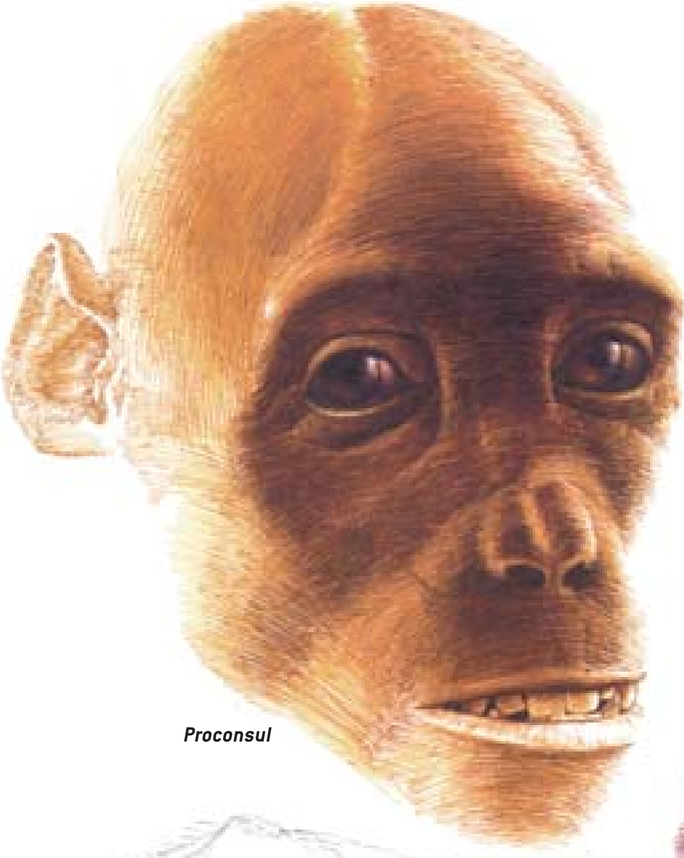
PLANET OF THE



Proconsul

Dryopithecus

Sivapithecus

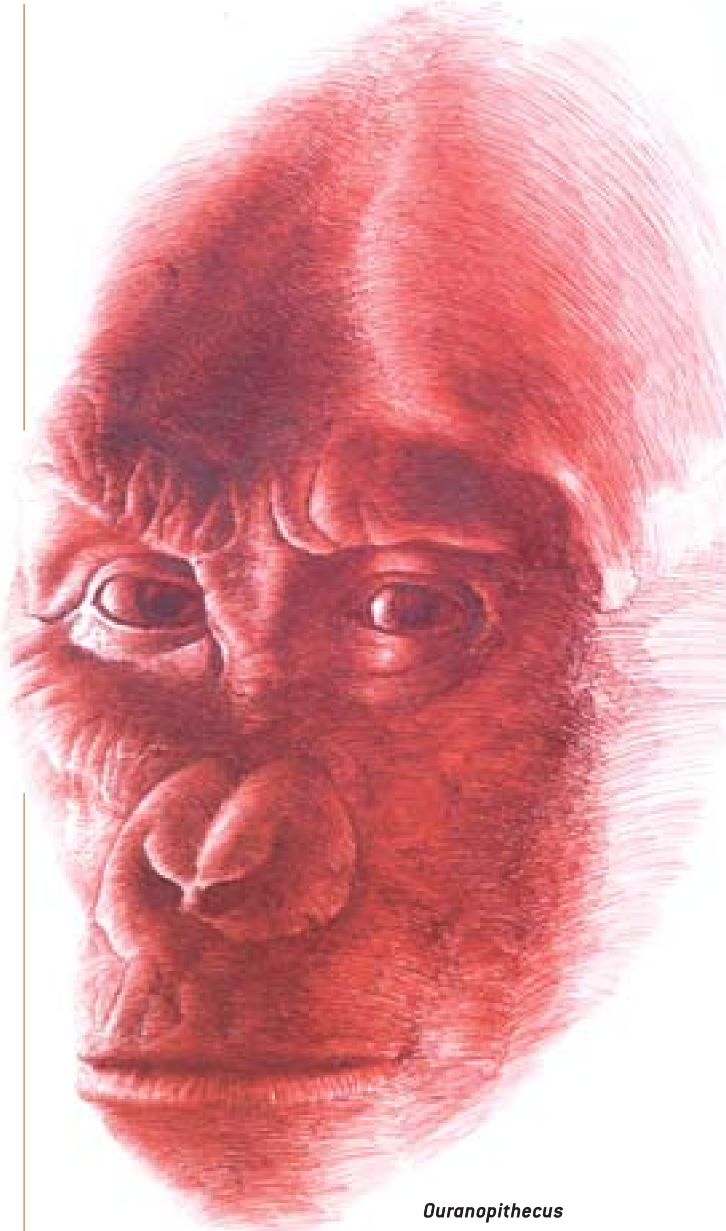
A DIVERSITY OF APES ranged across the Old World during the Miocene epoch, between 22 million and 5.5 million years ago. *Proconsul* lived in East Africa, *Oreopithecus* in Italy, *Sivapithecus* in South Asia, and *Ouranopithecus* and *Dryopithecus*—members of the lineage thought to have given rise to African apes and humans—in Greece and western and central Europe, respectively. These renderings were created through a process akin to that practiced by forensic illustrators. To learn more about how artist John Gurche drew flesh from stone, check out www.sciam.com/ontheweb

