



THE HUNT FOR THE
DAWN MONKEY

UNEARTHING THE ORIGINS OF
MONKEYS, APES, AND HUMANS



CHRIS BEARD

1

Missing Links and Dawn Monkeys

In rural China, the highest compliment you can get is not that you're attractive or smart. It's that you work really hard. As I shift to stay in the scant midday shade offered by a deep ravine on the northern bank of the Yellow River, this proletarian attitude makes a lot of sense. When I left the United States earlier this month, spring had barely begun. Checking the calendar in my field notebook, I see that it's only mid May—too early in the season for a heat wave. Yet for the past few days, my team has endured triple digit temperatures. Each of us sports a tan several shades deeper than our normal hue. A few yards away, where he chips at a piece of freshwater limestone that just might contain a fossil, my colleague Wang Jingwen is beginning to live up to his nickname, which translates roughly as “black donkey.” I'm told that the local villagers have been praising our work ethic, because when it gets this hot, even the peasants take a siesta under a shade tree.

We have no choice but to tolerate the heat of the noon sun, because it provides the best lighting conditions for finding fossils. At this time of day, there are no shadows to hide the small jaws and limb bones that have been entombed in these rock strata for the past forty thousand millennia or so. Having traversed twelve time zones to get here, I'm not about to forgo the chance to find an important specimen merely because of the

oppressive heat. My persistence is rewarded when I split apart another block of greenish-gray limestone. Inside I find a nearly complete maxilla, or upper jaw, of a small rodent, replete with three black teeth that glisten like fresh obsidian in the sunlight. Peering through a hand lens that I keep tied to a leather thong draped like a necklace under my tee shirt, the diagnostic pattern of cusps and crests on the fossilized teeth readily identifies the creature as *Pappocricetodon schaubi*. A primitive progenitor of modern mice, rats, and gerbils, *Pappocricetodon* is the most abundant fossil mammal known from this site.¹ Though it's not exactly the pivotal discovery I had hoped for, finding the mortal remains of any animal that lived millions of years ago invigorates the mind. I begin to contemplate the weighty scientific issues that have led me to travel halfway around the world, to this remote part of central China's Shanxi Province.

My particular area of scientific expertise, vertebrate paleontology, is in the midst of a sea change. Much of what I learned as a graduate student is being challenged by provocative new fossils and new methods of interpreting them, if not discarded altogether. Increasing globalization and the collapse of the Soviet Union and its satellite states have opened up most of the world to paleontological exploration, including places that, only a few years earlier, I never dreamed of being able to visit in search of fossils. On a separate front, molecular biologists are sequencing the DNA of various organisms at an increasingly frenetic pace, churning out megabytes of raw data that are being used to test old ideas, and to propose new ones, about the evolutionary relationships of living plants and animals. All in all, it feels like a unique moment in history and a great time to be a paleontologist, especially when you're involved in one of the most exciting debates to hit the field of paleoanthropology in many years.

Paleoanthropology is the scientific study of human origins. In the strictest sense, paleoanthropologists seek to illuminate the evolutionary history of the human lineage as it evolved from our more apelike ancestors. Fossil hominids are the crown jewels of paleoanthropology. Without them, theories about when, where, and how our species evolved would be helter-skelter, unconstrained by hard data. One of the great triumphs of twentieth century science has been the recovery of an amazing diversity of hominid fossils, mainly from eastern and southern Africa, but also from various parts of Eurasia, ranging from France and Spain to China and Indonesia. Discoveries of new fossil hominids continue unabated. Considered as a whole, the fossil record of early humans is now

complete enough that, at least in broad strokes, we know how humans evolved from more apelike precursors. Virtually all paleoanthropologists agree, for example, that the human lineage originated sometime between five and seven million years ago in Africa, and that early humans acquired the ability to walk upright on two legs millions of years before their brains enlarged much beyond those of chimpanzees.²

A fuller consideration of human origins requires us to place our own evolutionary history within a broader context. Did humans take longer to evolve our unique characteristics than other living primates, or did our ancestors simply experience unusually high rates of evolution? For that matter, how unique are humans with respect to other primates anyway? Which seemingly “human” traits are ours alone, and which are shared with various primate relatives? Where do humans lie on the family tree of all primates, and what does that tree look like? Where do primates lie on the larger family tree of all mammals? Were there particularly critical events during the earlier phases of our evolutionary history, before our own lineage branched away from those leading to chimpanzees and other living primates? Today, these questions pose far greater scientific challenges than simply filling in the constantly shrinking gaps in the human fossil record. Yet, ironically, when most people hear the term “missing link,” they think of a gap in the fossil record that supposedly fails to link modern humans with our apelike ancestors. The dirty little secret of paleoanthropology is that, while there are plenty of missing links, they don’t occur where most people think they do. They exist farther back in deep time. Ultimately, this is why I’m at the bottom of a ravine on the banks of the Yellow River.

The ravine itself is a natural erosional feature, an ephemeral drainage flowing into the Yellow River from the north. It dissects a relatively flat plateau, which—like most rural parts of central China—is now under intensive wheat cultivation. Standing on top of the plateau at the head of the ravine offers a panoramic view of the surrounding terrain. To the south, on the far side of the Yellow River in Henan Province, lie rugged mountains composed primarily of limestone of Ordovician age. Some 450 million years ago—about twice the age of the earliest known dinosaurs—the rock now forming the crest of this range was deposited in a warm, shallow sea not unlike that surrounding the modern Bahamas.

To the north and east, wheat fields extend across the plateau as far as the eye can see. Immediately west of the ravine, the sleepy village of Zhaili shelters the peasant farmers who tend the surrounding fields. A narrow path, hewn into the western wall of the ravine, provides access to the

bottom some 150 feet below for the villagers and their sheep and goats. Walking down this path, you can't help but notice the peculiar nature of the nearly vertical walls of the ravine. The rock defining both sides of the ravine is soft and pliable, so easy to work that many people in this part of China actually carve small caves into it, which function as storage rooms or even small homes. Geologically, this type of rock is known as loess. It is composed of wind-blown sediment laid down by countless dust storms that swept across this part of China during the Pleistocene Epoch, when vast ice sheets were expanding and contracting farther north in Siberia.

What is unique about this particular ravine, though, is not the loess. In this part of Shanxi Province, loess is ubiquitous, draping over older geological features like autumn leaves covering a well-kept lawn. But here, as the ravine approaches the Yellow River, it cuts deep into the loess. For the last fifty yards or so of its existence, the ravine finally succeeds in breaking through the loess altogether to expose the much older underlying strata. Even to the untrained eye, it is clear that these rocks are different, both in terms of their composition and their segregation into different layers or beds. They consist of alternating bands of blue-green mudstone, pale yellow and white limestone, and thick gray sandstones, the last of which show internal evidence of stratification in the form of minute swales of sand grains known as cross-bedding. The fossils we seek are concentrated in the layers of mudstone and limestone. They are roughly forty million years old, about six times older than the earliest putative hominids ever discovered. They pertain to an interval of Earth history known as the Eocene, the Greek roots of which translate more or less as "dawn of recent [life]."

