans. It is no exaggeration to say that monkeys are among the most intelligent creatures on the planet. However, compared with monkeys, apes are in another category altogether.

Most of the apes are much larger in both body size and brain size than monkeys and all apes lack tails. (I am talking about living or extant apes here; some of these attributes were not present in the earliest apes, as we shall see.) Their arms are long (longer than their legs), allowing them to swing below the branches, whereas monkeys mostly walk along the tops of the branches. Female apes go through a menstrual cycle rather than a more seasonal reproductive cycle (estrous), as female monkeys do. Apes live longer and have larger, more complex societies and more complex and social brains. Apes score higher than any monkey in lab tests of intelligence, and some researchers have even claimed to have been able to teach apes to communicate in a rudimentary language. Although there are detractors regarding the ape language experiments, it is clear that apes are capable of much more cognitively challenging tasks than monkeys. In the wild, great apes, especially chimpanzees, make and use tools in foraging. All great apes build nests to be comfortable and safe at night in the trees or on the ground, they make umbrellas and other devices to protect themselves from the elements, and they devise novel and intelligent solutions to the problems they face. In my opinion, ape intelligence, specifically great ape intelligence, is an order of magnitude above that of any monkey and makes an obvious comparison with early humans. That is really the main reason we study great ape behavior in the wild. They surely represent something close to the way the earliest humans, which were great apes themselves, behaved. We did not evolve from a living great ape, but the earliest human species anatomically resembled living great apes and surely behaved much more like living great apes than living humans. Why we have changed so much and apes so little is possibly the biggest puzzle in paleoanthropology.

Scientists divide the living species of apes into two groups. Lesser apes include the gibbons and a less familiar primate called the siamang. Gibbons and siamangs are placed in the family Hylobatidae, or hylobatids, more informally. As we learned earlier, the great apes include chimpanzees, bonobos (formerly known as pygmy chimps), gorillas, orangutans, and humans. They are collectively known as the Hominidae, or hominids. The vast majority of paleoanthropologists recognize this dichotomy and are okay placing humans and great apes in the same family (hominids), though there are some who continue to elevate humans to a unique family (hominid) and place great apes in another group called the pongids. This is an evolutionarily artificial classification that places the unique adaptations of humans above the genetic and anatomical evidence of our relationships with the great apes. It runs counter to normal taxonomic practice and, I would say, plays into the hands of those who refuse to accept that humans evolved from an apelike species, or evolved at all. Here I use "hominids" to refer to the great apes and humans (see plate 2).

The recognition of the similarities between great apes and humans is remarkable and recent. Up until the 1990s most researchers reserved the word "hominid" for humans and our ancestors—all species on our branch of the family tree after we split off from the last common ancestor we share with a great ape. In most of my publications through the mid-1990s, I had to justify the use of the term "hominid" as employed here as if it was controversial and confusing. Today, reserving the term "hominid" for humans has become controversial and confusing. Most researchers, myself included, place African apes (chimpanzees, bonobos, and gorillas) and humans (we and our fossil relatives) in the same subfamily, the Homininae (hominines) (table 0.1). A few researchers even advocate including the genus of chimpanzees and bonobos (*Pan*) within our genus *Homo*, as a subgenus. Most researchers today agree that chimps and gorillas are more closely related to humans than they are to orangutans. Furthermore, they agree that chimps are more closely related to humans than chimps are to gorillas. In a family

**TABLE 0.1.** A Classification of Living Hominoids.

| SUPERFAMILY | FAMILY | SUBFAMILY | TRIBE | GENUS |
|---|---|---|---|---|
| Hominoidea | | | | |
| | Hylobatidae (gibbons and siamangs) | | | |
| | | | | *Hylotbates* |
| | | | | *Nomascus* |
| | | | | *Hoolock* |
| | | | | *Symphalangus* |
| | Hominidae (great apes and humans) | | | |
| | | Homininae (African apes and humans) | | |
| | | | Hominini[1] | |
| | | | | *Homo* |
| | | | | *Ardipithecus* |
| | | | | *Australopithecus* |
| | | | Panini | |
| | | | | *Pan* |
| | | | Gorillini | |
| | | | | *Gorilla* |
| | | Ponginae (orangutans) | | |
| | | | Pongini | |
| | | | | *Pongo* |

[1]The hominini includes additional taxa not included here, for clarity.

tree, chimps are our sisters, gorillas our cousins, and orangs are our cousins once removed.