APES

By David R. Begun

Fossil ape reconstructions by John Gurche

During the Miocene epoch, as many as 100 species of apes roamed throughout the Old World. New fossils suggest that the ones that gave rise to living great apes and humans evolved not in Africa but Eurasia

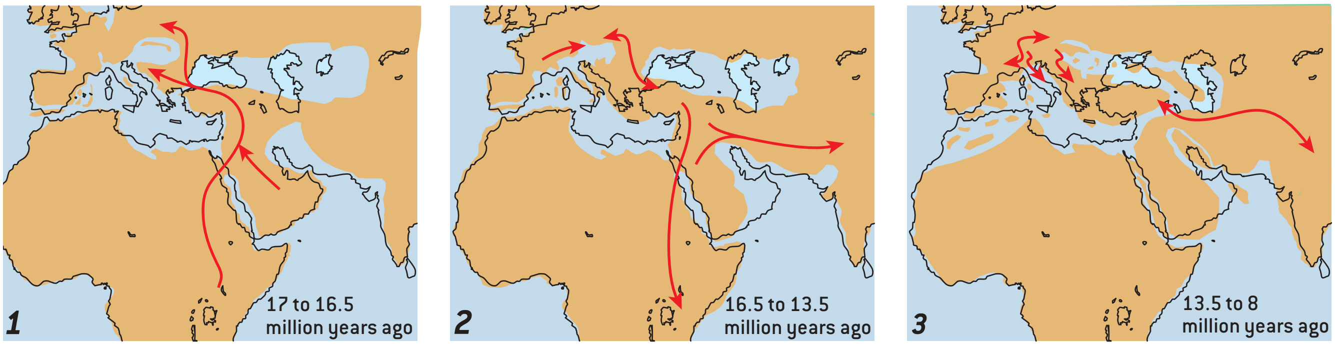


Ouranopithecus

Oreopithecus

"It is therefore probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee; as these two species are now man's closest allies, it is somewhat more probable that our early progenitors lived on the African continent than elsewhere."

So mused Charles Darwin in his 1871 work, *The Descent of Man.* Although no African fossil apes or humans were known at the time, remains recovered since then have largely confirmed his sage prediction about human origins. There is, however, considerably more complexity to the story than even Darwin could have imagined. Current fossil and genetic analyses indicate that the last common ancestor of humans and our closest living relative, the chimpanzee, surely arose in Africa, around six million to eight million years ago. But from where did this creature's own forebears come? Paleoanthropologists have long presumed that they, too,



had African roots. Mounting fossil evidence suggests that this received wisdom is flawed.

Today's apes are few in number and in kind. But between 22 million and 5.5 million years ago, a time known as the Miocene epoch, apes ruled the primate world. Up to 100 ape species ranged throughout the Old World, from France to China in Eurasia and from Kenya to Namibia in Africa. Out of this dazzling diversity, the comparatively limited number of apes and humans arose. Yet fossils of great apes—the large-bodied group represented today by chimpanzees, gorillas and orangutans (gibbons and siamangs make up the so-called lesser apes)—have turned up only in western and central Europe, Greece, Turkey, South Asia and China. It is thus becoming clear that, by Darwin's logic, Eurasia is more likely than Africa to have been the birthplace of the family that encompasses great apes and humans, the hominids. (The term "hominid" has traditionally been reserved for humans and protohumans, but scientists are increasingly placing our great ape kin in the definition as well and using another word, "hominin," to refer to the human subset. The word "hominoid" encompasses all apes—including gibbons and siamangs—and humans.)