As its etymology suggests, the Eocene was a pivotal period in the history of life on Earth—a time of transition from ancient to modern. The earliest members of most living orders of mammals first appeared and became geographically widespread, replacing more archaic forms that left no living descendants. Such distinctive and highly specialized types of modern mammals as bats and whales first showed up in the Eocene, together with the earliest odd-toed ungulates (horses, rhinos, and tapirs), even-toed ungulates (pigs, camels, and primitive relatives of deer and antelopes), and others. The order of mammals to which we belong, the Primates, also first became geographically widespread and ecologically prominent at the beginning of the Eocene, although a few scattered fossils hint that primates are somewhat older yet. At the same time, the Eocene witnessed the decline and extinction of many groups of mam-

mals that first evolved alongside the dinosaurs, or immediately following their demise. Examples include the vaguely rodentlike multituberculates, the raccoon- or bearlike arctocyonids, and the large herbivores known as pantodonts and uinatheres. The Eocene also witnessed a great evolutionary diversification of flowering plants, together with the insects that feed on them.³

In terms of its prevailing climate, the Eocene was virtually a mirror image of the Pleistocene or “Ice Ages,” when much of human evolution transpired. It began with a pronounced episode of global warming some fifty-five million years ago. Such optimal conditions allowed tropical and subtropical forests—and the animals that inhabit them—to occur at much higher latitudes than they do today. Because primates have always prospered in these warm forest habitats, the Eocene was truly a heyday for primate evolution. Among their other accomplishments, Eocene primates extended their geographic range far beyond its current limits. Fossils of Eocene primates have been found as far north as Saskatchewan in North America, England and Germany in Europe, and Mongolia in Asia. As I discuss in greater detail in subsequent chapters, the fossil record shows that during the Eocene, even these northern continental regions supported diverse evolutionary radiations of primates. After enduring for more than twenty million years, the greenhouse world of the Eocene ended thirty-four million years ago, when the Earth’s climate once again became cooler and drier. It is unlikely to be a coincidence that this severe climatic deterioration witnessed the extinction of primates in North America and Europe, where tropical and subtropical habitats disappeared.

The vast majority of the fossil primates known from the Eocene resemble the most primitive primates alive today. These animals, collectively known as prosimians, include the diverse radiation of lemurs native to Madagascar, the bushbabies of continental Africa, the lorises of Africa and southern Asia, and, perhaps strangest of all, the tarsiers of Southeast Asian islands. Prosimians resemble other primates, including humans, in possessing nails rather than claws on most digits of their hands and feet, and in having eyes that face forward to allow for enhanced, “stereoscopic” vision. Like all primates aside from humans, prosimians have a grasping big toe, functionally akin to the human thumb. Yet prosimians also differ from humans and our nearest primate relatives, the monkeys and apes, in many aspects of their anatomy, physiology, and behavior.

Monkeys, apes, and humans are collectively known as anthropoids or “higher primates.” Compared to prosimians, living anthropoids possess

larger brains, eye sockets that are almost completely surrounded by bone, a single lower jaw bone (or mandible) formed by the fusion of two separate bones at the chin, and many other anatomically advanced features. In terms of their behavior, anthropoids again differ from most prosimians, although there is some overlap between species of each group. In general, anthropoids tend to live in complex groups characterized by intricate social interactions among individual members. Some prosimian species, in contrast, live quite solitary lives. All anthropoids aside from the South American owl monkey (*Aotus*) are diurnal—that is, they are mainly active during daytime. Many prosimians, notably tarsiers, bushbabies, lorises, and some lemurs, strongly prefer to move about and feed at night. These profound differences between prosimians and anthropoids extend to the molecular level. Analyses of long sequences of the DNA of various species of monkeys, apes and humans show that all of these species are far more similar to one another than any of them are to prosimians. In an evolutionary context, this means that, whether we analyze anatomy, behavior, or DNA, the conclusion remains inescapable. We humans are much more closely related to monkeys and apes than we are to lemurs or tarsiers. Put slightly differently, monkeys share a more recent common ancestor with us than they do with prosimians.

Despite unanimous scientific agreement that humans share a close common ancestry with monkeys and apes, one of the most controversial issues in paleoanthropology today is how, when, and where the first anthropoids—the common ancestors of monkeys, apes, and people—evolved. In stark contrast to the relatively abundant fossil record for early humans, the fossil record for anthropoid origins is spotty, incomplete, and seemingly incoherent. Paleontology, like other branches of science, abhors such a vacuum. The main purpose of our expedition is to help flesh out this distant phase of our evolutionary history. Yet the simple fact that our team is searching for fossils of early anthropoid primates in Eocene rocks in central China is, in several respects, unorthodox—if not downright heretical.

Our goal is to test a bold new hypothesis about anthropoid origins—one that moves the birthplace of these remote human ancestors from Africa to Asia while it ruptures the established evolutionary timetable by tens of millions of years. This sweeping idea rests on the wobbly foundation provided by some fragmentary fossils from another Chinese site known as Shanghuang that I had recently named *Eosimias* (“dawn monkey” in Latin and Greek). If we are to have any hope of gaining scientific traction, we must find better fossils of *Eosimias* and animals like it. The

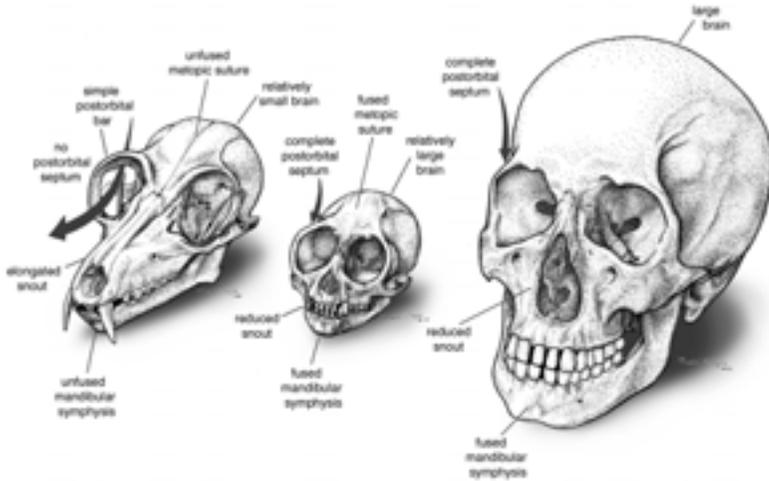


Figure 1. Major differences in cranial anatomy distinguish prosimians from anthropoids. Illustrated here (from left to right) are skulls of a ruffed lemur (*Varecia variegata*), a South American squirrel monkey (*Saimiri sciureus*), and a human (*Homo sapiens*). Note the basic similarity in skull form in the two anthropoids, which differ from the lemur in having a relatively larger brain, a reduced snout, fused mandibular symphysis and metopic suture, and a complete postorbital septum. Original art by Mark Klingler, copyright Carnegie Museum of Natural History.

bottom of the ravine on the northern bank of the Yellow River seems like a promising place to start.

To search for such elusive fossils, a highly interdisciplinary and international team of scientists has converged on this remote corner of central China. Each member brings a unique set of skills and knowledge to the table. On the Chinese side are four scientists from the Institute of Vertebrate Paleontology and Paleoanthropology (or IVPP), a branch of the Chinese Academy of Sciences. Tong Yongsheng, a veteran of numerous field campaigns all over the People's Republic, originally hails from Zhejiang Province, along China's southern coastline. A muscular man of medium build, Tong specializes in small mammals from the Eocene, especially rodents and insectivores (shrews, hedgehogs, and the like). Wang Jingwen, who grew up in Beijing, primarily studies ungulates, or hooved mammals, from the Eocene. Lately, though, Wang has developed an abiding interest in early primates, which allows the two of us to collaborate closely on joint research projects. Huang Xueshi boasts the most eclectic interests of any member of our team, having worked on fossils ranging in age from Paleocene to Oligocene. Huang's excellent mastery of English, combined with his strong local dialect, makes him the object

of the occasional joke. Other Chinese sometimes ask him to speak to them in English so that they can better understand him! Guo Jianwei, the youngest Chinese member of the team, focuses on the evolution of ruminant artiodactyls—the large group of even-toed ungulates that includes living deer, giraffes, antelopes, goats, and cattle.