## WHAT MAKES AN APE?

Earlier I listed a few broad characteristics of biology and behavior that distinguish monkeys from apes and humans. The distinctions are important because in a way they approximate the path of evolution from our more monkey-like ancestors to our apelike ancestors to us. It is important to remember again that none of the living primates are our ancestors and that they have all evolved their own special characteristics. But we can see in monkeys today the enhanced intelligence, adaptability, and agility that was present in our common ancestor with them. We can see in the apes the further development of the brain and changes in body plan. Looking at the differences between moneys and hominoids helps us to retrace, as an approximation, the course of our evolution. So let's look at this distinction in more detail.

First, there is the genetic evidence. We have known since the early part of the twentieth century that humans and apes are more similar to each other than to any other primate, when various organic molecules are compared. At first, comparisons among monkeys, apes, and humans involved proteins in the blood. Over a century ago researchers began to document similarities among Old World anthropoids to the exclusion of other primates.

In 1901 George Nuttall published a study in which he described a blood test to assess relationships among animals. Nuttall injected human blood serum (blood plasma from which the fibrogen, a clotting protein, has been removed) into rabbits. Blood collected from the rabbits was used to create an antiserum for human blood, that is, rabbit plasma with antibodies to human blood serum, produced by the rabbits as a natural immune reaction to human blood. Now he had a substance that he could use to detect human or humanlike blood. When Nuttall mixed this antiserum specific to humans with the sera from hundreds of different animals, he found that almost none of the mixtures reacted. In other words, there was nothing in the sera of any of these other animals that the human serum antibodies would react with—except monkey sera. The antibodies to human serum recognized something in the monkey sera.

Nuttall followed up this work in 1904 with a monograph entitled "Blood immunity and blood relationship: a demonstration of certain blood-relationships amongst animals by means of the precipitin test for blood." He concluded that humans share a close relationship with the great apes and that the next closest relatives, in order, were Old World monkeys, New World monkeys, and prosimians (lemurs, lorises, galagos, and tarsiers). This was really a remarkable conclusion for the time because it is essentially what we think today. Nuttall even suggested that, given the difficulty of finding informative fossils, molecular techniques might be the best way to classify species and determine their evolutionary relationships.

Whether relationships among species can be determined by morphology (which is essentially all we have for fossils) or whether genes are the only reliable source of information is a debate that rages on today. As a paleoanthropologist, I advocate using morphology, as well as molecules, to help unravel the mysteries of ape and human origins, and I think that most of my colleagues would agree—even the molecular systematists who use DNA to reconstruct the tree of life.

As techniques grew more refined, it became possible to begin to differentiate among the Old World anthropoids. In the 1960s, researchers first proposed, based on molecular evidence, that humans are specifically related to African apes (this of course had been concluded much earlier by Darwin, and especially by Huxley, from morphological evidence).

Today it is possible to make detailed comparisons among organisms based on the actual sequence of base pairs in their DNA. The vast majority of analyses comparing the DNA sequence of humans with those of other primates yield the same results. Humans share a most recent ancestor with chimpanzees and bonobos. Gorillas are next most closely related to humans and chimps, and orangs are the next group out. Gibbons and siamangs are the so-called lesser apes, the living hominoids that first branched from the line leading to the great apes and humans.

Let's put this in context.

Figure 0.2 is a diagram called a cladogram, which shows a nested set of relationships. It depicts the order of branching events but not direct ancestor-descendent relationships. You should read the cladogram as follows: New World monkeys branch off from the line leading to Old World anthropoids (catarrhines) and each goes on their own evolutionary path. This means that all New World monkeys have the same evolutionary relationship to all catarrhines. While this may seem counterintuitive (after all, we speak of both Old and New