Perhaps it should not come as a surprise that the apes that gave rise to hominids may have evolved in Eurasia instead of Africa: the combined effects of migration, climate change, tectonic activity and ecological shifts on a scale unsurpassed since the Miocene made this region a hotbed of hominoid evolutionary experimentation. The result was a panoply of apes, two lineages of which would eventually find themselves well positioned to colonize Southeast Asia and Africa and ultimately to spawn modern great apes and humans.

Paleoanthropology has come a long way since Georges Cuvier, the French natural historian and founder of vertebrate paleontology, wrote in 1812 that "*l'homme fossile n'existe pas*" ("fossil man does not exist"). He included all fossil primates in his declaration. Although that statement seems unreasonable today, evidence that primates lived alongside animals then known to be extinct—mastodons, giant ground sloths and primitive ungulates, or hoofed mammals, for example—was quite poor. Ironically, Cuvier himself described what scholars would later identify as the first fossil primate ever named, *Adapis parisiensis* Cuvier 1822, a lemur from the chalk mines of Paris that he mistook for an ungulate. It wasn't until 1837, shortly after Cuvier's death, that his disciple Édouard Lartet described the first fossil higher primate recognized as such. Now known as *Pliopithecus,* this jaw from southeastern France, and other specimens like it, finally convinced scholars that such creatures had once inhabited the primeval forests of Europe. Nearly 20 years later Lartet unveiled the first fossil great ape, *Dryopithecus,* from the French Pyrénées.

In the remaining years of the 19th century and well into the 20th, paleontologists recovered many more fragments of ape jaws and teeth, along with a few limb bones, in Spain, France, Germany, Austria, Slovakia, Hungary, Georgia and Turkey. By the 1920s, however, attention had shifted from Europe to South Asia (India and Pakistan) and Africa (mainly Kenya), as a result of spectacular finds in those regions, and the apes of Eurasia were all but forgotten. But fossil discoveries of the past two decades have rekindled intense interest in Eurasian fossil apes, in large part because paleontologists have at last recovered specimens complete enough to address what these animals looked like and how they are related to living apes and humans.

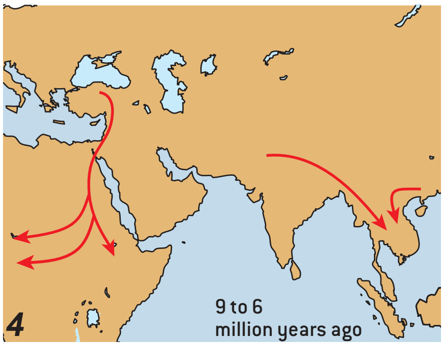
The First Apes

TO DATE, RESEARCHERS have identified as many as 40 genera of Miocene fossil apes from localities across the Old World—eight times the number that survive today. Such diversity seems to have characterized the ape family from the outset: almost as soon as apes appear in the fossil record, there are lots of them. So far 14 genera are known to have inhabited Africa during the early Miocene alone, between 22 million and 17 million years ago. And considering the extremely im-