The American members of the team include both paleontologists and geologists. Mary Dawson, my colleague at the Carnegie Museum of Natural History, specializes in the early evolution of rodents, rabbits, and their kin. Her role in the discovery of the first Eocene vertebrates north of the Arctic Circle, on Ellesmere Island in the Canadian Arctic archipelago, has won her widespread acclaim. John Kappelman, an anthropologist from the University of Texas, is a leading expert on the later phases of higher primate evolution, especially the evolution of apes during the Miocene Epoch. John's role in our expedition relates to his other professional hat, that of paleomagnetic stratigrapher. Together with Wulf Gose, a geologist from the University of Texas, and Tim Ryan, his graduate student, Kappelman hopes to determine the age of the fossils we find, using the episodic reversals in the Earth's magnetic field as a guide.

Wen Chaohua, a peasant farmer from the neighboring village of Zhaili, rounds out our field crew. I first met Mr. Wen the previous year, when we hired him as a manual laborer. Slight of build but surprisingly strong, Wen rapidly earned a spot on our team because of his solid work habits, his quick smile, and his unbridled enthusiasm for finding fossils. Though Wen has only the minimal educational background typical of rural Chinese of his generation, he shows plenty of raw intelligence. Had he been fortunate enough to grow up under different circumstances, I'm sure Wen could have been successful in almost any endeavor he chose to pursue. This year, Wen looks positively professorial wearing his new eyeglasses, which correct a minor astigmatism that had bothered him last year. Like me, Wen sports a small hand lens tied around his neck, which he uses to examine small fossils up close. In recognition of his hard work, Mary Dawson gave Wen her own hand lens at the conclusion of our previous field season. Now that he has the standard tools of the trade, Wen takes even greater pride in his work. Our reward is a steady stream of fossils.

Wen's role on our field crew is simply to extract large blocks of fossil-bearing rock from the bottom of the ravine. Other members of the team then break each block down more finely in search of any fossils that might lie inside. Wen's tool of choice for this enterprise is a large, steel rock pick hafted onto a stout wooden handle. This Wen wields with all of the exuberance of a forty-niner searching for a vein of gold. Invariably, Wen

himself uncovers many fossils, simply because he exposes so much fresh fossil-bearing rock with each powerful swing of his pick. At first, it was hard to restrain Wen from attempting to extricate the fossils he encountered during his daily assault on the layers of limestone and mudstone. Now, with a field season of experience under his belt, Wen understands that whenever he happens across a fossil, he must stop his work and alert the rest of the team.

I find that fieldwork in almost any locale quickly settles down into a daily routine. The work itself is often repetitive, even though the scientific results can vary dramatically from day to day. Our days in the bottom of the ravine by the Yellow River consist mostly of reducing large blocks of fossil-bearing rock to smaller ones, a process that is randomly punctuated by Wen's standard victory call—"You yige ya-chuang! You yige ya-chuang!" (I've got a jaw!)—whenever he finds something he thinks is interesting. Wen himself is particularly fond of large fossils, possibly because of his culture's long-standing fascination with "dragon bones." Usually, I know that Wen's most agitated cries mean that he has stumbled across the limb bones or jaws of the hippolike animal known as *Anthracoeryx*, the most common large mammal found at this locality. But Wen appreciates that the rest of us become more excited by relatively complete specimens of smaller mammals.

Today, Wen is in particularly fine form, whacking away at the freshwater limestone with gusto. It is May 21, 1995, and Wen knows that the field season is scheduled to end within the week, so that our team can return to Beijing in time to plan the logistics of future research before the American members have to catch their return flights home. The end of the field season means big changes in all of our daily lives. Most of us will return to our academic lifestyles, writing grant proposals and technical articles, preparing lectures, and attending administrative meetings. Wen will go back to being a farmer in the village of Zhaili. Maybe it's the thought of the upcoming changes that spurs Wen onward. In any case, he seems determined to find something important today. Looking back on it now, I doubt that Wen could possibly have dreamed of making such a momentous discovery as he hoisted his pick once more.

I can still hear the distinct thump of Wen's rock pick striking that fateful blow. Immediately, Wen's excited chatter makes me drop whatever I'm working on to see what all the fuss is about. Wen shouts: "Yige xiao ya-chuang, heng piao-liang! Ni kan-kan!" (A small jaw—very beautiful. You must see it for yourself!). As soon as I see what Wen's hefty pick has revealed, my heart begins to race. A large block of freshwater limestone



Figure 2. The author and Wen Chaohua at Locality 1 in the Yuanqu Basin of central China, where Mr. Wen discovered the complete lower dentition of *Eosimias centennicus* in 1995.

has been split cleanly in two by a single blow from Wen's pick. Through sheer luck, the plane in which the block has fractured corresponds exactly with the bedding plane on which both halves of an *Eosimias* lower jaw were entombed some forty million years ago. Unlike the fragmentary jaws of *Eosimias* we had collected at Shanghuang, this specimen is virtually complete, with all of the teeth intact and well preserved. The region near the chin makes it immediately apparent that the two halves of the lower jaw of *Eosimias* are not fused as they are in modern monkeys, apes, and humans. Despite the presence of this prosimianlike condition, I can also make out the remarkably anthropoidlike front teeth of *Eosimias*. Here, in a single specimen, lies compelling evidence that *Eosimias* occupies a critical position on the evolutionary tree of primates—one inter-

mediate between living prosimians and anthropoids. This precious fossil is exactly what we've been looking for—the pot of gold at the end of the rainbow!

Still reeling from the excitement of Wen's discovery, I realize that other members of the crew are crowding anxiously around me, waiting to learn what is so interesting. Mary Dawson approaches to peer at the block of stone in my hands. As soon as she sees the dual rows of teeth lying on the limestone slab like an exquisite string of black pearls she exclaims, "Chris, this specimen is going to confirm what we've thought all along! *Eosimias* is a primitive little monkey after all! No one will be able to complain about the Shanghuang specimens anymore." I grin and agree wholeheartedly. Tong Yongsheng and Wang Jingwen then come closer, converse briefly with Wen in Chinese, and begin to examine the amazing specimen for themselves. After a minute or so, they too look up at me with glints in their eyes. "This fossil is very important," intones Tong seriously. "Maybe it proves that all anthropoids began in China." Wang agrees, then adds, "Chris, you are very lucky! Everywhere you go in China you find interesting primates. Maybe it's because of your nickname." My Chinese nickname, *xiao hou-ze*, means "little monkey," in recognition of my favorite fossils.