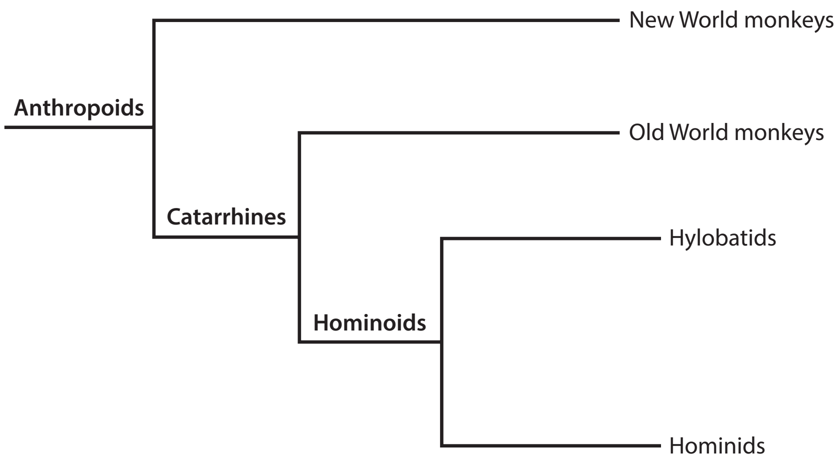


**FIGURE 0.2.** Cladogram of living anthropoids.

World monkeys), it is in fact documented by many lines of evidence, both morphological and molecular. So, New World monkeys as a group all have the same relationship with catarrhines (Old World monkeys, ape, and humans.) Both groups branched off from each other. Although capuchin monkeys from South America look a lot like vervet monkeys from Africa, they are in fact no more closely related to vervets than they are to Elvis (or any other hominoid). Vervets are more closely related to Elvis and all other hominoids, as well as to all other Old World monkeys, than they are to capuchins and all other New World monkeys. Get it? If not, have another look. It takes a while to properly understand a cladogram.

The next branching event separates the Old World monkeys from the apes (including humans). Again, this means that all Old World monkeys have the same evolutionary relationship to all hominoids. Although they may look to the lay person more like Old World monkeys than like humans, gibbons (hylobatids) are in fact more closely related to humans than they are to Old World monkeys.

And so it goes down the line. Gibbons branch off from the common ancestor of great apes and humans, and within this group, orangs diverge from African apes and humans, and finally gorillas diverge from chimps and humans. Despite the behavioral and morphological similarities that exist today among the African apes, chimpanzees and bonobos are more closely related to humans than they are to gorillas. This fact is reflected in the extreme similarity of the DNA of chimpanzees and humans, in the chimp-like anatomy of our ancestors, and in details of anatomy shared by humans, especially fossil humans, and chimps today (from now on, when I say "chimps" or "chimpanzees," I am including bonobos as well.) The reason that chimps and gorillas look more similar to one another than chimps resemble humans, even though chimps and humans are more closely related to one another, is that chimps and gorillas share primitive characters that humans have lost. Our earliest fossil ancestors looked much more like chimpanzees than we do today.

Let me return to the cladogram and the science behind it, cladistics. Why is it that evolutionary biologists do not simply rely on overall similarity in reaching their conclusions about evolutionary relationships? After all, geneticists determine relationships based on overall similarity of the genomes among species. The problem with morphology is that it is generally limited to a relatively small number of characters compared with the huge number of genes included in a genetic analysis. And anatomical characters do not all have the same usefulness for working out evolution in given lineages.

Species share anatomical features for three main reasons. They may have evolved in an ancient common ancestor shared by many other species. We have four limbs, like turtles, lizards, crocodyles, birds, and mammals, among other animals. But this does not mean that lizards and humans are more closely related to each other than humans are to dolphins, which lack externally visible limbs. It just means that lizards and humans evolved from a common ancestor that had four limbs (tetrapods). During the time since that ancestor lived, some descendants have lost their limbs (dolphins and whales; snakes). These shared characters (for example, having four limbs) are called primitive characters, and they are not helpful in deducing relationships among closely related species. Small brains (compared with humans'), long arms, short legs, large canines, and a hirsute appearance are all primitive characters that make chimps and gorillas resemble one another but do not tell us that they are most closely related. For much of our evolutionary history we looked like that as well.