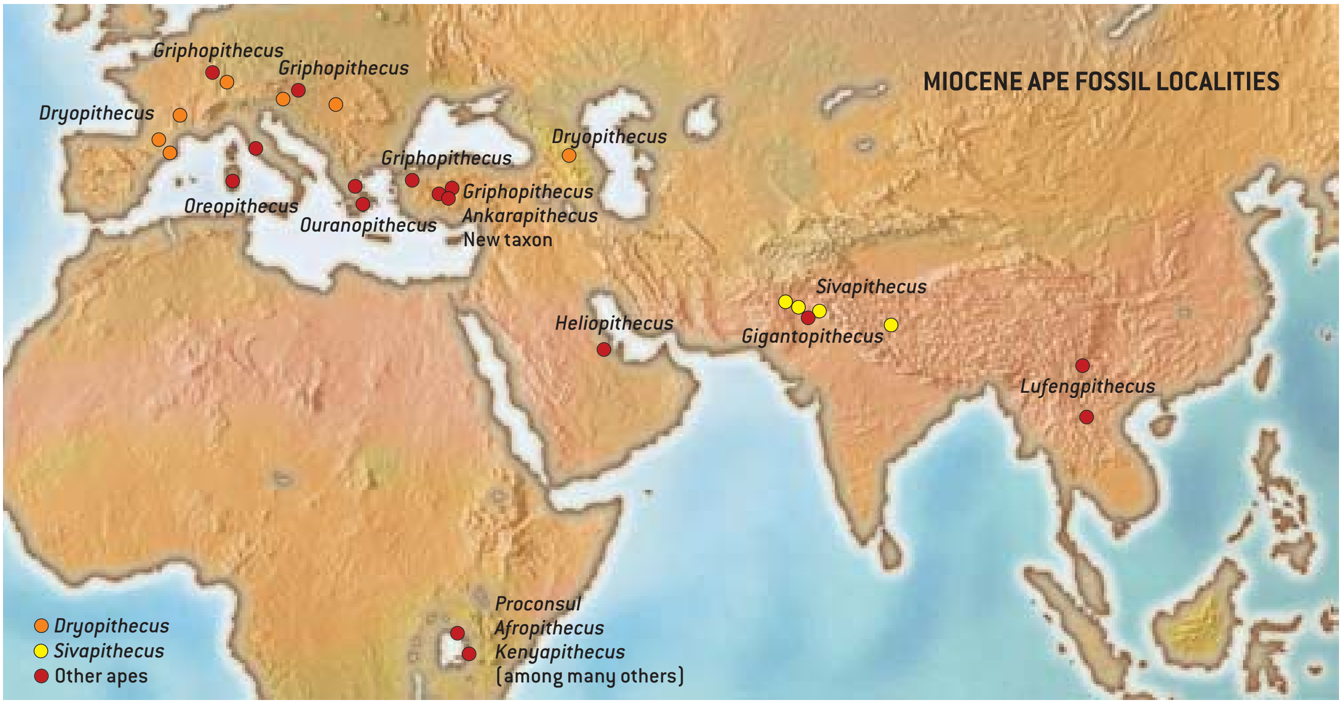
Overview/Ape Revolution

- Only five ape genera exist today, and they are restricted to a few pockets of Africa and Southeast Asia. Between 22 million and 5.5 million years ago, in contrast, dozens of ape genera lived throughout the Old World.
- Scientists have long assumed that the ancestors of modern African apes and humans evolved solely in Africa. But a growing body of evidence indicates that although Africa spawned the first apes, Eurasia was the birthplace of the great ape and human clade.
- The fossil record suggests that living great apes and humans are descended from two ancient Eurasian ape lineages: one represented by *Sivapithecus* from Asia (the probable forebear of the orangutan) and the other by *Dryopithecus* from Europe (the likely ancestor of African apes and humans).

LAURIE GRACE; MAP SOURCE: F. RÖGL IN *THE MIOCENE LAND MAMMALS OF EUROPE*, EDITED BY G. RÖSSNER AND K. HEISSIG. VERLAG DR. FRIEDRICH PFEIL, 1999



APES ON THE MOVE: Africa was the cradle of apekind, having spawned the first apes more than 20 million years ago. But it was not long before these animals colonized the rest of the Old World. Changes in sea level alternately connected Africa to and isolated it from Eurasia and thus played a critical role in ape evolution. A land bridge joining East Africa to Eurasia between 17 million and 16.5 million years ago enabled early Miocene apes to invade Eurasia (*1*). Over the next few million years, they spread to western Europe and the Far East, and great apes evolved; some primitive apes returned to Africa (*2*). Isolated from Africa by elevated sea levels, the early Eurasian great apes radiated into a number of forms (*3*). Drastic climate changes at the end of the Late Miocene wiped out most of the Eurasian great apes. The two lineages that survived—those represented by *Sivapithecus* and *Dryopithecus*—did so by moving into Southeast Asia and the African tropics (*4*).



perfect nature of the fossil record, chances are that this figure significantly underrepresents the number of apes that actually existed at that time.

Like living apes, these creatures varied considerably in size. The smallest weighed in at a mere three kilograms, hardly more than a small housecat; the largest tipped the scales at a gorillalike heft of 80 kilograms. They were even more diverse than their modern counterparts in terms of what they ate, with some specializing in leaves and others in fruits and nuts, although the majority subsisted on ripe fruits, as most apes do today. The biggest difference between those first apes and extant ones lay in their posture and means of getting around. Whereas modern apes exhibit a rich repertoire of locomotory modes—from the highly acrobatic brachiation employed by the arboreal gibbon to the gorilla's terrestrial knuckle walking—early Miocene apes were obliged to travel along tree branches on all fours.