As far as my new hypothesis about anthropoid origins was concerned, Wen's pivotal discovery couldn't have come at a better time. Ever since I had introduced *Eosimias* as a critical new link in the search for anthropoid origins, both the tiny fossil and I had been at the center of a controversy of monumental proportions, and I could not afford the luxury of ignoring the academic brouhaha. My career had barely begun, yet my scientific reputation was under assault. I needed fresh and compelling evidence if my new interpretation of anthropoid origins was to gain ground, and Wen's remarkable breakthrough promised to provide exactly that. Novel ideas in paleontology depend heavily on the fossils that support them. Until now, however, my biggest challenge had been that most of the fossil record seemed to be stacked against me.

For the past several decades, all undisputed early anthropoids had been discovered in Africa, mainly at a series of sites in the Fayum region of northern Egypt being excavated by Elwyn Simons of Duke University and his students and colleagues. This African dominance of the early fossil record of anthropoids dovetailed nicely with the broad consensus that later stages of anthropoid evolution, especially the origins of apes and humans, were confined to that continent. Yet I doubted that the geographical component of primate evolution could be as simple as this "Out

of Africa” theory implied. Did most, or even all, of the major evolutionary transitions in primate and human evolution occur in Africa? For me, Asia is a far more likely birthplace for the lineage we share with living apes and monkeys. Yet my views lie distinctly in the minority at present.

Despite Africa’s legitimate claim as a potential birthplace for the earliest anthropoids, three lines of evidence have persuaded me to focus my efforts on Asia. These include: (1) the geographic distribution of tarsiers, the group of prosimians that seems to be the nearest evolutionary cousins of anthropoids; (2) some fragmentary fossils from Myanmar (a nation formerly known as Burma), discovered decades ago, that appear to document the presence of early—and anatomically primitive—anthropoids in southeast Asia; and (3) results from my own earlier expeditions to China, which yielded the contentious fossils that had ignited the paleoanthropological firestorm in the first place.

The first important hint that Asia may have been the birthplace of all anthropoids comes from the geographic distribution of tarsiers, which live only on various offshore islands in southeast Asia. By any objective standard, tarsiers are among the strangest primates that have ever lived. Tarsiers are the only primates that eat nothing but live animal prey—mainly insects, but also small vertebrates such as lizards, snakes, and even birds, which tarsiers have been reported to catch in midflight.⁴ In contrast, most other primates tend to be vegetarians; yet others, like most humans, consume lots of vegetables along with their meat. Although tarsiers are not habitual bipeds like us, their own special way of moving about is at least as distinctive. The hindlimbs of tarsiers are extremely long and muscular, allowing them to leap across distances many times their own body length. Finally, tarsiers resemble many other prosimians in that they are most active at night. Yet tarsiers lack the familiar “glow-in-the-dark” structure in the back of their eyes (technically known as the tapetum lucidum) that concentrates diffuse nighttime light in the eyes of lemurs, cats, and many other mammals. To compensate for this anatomical deficiency, tarsiers have evolved the largest eyes of any living primate. Indeed, the volume of a tarsier eyeball more or less equals that of a tarsier brain!⁵

Despite the generally odd biology of tarsiers, a great deal of evidence suggests that these animals are the nearest living relatives of anthropoids. For example, the noses of tarsiers resemble those of humans and other anthropoids in lacking the moist, hairless region between the nostrils, known as the rhinarium, that creates the familiar “wet nose” of dogs, lemurs, and many other mammals. Like those of anthropoids, the eye

sockets of tarsiers are almost completely enclosed by bone. In contrast, lemurs have much simpler eye sockets, in which the outer margin is defined by a simple, rodlike strut of bone. Although the hindlimbs of tarsiers are highly specialized and differ from those of anthropoids, some of the individual bones (especially the talus—the ankle bone that articulates with the bones of the lower leg) closely resemble those of certain monkeys. Lemurs differ appreciably from both tarsiers and anthropoids in these respects. Both tarsiers and anthropoids lack the tapetum lucidum layer in the back of the eyeball, while lemurs still retain this ancient mammalian structure. Evidence from physiology and molecular biology likewise indicates that tarsiers and anthropoids are more closely related to one another than either group is to lemurs. For example, in contrast to lemurs and most other mammals, neither tarsiers nor anthropoids have the ability to synthesize vitamin C. Like humans, tarsiers must therefore ingest sufficient quantities of this compound to meet their daily nutritional requirements.⁶ Similarly, DNA sequencing has shown that the genomes of tarsiers and anthropoids have been modified from the ancestral primate condition in exactly the same way, by having chunks of extraneous DNA included in their genomes in precisely the same locations.⁷ Although some of these similarities between tarsiers and anthropoids may be spurious (caused by convergent evolution from different ancestral conditions), it seems very unlikely that all of them are. Instead, the simplest hypothesis requires us to view tarsiers and anthropoids as descendants of a common ancestor—one that possessed most, if not all, of the preceding biological traits. This common ancestry shared by tarsiers and anthropoids existed for some unknown length of time after the evolutionary schism that produced the ancestors of all other living primate lineages (lemurs, lorises, and bushbabies).

Accepting a unique common ancestry between tarsiers and anthropoids has significant implications for reconstructing the geography of anthropoid origins. By definition, the anthropoid lineage originated when ancestral tarsiers first diverged from ancestral anthropoids. Ultimately, this evolutionary divergence between tarsiers and anthropoids corresponded to a single episode of speciation. Documenting such a geologically brief event typically lies beyond the power of resolution of paleontology. However, from everything we currently know about speciation, it occurs on a local, rather than global, scale. Accordingly, the pivotal speciation event that gave rise to the tarsier and the anthropoid lineages must have occurred at a unique (if currently unknown) point in space and time. Once we conclude that tarsiers and anthropoids are each other's

nearest evolutionary cousins, we must also assume that both lineages originated in the same place (since speciation, like politics, is local). As it happens, ascertaining the birthplace of tarsiers is more straightforward than doing the same for anthropoids.

Today, tarsiers are found only on the Indonesian islands of Sumatra, Borneo, and Sulawesi, some of the more southerly islands of the Philippine archipelago, and small satellite islands nearby. Undoubted fossil tarsiers are rare, and individual specimens are highly fragmentary, but these too have only been found in Asia.⁸ Fossils pertaining to extinct prosimians that may be closely related to tarsiers have been found in North America, Europe, and Asia (these animals will be explored more fully in chapter 3). Significantly, fossil tarsiers—or even plausible fossil relatives of tarsiers—have never been found in Africa.⁹ The narrow geographic range of tarsiers throughout their evolutionary history therefore provides an important guide to where tarsiers and anthropoids first diverged, with the simplest hypothesis being that this evolutionary split took place in Asia. If so, some of the more adventurous members of the anthropoid lineage later migrated to Africa, where many subsequent events in anthropoid evolution apparently occurred. Eventually, anthropoids even reached South America, although no one believes anthropoids originated there. On the other hand, there is no evidence that tarsiers ever left their Asian homeland. A major problem, then, for anyone who would argue that anthropoids originated in Africa is the absence of any living or fossil tarsiers from that landmass.

Long before there was any substantial fossil record for early humans, Charles Darwin used similar logic to conclude that Africa may have been the ancestral homeland for our own lineage. In *The Descent of Man*, Darwin noted that:

In each great region of the world the living mammals are closely related to the extinct species of the same region. It is therefore probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee; and as these two species are now man's nearest allies, it is somewhat more probable that our early progenitors lived on the African continent than elsewhere.¹⁰

Decades after the original publication of *The Descent of Man* in 1871, discoveries of early hominid fossils in Africa convincingly upheld Darwin's prediction about the geography of human evolution.