We know that lizards and snakes are more closely related to each other than either one is to turtles or humans because they share features inherited from their last common ancestor, an animal that lived after turtles branched off but before mammals appeared on the scene. In the same way, humans and dolphins share many features with each other that nonmammals do not have because they were inherited from the common ancestor of dolphins and humans, an early mammal. Characters inherited from the last common ancestor of a group of organisms are referred to as derived characters. These are the characters that we need for establishing evolutionary relations.

I mentioned that there are three main ways in which characters can be shared among species. The third process that can lead to shared characters is parallel evolution. I will discuss this in more detail later, but for now let's just say that it is the independent evolution of similarities. In primate evolution, adaptations allowing species to hang below branches evolved independently quite a few times: in lemurs, New World monkeys, and maybe even more than once in apes. Thickly enameled teeth set in massive jaws also evolved multiple times in apes. We will explore the reasons for these fascinating parallel events later in the book.

The difficulty that some people have in accepting the idea that chimpanzees could be more closely related to humans than to gorillas, or that we could be related in any way to apes, is really an artifact of our perceptions of humans as apart from the other animals. We all know that humans are animals (as opposed to plants or fungi or bacteria), but we often separate the two categories in our minds. Many religions also teach that humans are separate from animals and have a special and unique origin. So our understanding of a chimpanzee is biased by the influence of our cultural traditions. When we consider them outside of this frame of reference (as much as we can), it becomes obvious that chimps and humans share a special, extremely close relationship.

We've known since the work of Mary-Claire King and her dissertation supervisor, Allan Wilson, at Berkeley in the early 1970s that chimpanzees and humans share almost 99% of their DNA in common. However, this also needs to be placed in context. It is estimated that there are between about 20,000 and 30,000 genes in the genome of every mammal. In the case of humans and chimpanzees, when comparing the same gene, there is on average about a 98.8% similarity in the base pairs. Base pairs are the nucleotide pairs that make up the rungs of double helix molecule. But humans and chimps have about 3.3 billion base pairs, so when you multiply the relatively small difference between the genomes of chimps and humans by 3.3 billion, the estimated number of genetic differences between humans and chimps adds up to quite a few, about 40 million, in fact. While many of these base pairs do not contribute to the functional portion of the genome (genes), the number of differences among genes is still large. Scientists also estimate that a good number of genes are unique to chimpanzees and others are unique to humans, adding to the difference. Furthermore, it is likely that many of the genes that distinguish humans and chimps are regulatory genes, which have multiple so-called downstream effects. A few regulatory gene differences can probably make the difference between a chimp and a human pattern of growth and development. So, although 98.8% sounds like a small difference, given the number of genes in the chimp and human genomes and the effect of regulatory genes, it amounts to more than enough genetic divergence to account for the differences in biology and behavior between chimps and humans.

While chimps and humans are genetically closer to one another that either is to any other primate, all hominoids share the vast majority of their DNA sequence. In fact, all vertebrates share most of their DNA. It is estimated that we have 88% of our genes in common with mice, 65% with chickens, and even 25% with grapes. For the most part, the same genes make all organisms work the way they are supposed to, and if it ain't broke, don't fix it. However, all hominoids share a range of anatomical characteristics that distinguish them from other primates. The list is long, so I will focus on the major features.

**A larger brain.** Once body size is taken into account, all hominoids have larger brains, on average, than other primates. If you were to make a comparison between the brain and body mass ratios of humans and mice, you would find that the mouse has a brain about the same size as humans relative to overall body mass, roughly 2%. So it sounds as if mice have brains comparable with those of humans.

The problem with this sort of comparison is that it does not take into account the fact that different attributes of the body change size and shape at different rates, a phenomenon known as scaling. When you compare brain and body size ratios across a wide spectrum of mammals (the so-called mouse-to-elephant curve), you see that overall body mass increases much more rapidly than brain mass (figure 0.3).

Elephants, for example, have brains that weigh less than 0.2% of their overall body mass. That is roughly 10 times smaller than for the mouse. The reason is that an elephant is not a gigantic mouse. The ancestor of all elephants was an animal the size of a rabbit that lived 60 million years ago. As the elephant grew in size during the course of its evolutionary history, its brain grew as well, but much more slowly. This is expected because brains are, metabolically speaking, extremely expensive, more so than any other organ. An elephant could not feed a brain 10 times the size of its actual brain, not to mention the problem of fitting such a large brain into the skull or getting a big-brained baby elephant through a birth canal.