To understand why the first apes were restricted in this way, consider the body plan of the early Miocene ape. The best-known ape from this period is *Proconsul*, exceptionally complete fossils of which have come from sites on Kenya's Rusinga Island [see "The Hunt for Proconsul," by Alan Walker and Mark Teaford; SCIENTIFIC AMERICAN, January 1989]. Specialists currently recognize four species of *Proconsul*, which ranged in size from about 10 kilograms to possibly as much as 80 kilograms. *Proconsul* gives us a good idea of the anatomy and locomotion of an early ape. Like all extant apes, this one lacked a tail. And it had more mobile hips, shoulders, wrists, ankles, hands and feet than those of monkeys, presaging the fundamental adaptations that today's apes and humans have for flexibility in these joints. In modern apes, this augmented mobility enables their unique pattern of movement, swinging from branch to branch. In humans, these capabilities have been exapted, or borrowed, in an evolutionary sense, for enhanced manipulation in the upper limb—something that allowed our ancestors to start making tools, among other things.

At the same time, however, *Proconsul*

THE AUTHOR

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What Is an Ape, Anyway?

MONKEY *PROCONSUL* GREAT APE

LIVING APES—chimpanzees, gorillas, orangutans, gibbons and siamangs—and humans share a constellation of traits that set them apart from other primates. To start, they lack an external tail, which is more important than it may sound because it means that the torso and limbs must meet certain requirements of movement formerly executed by the tail. Apes and humans thus have highly flexible limbs, enabling them to lift their arms above their heads and to suspend themselves by their arms. (This is why all apes have long and massive arms compared to their legs; humans, for their part, modified their limb proportions as they became bipedal.) For the same reason, all apes have broad chests, short lower backs, mobile hips and ankles, powerfully grasping feet and a more vertical posture than most other primates have. In addition, apes are relatively big, especially the great apes (chimps, gorillas and orangutans), which grow and reproduce much more slowly than other simians do. Great apes and humans also possess the largest brains in the primate realm and are more intelligent by nearly all measures—tool use, mirror self-recognition, social complexity and foraging strategy, among them—than any other mammal.

Fossil apes, then, are those primates that more closely resemble living apes than anything else. Not surprisingly, early forms have fewer of the defining ape characteristics than do later models. The early Miocene ape *Proconsul,* for example, was tailless, as evidenced by the morphology of its sacrum, the base of the backbone, to which a tail would attach if present. But *Proconsul* had not yet evolved the limb mobility or brain size associated with modern apes. Researchers generally agree that the 19-million-year-old *Proconsul* is the earliest unambiguous ape in the fossil record. The classification of a number of other early Miocene "apes"—including *Limnopithecus, Rangwapithecus, Micropithecus, Kalepithecus* and *Nyanzapithecus*—has proved trickier, owing to a lack of diagnostic postcranial remains. These creatures might instead be more primitive primates that lived before Old World monkeys and apes went their separate evolutionary ways. I consider them apes mainly because of the apelike traits in their jaws and teeth. *—D.R.B.*

and its cohorts retained a number of primitive, monkeylike characteristics in the backbone, pelvis and forelimbs, leaving them, like their monkey forebears, better suited to traveling along the tops of tree branches than hanging and swinging from limb to limb. (Intriguingly, one enigmatic early Miocene genus from Uganda, *Morotopithecus,* may have been more suspensory, but the evidence is inconclusive.) Only when early apes shed more of this evolutionary baggage could they begin to adopt the forms of locomotion favored by contemporary apes.