Although Darwin's logic remains impeccable, and despite the fact that

his views were subsequently vindicated, it is still something of an intellectual leap to apply Darwin's approach to an event that happened so much farther back in time. I suspect that the antiquity of anthropoid origins is almost an order of magnitude greater than the birth of the hominid lineage (about fifty-five million years ago for anthropoids, and five to seven million years ago for hominids). Relying too heavily on the geographic distribution of living tarsiers to reconstruct such an ancient chapter in our evolutionary history has obvious drawbacks. Fortunately, the fossil record, fragmentary and imperfect though it may be, provides crucial evidence that bolsters an Asian origin for the lineage we share with monkeys and apes. Critical fossils from Myanmar and China form the second and third lines of evidence favoring an Asian origin for anthropoids.

The first putative fossil anthropoids to be unearthed in Asia were discovered in Myanmar during the early part of the twentieth century. After a series of wars between the Burmese and the British during the late nineteenth century, Burma was annexed to India, then a British colony. As a result, the first significant paleontological exploration of Myanmar was conducted by British paleontologists and geologists employed by the Geological Survey of India. In 1913 a British paleontologist named G. D. P. Cotter, working in Eocene strata in the region of the Pondaung Hills in central Myanmar, found three fossilized fragments of upper and lower jaws, all of which appeared to belong to a single individual. The specimens were so incomplete and so poorly preserved that they were not made known to science until fourteen years later, when they were formally described by Cotter's supervisor at the Geological Survey of India, Guy Pilgrim.

Pilgrim's analysis of these fossils, which he named *Pondaungia cotteri* in honor of his colleague, was meticulous, cautious, and surprisingly prescient. Pilgrim acknowledged that the scrappy nature of the specimens left open the possibility that *Pondaungia* might not be a primate at all. Nevertheless, he proceeded to point out anatomical details of the preserved cheek teeth that suggested, not only that *Pondaungia* was a primate, but that it was actually the most primitive anthropoid known at the time. In his own words, Pilgrim noted that:

If my interpretation of the structure of the teeth in *Pondaungia* is correct, and if it really is a Primate, then it must represent an earlier Anthropoid stage than *Propithecus* [one of the few anthropoid fossils known at that time, from the Fayum region of Egypt]. . . . It seems, however, worthy

of consideration whether *Pondaungia* does not partially fill the gap between the definitely Anthropoid *Propliopithecus* and some Lower or Middle Eocene Tarsioid.¹¹

By the time Pilgrim got around to publishing his description of *Pondaungia* in 1927, a second fossil primate had already been discovered in the same vicinity, this time by the famous American paleontologist Barnum Brown, primarily known for his expeditions to western North America, where he collected numerous dinosaurs for the American Museum of Natural History in New York. Brown and his wife, Lilian, traveled to the Pondaung Hills in early 1923, with a retinue of Burmese assistants and servants. Virtually impassable roads and primitive modes of local transportation hindered the expedition's work. The threat of malaria was constant, and it eventually claimed the life of one of Brown's Burmese servants. Brown himself contracted malaria later in the expedition, which prevented him from extending his paleontological exploration farther north, into China's Yunnan Province.¹² Despite these hardships, Brown's campaign succeeded in amassing an important collection of fossil mammals, some of which proved to be more nearly complete than those collected by the earlier Geological Survey of India expeditions. The vast majority of the specimens uncovered by Brown belonged to large mammals, including extinct rhinolike forms known as brontotheres and amynodonts and primitive hippolike animals called anthracotheres. When the collection was initially unpacked and curated at the American Museum, a single, rather innocuous-looking specimen was considered insufficiently important to warrant its own entry in the museum's permanent catalogue. Fourteen years later, it would finally be recognized as the second species of fossil primate from the Pondaung Hills.

The task of studying and describing the fossils collected by Barnum Brown's expedition to Myanmar fell to Edwin H. Colbert, who was then a young assistant curator of vertebrate paleontology at the museum. Like Brown, Colbert would eventually gain scientific celebrity for his work on dinosaurs. During the 1930s, however, the trajectory of Colbert's career was dictated by Brown's field expeditions in southern Asia, which aimed primarily to find and collect fossil mammals. As Colbert began his research on the Myanmar fossils, it became apparent that most of the specimens belonged to species that had already been described and named by Pilgrim and Cotter, whose teams had gotten there first. The most important exception was a fragment of a lower jaw preserving the crowns of three teeth and part of the region near the chin. This area, known as

Hills.
[Figure 3
near
here.]



Figure 3. Barnum Brown (on horseback), leading the American Museum of Natural History expedition to the Pondaung region of Myanmar (formerly Burma) that recovered the holotype lower jaw of *Amphipithecus mogaungensis*. Photograph courtesy of and copyright American Museum of Natural History Library.

the symphysis, is the site where the two separate bones of the lower jaw meet to form a joint at the midline. Colbert's rapidly growing expertise on early mammals allowed him to recognize immediately that this broken bit of jawbone pertained to an early primate.

Most living and fossil species of mammals, including primates, can be distinguished from their closest relatives on the basis of their teeth alone. This may sound trivial, but for paleontologists, the evolutionary fingerprint stamped onto the anatomy of mammalian teeth is both critical and fortuitous. Early mammals owed their evolutionary success to the complicated structure of their teeth, which allowed them to chew their food prior to swallowing it. This ability, absent in birds and reptiles, lets mammals eat a wider variety of foods more efficiently than other vertebrates can. As mammals evolved, their diets often changed, and the anatomy of their teeth and jaws responded in kind. At the same time, mammalian teeth are the hardest, most durable parts of the mammalian body. How fortunate for paleontologists that the most diagnostic elements of the mammalian skeleton are precisely those that are most likely to be preserved as fossils.

The teeth of primates, like those of most mammals, can be segregated into four different classes. From front to back in the jaw, these basic tooth

types include incisors, which in humans are roughly chisel-shaped; canines, which are simple and fairly conical in structure; premolars, which dentists call bicuspids because of their two main cusps; and molars, the relatively large teeth at the back of the jaw that do most of the actual chewing. Humans normally have two incisors, one canine, two premolars, and three molars (one of which is known as a “wisdom tooth” because it is the last tooth to erupt as teenagers reach adulthood) on each side of their upper and lower jaws.

In the jaw fragments of *Pondaungia cotteri* described by Pilgrim, only upper and lower molars were preserved. But the new specimen described by Colbert had two premolars and a single molar still intact. The rest of the teeth were broken away long ago, perhaps not long after the animal died. Thus, Colbert had the luxury of being able to analyze the anatomy of the premolars and the symphysis for the first time. These new pieces of the puzzle gave Colbert more confidence than Pilgrim had, although the two men reached virtually identical conclusions about the evolutionary position occupied by these Burmese fossil primates.

Colbert formally described the second Burmese primate, which he named *Amphipithecus mogaungensis*, in 1937.¹³ Citing the peculiar anatomy of the premolars and the great depth and robusticity of the jaw, Colbert concluded that *Amphipithecus* represented an anthropoid rather than a relative of lemurs or tarsiers. A surprising feature shown by the lower jaw of *Amphipithecus* was that, in life, it would have possessed three premolars on each side (only two of these teeth remained intact in the fossil, but the presence of the other premolar could readily be inferred from its broken root). Among living anthropoids, only the monkeys of Central and South America possess three premolars on each side of their lower jaws. All living anthropoids of the Old World resemble humans in having only two premolars. Rather than interpret *Amphipithecus* as a relative of South American monkeys that somehow happened to live in Myanmar, Colbert concluded that *Amphipithecus* was related to living and fossil anthropoids from the Old World, especially *Propliopithecus* from the Fayum region of Egypt. Possibly, the retention of an additional premolar that was lacking in other Old World anthropoids merely signified the primitive evolutionary status of *Amphipithecus*.