So brains and body masses do not scale at a ratio of one to one. If you compare the average brain-to-body mass of a large number of mammals you see a trend, and you can use this trend line, or regression, to predict how big a "typical" mammal's brain should be for a given body mass. It turns out that primates in general have significantly larger brains than most mammals at the same body masses. Within primates, monkeys scale with larger brains than lemurs and lorises, and apes have the largest brains, with a few exceptions (for instance, gibbon brains are about the same size as baboon brains after body mass is taken into account).

Among the hominoids, modern humans have much larger brains than a typical mammal of our body mass. For example, a fallow deer weighing about 70 kilograms (154 pounds) has a brain size of about 160 grams (5.6 ounces), while a human of the same body mass can easily have a brain 10 times that size. In great apes, the figure would be about 3.5 times the size of the deer's brain.

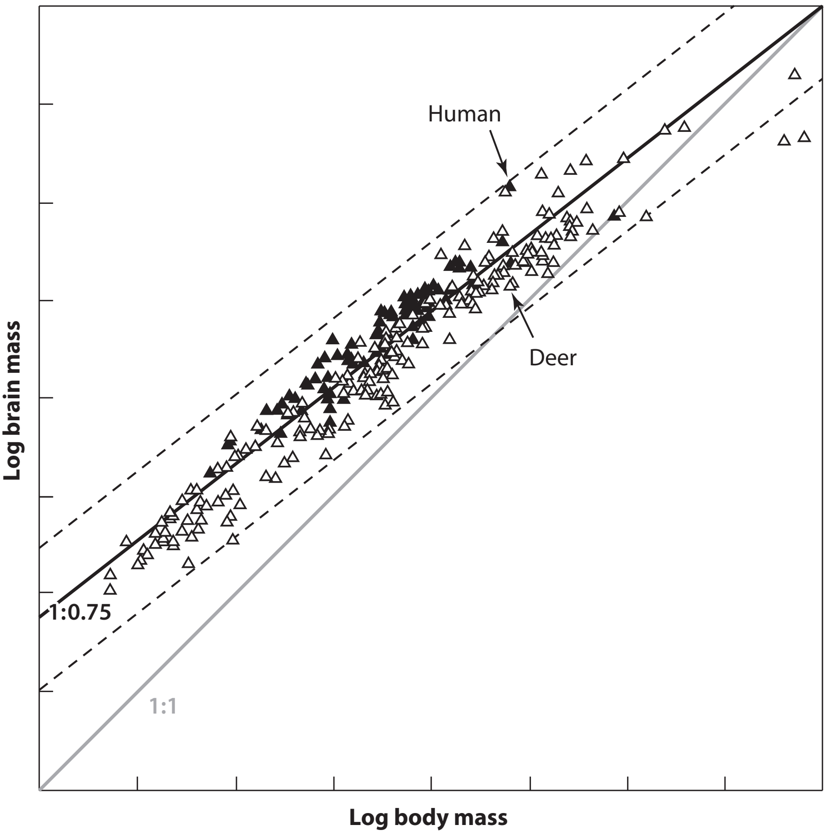


**FIGURE 0.3.** The mouse-to-elephant curve. The solid black line approximates the curve based on data gathered on the brain and body masses of hundreds of individual mammals. A slope of 1 (*gray line*), indicates that both variables are changing at the same rate. The actual line (solid black) is below 1 (0.75), indicating that brain size is increasing more slowly than body mass. The position of humans and the fallow deer show how much brainier we are; that is, how much larger our brains are than expected for animals of our size. The data point close to the human point (*black arrow*) is *Homo erectus*. (Modified from Martin 1990.)

We know that brain size is somehow related to information processing, or intelligence in some sense, but the relationship is not clear. In general, mammal species with larger brains tend to outperform those with smaller brains in various tests, but this link between brain size and cognitive performance is far from universal. *Within* species, however, there is no clear documented relationship between brain size and intelligence. In humans, for example, individuals of average or even exceptional intelligence and achievement in life can range in brain volume from under 1000 cubic centimeters to about 2000 cubic centimeters. The fascinating but somewhat morbid practice in the past of weighing, examining, and preserving the brains of renowned historical geniuses has shown that they can have brains anywhere in this range. Albert Einstein's brain is famously average in size (1230 grams upon his death in 1955).