Passage to Eurasia

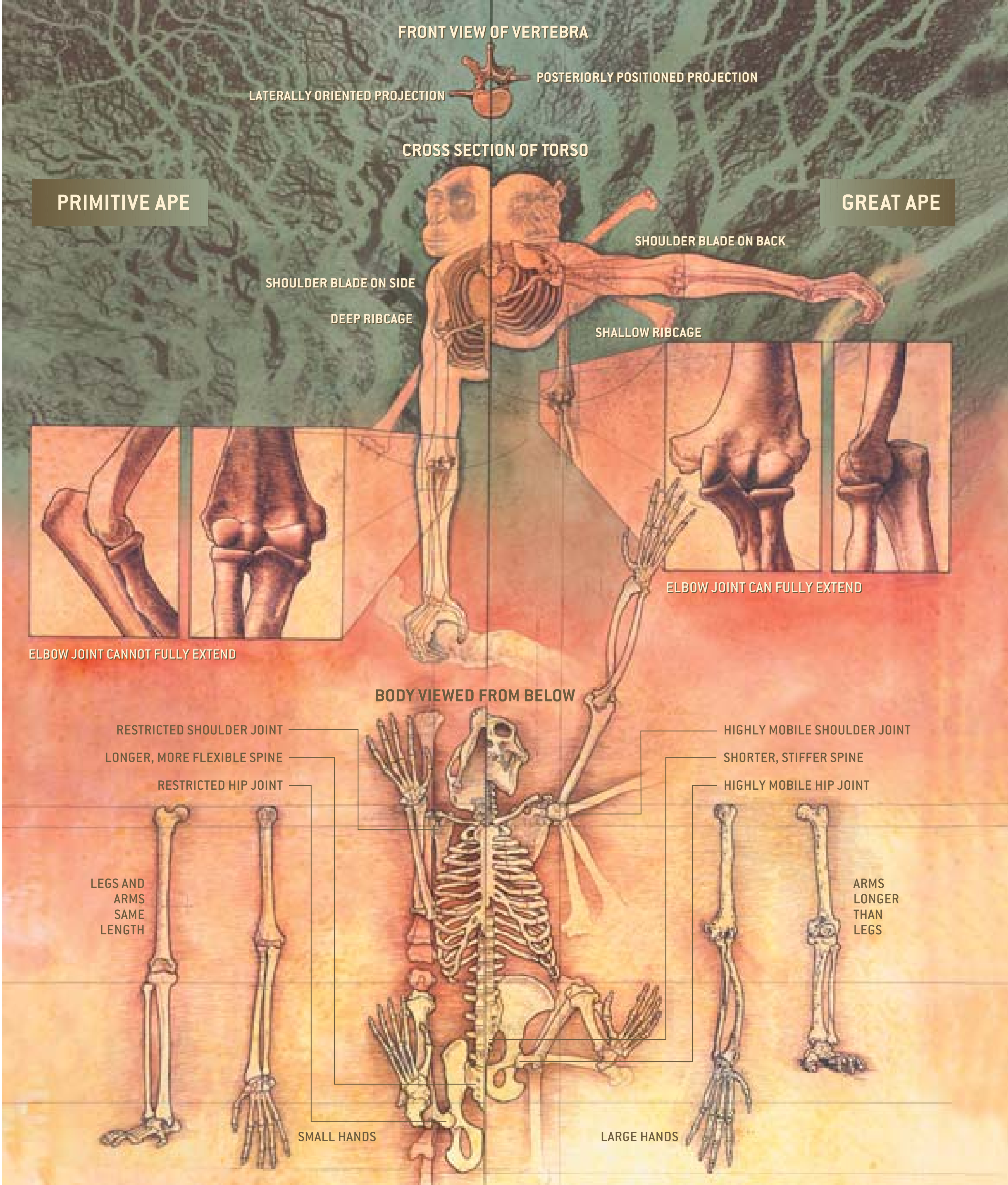
MOST OF THE EARLY Miocene apes went extinct. But one of them—perhaps *Afropithecus* from Kenya—was ancestral to the species that first made its way over to Eurasia some 16.5 million years ago. At around that time global sea levels dropped, exposing a land bridge between Africa and Eurasia. A mammalian exodus ensued. Among the creatures that migrated out of their African homeland were elephants, rodents, ungulates such as pigs and antelopes, a few exotic animals such as aardvarks, and primates.

The apes that journeyed to Eurasia from Africa appear to have passed through Saudi Arabia, where the remains of *Heliopithecus,* an ape similar to *Afropithecus,* have been found. Both *Afropithecus* and *Heliopithecus* (which some workers regard as members of the same genus) had a thick covering of enamel on their teeth—good for processing hard foods, such as nuts, and tough foods protected by durable husks. This dental innovation may have played a key role in helping their descendants establish a foothold in the forests of Eurasia by enabling them to exploit food resources not available to *Proconsul* and most earlier apes. By the time the seas rose to swallow the bridge linking Africa to Eurasia half a million years later, apes had ensconced themselves in this new land.