Pondaungia and *Amphipithecus*, from the Eocene of Myanmar, are roughly from thirty-seven to thirty-eight million years old, which makes them about three to four million years older than *Propliopithecus* and its contemporaries from the early Oligocene of Egypt.¹⁴ This fact alone

primates.
[Figure 4
near here.]



Figure 4. The holotype lower jaw of *Amphipithecus mogaungensis* from the Pondaung Formation of Myanmar, collected by Barnum Brown in 1923. Photograph courtesy of and copyright American Museum of Natural History Library.

caused the Burmese fossils to play a central role in debates about anthropoid origins throughout the twentieth century. Yet, from the very beginning, these Burmese primates inspired controversy. For example, although Colbert's ideas about the evolutionary position of *Amphipithecus* converged neatly on those of Pilgrim regarding *Pondaungia*, Colbert himself doubted that the two Burmese primates were closely related. He even hinted that *Pondaungia* might not be a primate at all, referring to it derisively as a "supposed primate." In retrospect, it is clear that Colbert made too much of relatively minor anatomical differences between *Am-*

phipithecus and *Pondaungia*. Indeed, the fragmentary specimens that were known at the time shared no parts in common. In a very real sense, Colbert was comparing apples and oranges.

Incomplete fossils, like all of the specimens of *Pondaungia* and *Amphipithecus* available to Pilgrim and Colbert, are almost inherently controversial. The problem is exacerbated in the case of fossils that lie near the origin of groups, like the anthropoids, that attract lots of scientific attention. From a purely practical perspective, the only way to resolve these sorts of disputes is by finding more—and preferably more complete—fossils. As the decades passed, however, only a few additional fragments of *Pondaungia* and *Amphipithecus* were collected and described, and these specimens added little new anatomical information.¹⁵ During the second half of the twentieth century, Myanmar became politically isolated from much of the West because of its record of military dictatorship. Political isolation hindered scientific collaboration, and efforts to advance our understanding of *Pondaungia* and *Amphipithecus* effectively ceased. Over this same interval of time, the fossil record of early anthropoids in Africa grew by leaps and bounds. By the early 1990s, the disparity was so severe that most experts believed that anthropoids must have originated in Africa, and that *Pondaungia* and *Amphipithecus* might not be anthropoids after all.¹⁶

I remained agnostic about the geography of anthropoid origins until I began fieldwork in China in early 1992. That project, undertaken in collaboration with colleagues from the IVPP, focused on a newly discovered series of ancient fissure-fillings near the village of Shanghuang, not far west of Shanghai. Fissures form whenever limestone rock formations are exposed to the elements, because limestone dissolves in rain-water. Over time, as water percolates through structures that originated as tiny cracks, they enlarge. Forming low points on the local terrain, these limestone fissures naturally tend to fill up with mud and any other debris, such as animal bones and carcasses, that happen to wash into them. As luck would have it, the Shanghuang fissure-fillings formed during the middle Eocene, about forty-five million years ago. The abundant fossils that our team recovered there include small, primitive primates that are roughly seven or eight million years older than *Pondaungia* and *Amphipithecus*. For the first time, these fossils placed me squarely in the center of the debate over when, where, and how the common ancestors of monkeys, apes, and humans evolved.

Certain fossils require radical adjustments to theories of how various forms of life evolved. One of the small primates we found at Shanghuang

rapidly became such a pivotal fossil. Like several other “missing links” in evolutionary biology, this new primate, which we later described as *Eosimias sinensis* (“dawn monkey from China”), possessed a unique combination of primitive and advanced anatomical features.¹⁷ Eventually, its age and anatomy would force me to disagree with decades of earlier research on anthropoid origins. In retrospect, the poor quality of the fossil record of early anthropoids at the time meant that earlier theories were ripe for being overturned. As already noted, living anthropoids differ in numerous fundamental ways from living prosimians. Prior to our discoveries at Shanghuang, however, the fossil record did little to blur the distinction. The earliest fairly complete anthropoid fossils then known, from the Fayum region of Egypt, were obviously anthropoidlike in all major respects. Although the advanced anatomy of these Egyptian fossils rendered their anthropoid status uncontroversial, this also left a gaping hole in the fossil record that could only be filled by more primitive fossils. *Eosimias* clearly met this criterion. It wasn’t immediately obvious to me (and it still isn’t obvious to some of my colleagues) that, in stark contrast to the Fayum anthropoids, *Eosimias* is a primitive anthropoid. It resembled neither Eocene prosimians nor other anthropoids known at the time. Before I could fully comprehend its evolutionary significance, however, I had to undertake a thorough analysis of its anatomy.

Any anatomical study of a previously unknown fossil is constrained by the quality of the material that is recovered. Like Pilgrim and Colbert before me, at first I had only fragmentary jaws and teeth of *Eosimias*, and nothing more, to go by. The best specimen we unearthed from the Shanghuang fissure-fillings was a lower jaw with three teeth intact—the last premolar and the first two molars. Crucial features, like the anatomy of the incisors, the canine, and the front part of the jaw, remained ambiguous at best. To make matters worse, *Eosimias* was considerably more primitive than either *Pondaungia* or *Amphipithecus*, making it even more difficult to evaluate. Yet despite these problems, my examination of these first fragmentary specimens convinced me that *Eosimias* qualified fully as a primitive anthropoid. My confidence derived partly from the utter lack of evidence supporting a different position for *Eosimias* on the primate evolutionary tree. The anatomical details underpinning my views are discussed in chapter 7. The important point to make here is that, for most scientists, remarkable claims require remarkable evidence. By any standard, the first fossils of *Eosimias* we found at Shanghuang were unremarkable, at least in terms of their completeness. This led many ex-

perts to doubt the anthropoid status of *Eosimias*. As a result, our fateful expedition to the little ravine near the Yellow River was launched as a conscious effort to uncover anatomically superior specimens of *Eosimias*. Thanks to Wen's landmark discovery, we succeeded beyond our wildest expectations.

In fact, the discovery of this single specimen has catapulted *Eosimias* to an elite position among Eocene primates. Although many primates have been described from the Eocene, few of them are documented by reasonably complete remains. Fewer still are known from truly superior anatomical specimens—either skulls or complete or partial skeletons. Of those rare species that are represented by such extraordinary fossils, such as *Adapis parisiensis* from France and *Notharctus tenebrosus* and *Shoshonius cooperi* from Wyoming, all are clearly fossil prosimians. They are only distantly related to the lineage that ultimately gave rise to modern monkeys, apes, and humans.