In the lab setting, great apes routinely outperform monkeys in tests that require memory, recognizing objects, understanding symbols (including language), and recognizing their own reflection in a mirror. Great apes in captivity assemble objects to make compound tools. In the wild, great apes also make tools, with chimpanzees by far the most prolific and skillful tool makers. The social interactions among great apes are considered to be more complex than those of other primates, (the relationship between sociality and brain size isn't universally accepted) and can include recognition of roles and social status and anticipation of actions by other apes. Apes can also adjust their behavior based on a given situation. They may behave differently in a one-on-one situation than they would if a third ape were present.

One way apes use their larger brains is by developing what some researchers call culture, a concept that many anthropologists usually reserve for humans. However, wild chimpanzees have documented traditions that are passed along socially from one generation to the next and are unique to individual groups. Chimps in different populations have their own ways of making tools and their own sets of tools for specific tasks. The way a chimp uses stones to crack nuts in one area differs from the way stones are used in another. Hunting is relatively common in some chimp populations and rare in others. In other words, these chimps are carrying on traditions of learned behavior unique to their specific groups, just like humans. Bonobos, on the other hand, have not been observed to make tools in the wild, and when they do hunt, it is for small vertebrates such as frogs. However, in captivity bonobos are very proficient at making tools.

There are many other aspects of great ape behavior that are much more similar to human behavior than may appear at first glance. This is especially true for chimpanzees. In addition to making and using tools more frequently than other great apes, chimpanzees form coalitions, especially among males, to attack other groups or to defend themselves. They cooperate in hunting forays and, unlike other great apes, manage to capture and kill a variety of mammals, including red colobus monkeys and bush babies. While this behavior occurs occasionally in other primates, particularly baboons, it appears to be more common in chimpanzees. On the darker side, like humans, these coalitions of male chimps sometimes wage war on other groups; they deliberately and strategically kill, that is, murder, members of rival "gangs" and commit infanticide.

Female chimps also form coalitions; in fact, at many field sites where they have been studied, core groups of females appear to form the most stable components of chimp societies. Females do seem to compete among one another and are at least as antagonistic among themselves as are male chimps. Despite this competition and squabbling, females appear to be the glue that holds chimp societies together. I am not a psychologist, but my understanding of the research on great apes suggests that the way men and women behave socially is so similar to chimp behavior as to suggest that it is at least in part due to genes inherited from the common ancestor we share with chimps. The popular observation that men are from Mars and women are from Venus may in part be a legacy of the common ancestor we share with chimpanzees.

**A straight spine and long arms.** Below the neck we share many similarities with the other apes. All hominoids (apes including humans) have a relatively vertical posture compared with the Old World monkeys. Humans have a completely vertical posture, but gibbons and orangutans have vertical backbones as well, because they spend a great deal of their time hanging from branches. Apes have short lower backs compared with the rest of the vertebral column. This probably increases their stability in vertical positions. Their arms are so long that both gibbons and orangutans often walk upright on the ground or on the tops of branches with their arms held above their heads. Gorillas and chimpanzees have angled or obliquely oriented vertebral columns. Because their arms are longer than their legs, when they walk on all fours, their shoulders are above their hips. In fact, all nonhuman apes have arms that are much longer than their legs, unlike any other living primate (plate 3).

All apes except humans are exceptional climbers and tend to move along the branches from underneath rather than above. For the most part, monkeys move on the tops of branches. Apes swing arm-to-arm below the branches, which primatologists call suspensory locomotion, or brachiation. African apes spend much more time on the ground than the orangutan of Asia, but they are still very adept at swinging through the trees.

**Shoulders for motion, hands for grasping.** In addition to the structure of their vertebral columns and long arms, apes have a number of other characteristics that help them swing beneath the branches. Apes have broad chests with their shoulder blades positioned on the back, which moves their arms out to the side of their chests, rather than beneath their chests, as in monkeys and most other quadrupeds. Apes have highly mobile shoulder joints, which allow them to place their arms in many different positions, an ability that is critical to maintaining their balance in the trees. A fall could be fatal. While many other mammals spend most of their time in the trees, few are as large as apes.