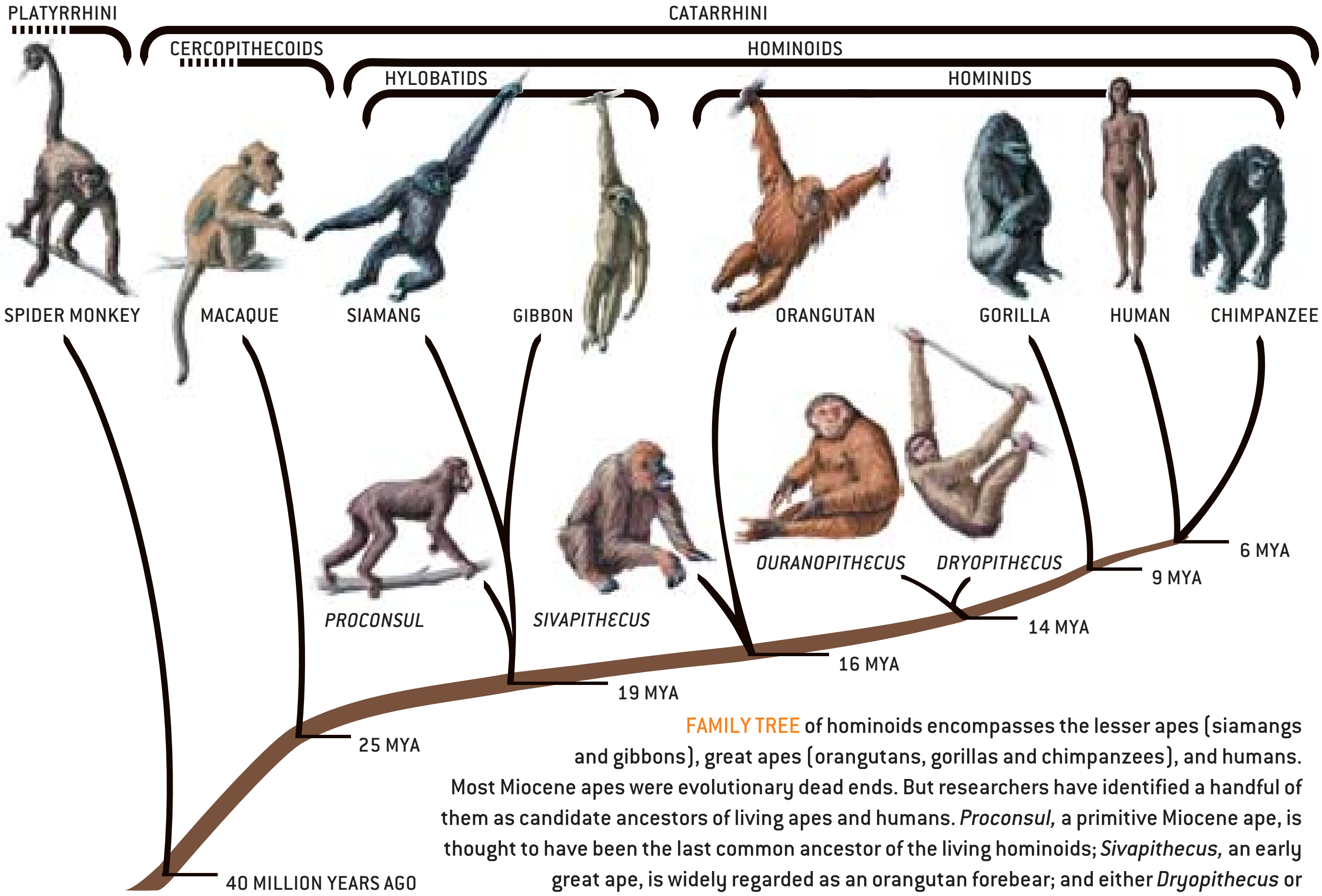
The movement of organisms into new environments drives speciation, and the arrival of apes in Eurasia was no exception. Indeed, within a geologic blink of an eye, these primates adapted to the novel ecological conditions and diversified into a plethora of forms—at least eight known in just 1.5 million years. This flurry of evolutionary activity laid the groundwork for the emergence of great apes and humans. But only recently have researchers begun to realize just how important Eurasia was in this regard. Paleontologists traditionally thought that apes more sophisticated in their food-processing abilities than *Afropithecus* and *Heliopithecus* reached Eurasia about 15 million years ago, around the time they first appear in Africa. This fit with the notion that they arose in Africa and then dispersed northward. New fossil evidence, however, indicates that advanced apes (those with massive jaws and large, grinding teeth) were actually in Eurasia far earlier than that. In 2001 and 2003 my colleagues and I described a more modern-looking ape, *Griphopithecus,* from 16.5-million-year-old sites in Germany and Turkey, pushing the Eurasian ape record back by more than a million years.