Wen's specimen reveals that *Eosimias* differs dramatically from these Eocene prosimians. Like living anthropoids, *Eosimias* has deep, powerfully constructed lower jaws. Its front teeth or incisors resemble those of living anthropoids in both their vertical orientation and small size. Living and fossil prosimians almost always have jaws that are more gracile, especially up front near the symphysis. As a result, their incisors tend to protrude forward, rather than being erect like ours. Immediately behind the incisors, the large, daggerlike canine of *Eosimias* also looks distinctly like that of an anthropoid. The premolars of *Eosimias* are very primitive, but again they resemble those of other early anthropoids, including *Amphipithecus* from Myanmar, in being oriented obliquely in the jaw. In Eocene prosimians, the long axis of each premolar is oriented front to back. The molars of *Eosimias* differ from those of all other primates. They are primitive in the sense that an extra cusp called the paraconid is still present. This cusp was suppressed later in the evolutionary history of anthropoids. In other details of their anatomy, however, even the molars of *Eosimias* show anthropoid features. As in other early anthropoids, the rear part (or talonid) of the last molar is highly abbreviated in *Eosimias*. This region is often greatly enlarged in Eocene prosimians.

Although it's too early to speculate about what *Eosimias* might have looked like in the flesh, a few important details are already clear. For example, we have a good idea of how big *Eosimias* was, because the size of the lower molars correlates closely with body size in living primates. *Eosimias sinensis* from Shanghuang probably weighed about three and a half ounces (100 grams). Wen's *Eosimias*, which appears to document

a new species, would have weighed slightly more (about four and a half ounces, or 130 grams). The smallest living monkeys, the pygmy marmosets of South America (*Cebuella pygmaea*), overlap *Eosimias* in body size, but most living anthropoids are substantially larger, typically by an order of magnitude or more. Indeed, even most tarsiers would tip the scales at a heavier weight than *Eosimias*. Small body size alone would have forced *Eosimias* to consume a diet rich in calories. *Eosimias* therefore probably ate a variety of insects, small vertebrates, and fruits. The relatively foreshortened lower jaw of *Eosimias* indicates that its muzzle must also have been abbreviated, like that of most monkeys. All modern primates the size of *Eosimias* live in trees, not on the ground. It therefore seems likely that *Eosimias* was a denizen of the forest as well. Beyond this, it is premature to predict much about the biology of *Eosimias*. Its intermediate evolutionary position between modern prosimians and anthropoids means that *Eosimias* may have been either prosimianlike or anthropoidlike in most of its biological attributes. Such a transitional spot on the evolutionary tree hinders attempts to reconstruct the habits and appearance of *Eosimias*, at least until more complete specimens are found. Yet at the same time, this makes *Eosimias* crucial in the search for anthropoid origins.

Exceptional fossils serve as critical guideposts for deciphering evolutionary history. Fossils often demonstrate that real animals once possessed combinations of features that are never found together in their living relatives. The famous “feathered dinosaurs” from northeastern China provide a classic example of this phenomenon, because they show that animals with skeletons that are undeniably dinosaurian in overall form were also covered with an external coat of feathers like that of modern birds.¹⁸ Such genuine chimeras from deep time can be pivotal when it comes to reconstructing the family tree of a group of organisms. In the example given above, new and spectacular specimens have dramatically illuminated the family tree encompassing birds and theropod dinosaurs. Exceptional fossils can also show the sequence in which certain anatomical features, and their associated functions, evolved. Again, in the case of the feathered dinosaurs, it now seems clear that feathers evolved long before other features that are characteristic of modern birds, like their toothless, horny beak. The relatively primitive forelimbs and breasts of the feathered dinosaurs demonstrate that these animals could not fly. Feathers must therefore have originally evolved to serve some other function, like courtship display or the conservation of body heat. At the same time, exceptional fossils testify that such transitional animals lived in a

specific place at a certain time. This information can be crucial in determining when and where major lineages first evolved.

By any of these criteria, *Eosimias* qualifies as an exceptional fossil. For me, *Eosimias* functions as a Rosetta Stone for reconstructing the ancestry of monkeys, apes, and humans, in much the same way that feathered dinosaurs have fundamentally resolved the origin of birds. But not all scientists agree that *Eosimias* is so critical for understanding anthropoid origins. Indeed, not all scientists agree on the importance of feathered dinosaurs for reconstructing the origin of birds. Consensus rarely emerges along the cutting edge of any scientific issue. Yet the following two points seem beyond dispute. First, *Eosimias* is far more primitive than any other fossil thought to be related to the origin of anthropoids. It is so primitive, in fact, that some experts continue to deny that *Eosimias* has any relevance for solving the mystery of anthropoid origins. Second, *Eosimias* is millions of years older than any other fairly complete fossil thought to belong to the anthropoid lineage. It is so old, in fact, that its age alone conflicts with widely accepted theories about when the anthropoid lineage was born. At the core of these disagreements regarding *Eosimias* lie two very different paradigms for reconstructing the evolutionary history of primates.

I refer to these two evolutionary paradigms as the ladder and the tree. The older ladder paradigm has largely withstood the test of time, a major criterion bolstering the scientific impact of any theory or model. In order to convey the underlying philosophy, methods, and goals of these competing evolutionary paradigms, let's make an analogy between the large-scale evolution of life on Earth (known as phylogeny) and the much smaller-scale family trees that are more familiar to most of us (known as genealogy). The ladder paradigm attempts to establish the phylogenetic line of descent from a remote ancestor to whatever descendant species is of interest. In genealogy, a similar goal would be to chart your direct ancestors (great great grandparents and such), with little regard for determining your distant aunts, uncles, and cousins.

Within the field of paleoanthropology, the ladder paradigm owes much to the influence of Sir Wilfrid E. Le Gros Clark, a British anatomist and primatologist whose publications dominated the study of primate evolution for much of the mid twentieth century. Although one might easily oversimplify the complex views of such an important scientific figure, it is fair to say that Le Gros Clark perceived the entire span of primate and human evolution as a steady progression from primitive to advanced. In Le Gros Clark's view, the original gamble made by the earliest

primates—to invade the trees and take on a highly arboreal lifestyle—led almost inexorably to a series of evolutionary trends that reached its climax with the advent of *Homo sapiens*. Le Gros Clark summed it all up rather nicely in his seminal book, *The Antecedents of Man*:

Among the Primates of today, the series tree shrew—lemur—tarsier—monkey—ape—man suggests progressive levels of organization in an actual evolutionary sequence. And that such a sequence did occur is demonstrated by the fossil series beginning with the early plesiadapids [so-called “archaic primates” from the Paleocene] and extending through the Palaeocene and Eocene prosimians, and through the cercopithecoid [Old World monkeys] and pongid [apes] Primates of the Oligocene, Miocene, and Pliocene, to the hominids of the Pleistocene. Thus the foundations of evolutionary development which finally culminated in our own species, *Homo sapiens*, were laid when the first little tree shrew-like creatures advanced beyond the level of the lowly insectivores which lived during the Cretaceous period and embarked on an arboreal career without the restrictions and limitations imposed by . . . a terrestrial mode of life.¹⁹

According to Le Gros Clark’s ladder paradigm of primate evolution, the origin of anthropoids was simply one of several important steps along the path from tree shrew to human. This particular step corresponds to a significant evolutionary transition, from more primitive prosimians to more advanced anthropoids, marked by such novel anatomical features as a bigger brain, more forward-facing eyes enclosed in bony eye sockets, and a reduction of the snout. Needless to say, because anthropoids evolved from prosimians, they must have originated later in time.