All apes can straighten their arms completely at the elbow, and they all have flexible elbow and wrist joints that bend and rotate, giving them a wide range of motion. Monkeys have much less mobility at the elbow because they are adapted more for speed than for swinging under branches. Apes use their large and powerful hands to grasp branches and to climb, whereas monkey hands tend to resemble their feet and are usually rotated so that the palm is on the ground or branch as they walk on all fours. Monkeys and apes both have relatively dexterous hands, but apes more so, and humans are the most dexterous of all.

**Short legs, powerful hips.** In the lower or hind limb, apes are perhaps a bit less distinctive, but we can still identify important differences from other primates. Apes all have shorter legs than arms, as I've already noted. The hips have a massive ball-and-socket joint, which both supports the body mass and also gives apes a great deal of mobility at the hip. This allows the larger apes to spread their body mass across several branches in the trees, reducing the chance that a branch will break under their weight.

In many of these features, humans are like other apes. Our lower backs are shorter than those of Old World monkeys but longer than those of the other great apes (we have five lumbar vertebrae on average, like gibbons). We have broad chests, shoulder blades positioned on the back, highly mobile shoulders, fully extendible elbows, wrists that rotate through a wide range of motion, and hands and feet that are quite distinct from each other in shape. To me this is clear evidence that humans evolved from a suspensory, apelike ancestor. To deny this, as, for example, the researchers working on *Ardipithecus* do, means that all of the similarities between ape and humans must have evolved independently. Given the huge number of traits we share with the apes, I find the hypothesis that they all evolved independently, and for no apparent reason, highly unlikely.

Of the many differences between apes and humans below the neck, almost all are related to one thing: our ability to walk on two feet. As we became bipedal, humans switched the ratio of arm-to-leg length. Longer legs made for more efficient walking and running. When compared with trunk length, our arms are much shorter than those of the apes. Our hands are smaller and less powerful than those of apes, except for our thumbs, which are very long and well supplied with strong muscles. Our hips have lost some of the mobility seen in apes, and our feet have become highly specialized for bipedalism. We have lost the opposable big toe found in all other primates, and our feet have become stable platforms with a variety of intricate mechanisms for making bipedalism efficient.

All of the features of human anatomy are built on the ape body plan. Without this evolutionary history we would not have our large brains and dexterous hands and our incredibly complex behavior. It is impossible to understand and explain the course of human evolution without recognizing the tremendous similarities between us and the apes.

## WHEN DID APES FIRST ARISE?

Many researchers have tried to date when apes diverged from Old World monkeys by comparing DNA and calculating a rate of change based on the known rate of background mutation. This dating technique, known as the molecular clock, is the basis of many reconstructed branches on the tree of life, but it is not without its fair share of difficulties and controversies.

Here's how the molecular clock works. Mutations occur spontaneously in all genomes. It is an inherent property of DNA replication. This background mutation process is thought to have a characteristic rate, like the ticking of a clock. However, although we know that the rate can be different between organisms, it is likely to be similar among closely related animals like great apes. But how do we calculate the rate of mutation?

To calculate the rate, we need to know how much difference exists in the genomes of each species and how long it took to accumulate. Here is where paleontology and molecular biology join forces. If you know roughly how long ago one organism branched off from its closest relatives, and you know how many genetic differences there are between the two, you can calculate a rate. For example, if the fossil record tells us that species A and species B branched off 1 million years ago, and if the DNA tells us that there are one million differences in the genomes of each, then the rate of mutation is on average one per year. Once a rate is established, it can be used to estimate the divergence dates between other pairs of organisms. This process is called calibration.