Later students of the primate fossil record eventually abandoned Le Gros Clark’s concept that the evolution of this group entailed a steady progression toward humans. But Le Gros Clark’s ladder continues to influence studies of primate evolution to this day. In terms of interpreting the primate fossil record, the ladder paradigm sustains modern attempts to link undoubted anthropoids with earlier fossil prosimians in a simple ancestor-descendant fashion.²⁰ Given this mind-set, the earliest anthropoids must have evolved from a group of anatomically advanced prosimians. Because most of these advanced prosimians lived toward the end of the Eocene, the idea that anthropoids originated relatively recently, near the Eocene-Oligocene boundary (about thirty-four million years ago), follows logically from Le Gros Clark’s ladder. Indeed, this notion of a relatively recent origin for anthropoids is intimately related to the ladder’s expectation that a sequence of fossils traversing the “prosimian-anthropoid boundary” will ultimately be uncovered.²¹

uncovered,²¹
[Figure 5
near here.]

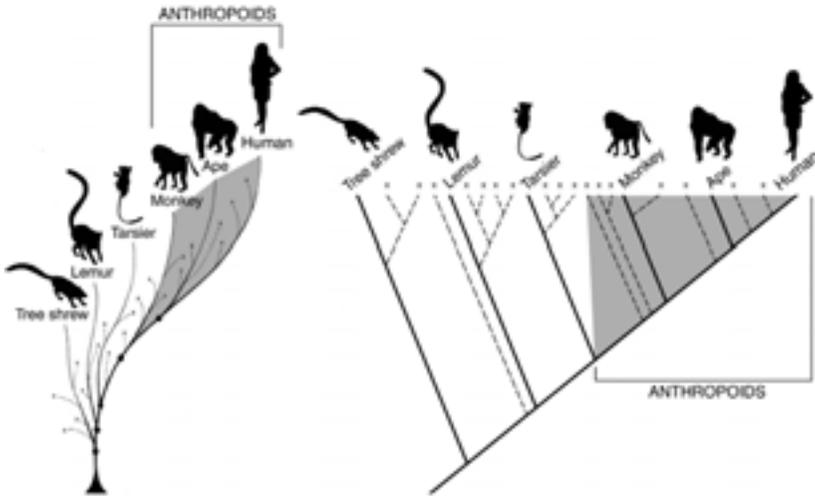


Figure 5. Divergent evolutionary paradigms lead to very different notions of how anthropoids (denoted by stippling) should be defined. According to the ladder paradigm (shown on the left), the earliest anthropoids not only follow prosimians in the fossil record but also differ from them in possessing most of the diagnostic features found in living anthropoids. In contrast, the tree paradigm (shown on the right) posits that the anthropoid lineage originated whenever the lineage leading to living tarsiers bifurcated away from it. In this case, the earliest anthropoids may have been quite ancient, and they may have lacked many, if not most, of the diagnostic features that characterize living anthropoids. Original art by Mark Klingler, copyright Carnegie Museum of Natural History.

The alternative tree paradigm flows from the work of the German entomologist Willi Hennig, whose methodology for reconstructing evolutionary relationships is known as cladistics. Returning once again to the analogy between phylogeny and genealogy, Hennig's approach makes no attempt to identify direct ancestors. Instead, the tree paradigm seeks to determine which species are closer evolutionary cousins. Identifying these closely related species hinges on documenting their shared biological features, especially those features that have arisen relatively recently in evolutionary history. Assuming that all of life on Earth ultimately derives from a single ancestral source, all species must eventually converge at some level on the tree of life. The goal of cladistics is to identify which limbs of this tree sprout nearest one another from a larger, common trunk.

The ladder and tree paradigms differ in several fundamental ways. The tree paradigm views the product of evolution as a constantly branching sequence of lineages, while the ladder paradigm envisions a simpler, ladderlike progression from primitive to advanced. Thus, the tree paradigm

recognizes that the ancient bifurcation between tree shrews and humans established two independent lineages, each of which subsequently experienced its own unique evolutionary history. There is no reason to presume that tree shrews have been frozen in time since they split away from the human lineage, nor is it necessary to postulate that humans underwent a “tree shrew stage” at some early phase in their evolutionary history.

Paleontologists who follow the tree and ladder paradigms often interpret fossils in very different ways. Both sides agree that the quality of the fossil record varies dramatically across space and time. In a few special places, like the Bighorn Basin of Wyoming or the White River Badlands of South Dakota, several million years of evolutionary history are reasonably documented by abundant fossils. These rich sequences of fossil-bearing strata provide a great deal of information about the kinds of animals that inhabited these particular regions during a finite interval of time. Taking the exceptional fossil records from these areas as a kind of gold standard, it is clear that, even in such best-case scenarios, certain animals are well represented as fossils while others are not. In the latter case, there may be major gaps in our knowledge of their anatomy and evolutionary significance. Even if we disregard any distinction between well-known and poorly documented fossils, we must admit that both classes of fossils combined document only a tiny fraction of the Earth’s ancient biological diversity. Once we acknowledge these inherent limitations of the fossil record, the slim chance that any fossil is the direct ancestor of another (or of a living species) becomes immediately apparent.²² Accordingly, the tree paradigm treats fossil species in much the same way that it deals with living ones. They are assumed to be evolutionary cousins, not direct ancestors. The ladder paradigm, on the other hand, is fixated on the issue of direct ancestry. As such, followers of the ladder paradigm are far more likely to propose that a given fossil is directly ancestral to, or near the ancestry of, some later group of organisms.

How do these different evolutionary paradigms bear on the search for anthropoid origins? I believe the paradigms have exerted an enormous influence, because they have affected the way in which different scientists frame the entire debate. Under the tree paradigm, the anthropoid lineage was established, by definition, when the tarsier lineage bifurcated from that leading to anthropoids. It is at least conceivable under the tree paradigm that the origin of anthropoids was very ancient (corresponding to whenever the tarsier and anthropoid lineages split) and that the earliest members of the anthropoid lineage were extremely primitive in their anatomy and other biological attributes. In contrast, the ladder par-

adigm equates the origin of anthropoids with achieving an important evolutionary stage. In this case, anthropoids should differ from prosimians by their acquisition of some key set of anatomical features, or by having crossed a biological threshold separating primitive prosimians from more advanced anthropoids. Hence, the ladder paradigm predicts that the origin of anthropoids was relatively recent (at least compared to their prosimian ancestors) and that the earliest anthropoids must have been anatomically quite advanced.

Given its great antiquity and primitive anatomy, I suspect that *Eosimias* is the key to resolving this dispute about which evolutionary paradigm—the ladder or the tree—best illuminates the deep recesses of our distant past. Looking up from the rock that contains Wen’s small treasure, the oblique rays of light now striking the walls of the ravine remind me once again of the massive timescales that are at play here. The limestone block in my hand containing the world’s oldest fairly complete fossil anthropoid dates to the latter part of the middle Eocene, some forty thousand millennia before our time. The loess walls of the ravine, ancient themselves by human standards, began to be deposited some two thousand millennia ago. The evolutionary history of the human lineage corresponds, in large measure, to the loess. The origins of the anthropoid lineage are at least as ancient as the limestone. The stratigraphic unconformity separating the limestone from the overlying loess equals roughly thirty-eight thousand millennia.

Two conclusions emerge from the mathematics of the ravine’s stratigraphic column. First, the common evolutionary history that we share with other anthropoids far outweighs the unique evolutionary history that is ours alone. Second, if we want to get a better picture of how *Eosimias* fits into the grander scheme of primate and human evolution, we’ve got to venture well beyond this ravine. Our itinerary begins on the other side of the vast Eurasian landmass, where the first chapter in this saga was written some two hundred years ago.