In paleoanthropology, we commonly calibrate ape divergence times based on the divergence of the orangutan. Ancestors of modern orangutans are well represented in the fossil record. The oldest fossil members of the orangutan lineage are known from coal deposits in Thailand and from sand and clay deposits in Pakistan that are both about 12.5 million years old. We estimate that orangs diverged from the other great apes sometime before the first pongines (orangs and their ancestors) appear in the fossil record, possibly about 14 to 16 million years ago. We know how much genetic "distance" there is between orangutans and African apes and humans from molecular data. So, we can calculate an estimate of the rate of mutation among apes and humans from the amount of time since the divergence of orangs from African apes and humans and the number of genetic differences between the two groups. We then take this rate and use it to calculate a time of divergence between other pairs of species or groups of species. The time of divergence is the number of differences divided by the calibrated rate.

This type of analysis has been used to estimate when chimpanzees and humans diverged from a common ancestor. The estimates usually range from about 5 to 7 million years ago, although some estimates are as old as 14 million years and others as young as 3.5 million years. The 5-to-7-million-year estimate is broadly consistent with the fossil record of the earliest members of our evolutionary group, the hominins, although at 5 million, this would exclude a number of fossils widely accepted as hominins (*Orrorin*, *Ardipithecus*, *Sahelanthropus*) from our group. (We'll meet these fascinating recent finds in chapter 9.) Nevertheless, a broad if not quite complete consensus is emerging that humans and chimps diverged between 7 and 8 million years ago, gorillas around 9, and orangs, by definition, between 14 and 16 million years ago.

Of course, we are talking here about each individual lineage of living great apes and humans. What about, for example, the common ancestor of the living African apes and humans, an extinct species? When can that species, the first hominine, be expected to have arisen? Well, the answer is among the divergence dates of the living ape lineages. When we say that the orangutan, a pongine, branched off between 14 and 16 million years ago, we are essentially saying that the ancestor of the modern orangutan, the first pongine, branched off from the common ancestor of the African apes and humans, the first hominine, 14 to 16 million years ago. Since they are sister clades (most closely related organisms), hominines and pongines must have come into being at the same time, as a result of the same branching event.

Yet it is always wise to be a little cautious. The earliest members of any lineage will be very difficult to detect in the fossil record because they haven't changed much from their ancestors. Researchers need to estimate the amount of time that is missing, and it is really anyone's guess. As I said, most scientists accept a date that puts the branching-off of the pongines at about 14 to 16 million years ago, but there is no definitive evidence for this date. In other words, the oldest identifiable pongine fossils are 12.5 million years old, and we guestimate that another 1.5 to 3.5 million years are missing from the fossil record. In this particular case I don't think we could be too far off.

As we will see in later chapters, there were very interesting apes running around in Europe and Africa between 14 and 16 million years ago, and none of them looked very much like either pongines or hominines. They were more primitive looking, as we will see, and lacked characters such as limb structure and growth rates that are shared by pongines and hominines. So the split between pongines and hominines is not likely to have been before these more primitive apes lived. In addition, when we calculate a rate of change, we assume that the rate has remained constant through time and across different species. But this may not be the case.

Using this approach, molecular biologists have produced a number of different estimates for the time of divergence between the Old World monkeys and the apes. The different estimates reflect the fact that scientists have used different parts of the genome and made different assumptions about the rates of change. Dates for the Old World monkey–ape split range from about 31 to 38 million years ago. This means that we should start finding evidence of Old World monkeys that can be distinguished from apes in the fossil record around this time. Or does it?

While it is relatively easy to define living hominoids and to understand why humans are hominoids, when the fossil evidence is added to the equation it becomes much more difficult. This should come as no surprise. The attributes that characterize all hominoids today took time to evolve, and at the beginning of hominoid evolution, none of these features were present. There was a single population that was our last common ancestor with Old World monkeys.

Whatever the cause, a split happened. It probably occurred by chance, perhaps when two populations became separated from one another by a natural barrier, such as a river, or they may simply have drifted apart. Each population had its own unique combination of variations. With space between them and slightly different ecological settings, each was now subject to different selection pressures. Over time those would lead to different adaptations developing in each lineage that would eventually be pronounced enough that we can tell them apart in the fossil record.

However, because it took millions of years for even a few of the clear distinctions between monkeys and apes to evolve, it is a big challenge to decide which fossil is really an early ape. Even if the divergence of Old World monkeys and apes is as late as 31 million years ago, there is a big gap between this divergence estimate and the first appearance in the fossil record of anything we might want to call an ape or an Old World monkey. We take up this part of the story next.