The apparent absence of such newer models in Africa between 17 million and 15 million years ago suggests that, contrary to the long-held view of this region as the wellspring of all ape forms, some hominoids began evolving modern cranial and dental features in Eurasia and returned to Africa changed into more advanced species only after the sea receded again. (A few genera—such as *Kenyapithecus* from Fort Ternan, Kenya—may have gone on to develop some postcranial adaptations to life on the ground, but for the most part, these animals still looked

PORTIA SLOAN (*this page*); JOHN GURCHE (*opposite page*)



GOING GREAT APE: Primitive ape body plan and great ape body plan are contrasted here. The earliest apes still had rather monkeylike bodies, built for traveling atop tree limbs on all fours. They possessed a long lower back; projections on their vertebrae oriented for flexibility; a deep rib cage; elbow joints designed for power and speed; shoulder and hip joints that kept the limbs mostly under the body; and arms and legs of similar length. Great apes, in contrast, are adapted to hanging and swinging from tree branches. Their vertebrae are fewer in number and bear a configuration of projections designed to stiffen the spine to support a more vertical posture. Great apes also have a broader, shallower rib cage; a flexible elbow joint that permits full extension of the arm for suspension; highly mobile shoulder and hip joints that allow a much wider range of limb motion; large, powerful, grasping hands; and upper limbs that are longer than their lower limbs.



FAMILY TREE of hominoids encompasses the lesser apes (siamangs and gibbons), great apes (orangutans, gorillas and chimpanzees), and humans. Most Miocene apes were evolutionary dead ends. But researchers have identified a handful of them as candidate ancestors of living apes and humans. *Proconsul,* a primitive Miocene ape, is thought to have been the last common ancestor of the living hominoids; *Sivapithecus,* an early great ape, is widely regarded as an orangutan forebear; and either *Dryopithecus* or *Ouranopithecus* may have given rise to African apes and humans.

PORTIA SLOAN

like their early Miocene predecessors from the neck down.)

Rise of the Great Apes

BY THE END of the middle Miocene, roughly 13 million years ago, we have evidence for great apes in Eurasia, notably Lartet's fossil great ape, *Dryopithecus,* in Europe and *Sivapithecus* in Asia. Like living great apes, these animals had long, strongly built jaws that housed large incisors, bladelike (as opposed to tusklike) canines, and long molars and premolars with relatively simple chewing surfaces—a feeding apparatus well suited to a diet of soft, ripe fruits. They also possessed shortened snouts, reflecting the reduced importance of olfaction in favor of vision. Histological studies of the teeth of *Dryopithecus* and *Sivapithecus* suggest that these creatures grew fairly slowly, as living great apes do, and that they probably had life histories similar to those of the great apes—maturing at a leisurely rate, living long lives, bearing one large offspring at a time, and so forth. Other evidence hints that were they around today, these early great apes might have even matched wits with modern ones: fossil braincases of *Dryopithecus* indicate that it was as large-brained as a chimpanzee of comparable proportions. We lack direct clues to brain size in *Sivapithecus,* but given that life history correlates strongly with brain size, it is likely that this ape was similarly brainy.

Examinations of the limb skeletons of these two apes have revealed additional great ape–like characteristics. Most important, both *Dryopithecus* and *Sivapithecus* display adaptations to suspensory locomotion, especially in the elbow joint, which was fully extendable and stable throughout the full range of motion. Among primates, this morphology is unique to apes, and it figures prominently in their ability to hang and swing below branches. It also gives humans the ability to throw with great speed and accuracy. For its part, *Dryopithecus* exhibits numerous other adaptations to suspension, both in the limb bones and in the hands and feet, which had powerful grasping capabilities. Together these features strongly suggest that *Dryopithecus* negotiated the forest canopy in much the way that living great apes do. Exactly how *Sivapithecus* got around is less clear. Some characteristics of this animal's limbs are indicative of suspension, whereas others imply that it had more quadrupedal habits. In all likelihood, *Sivapithecus* employed a mode of locomotion for which no modern analogue exists—the product of its own unique ecological circumstances.

The *Sivapithecus* lineage thrived in Asia, producing offshoots in Turkey, Pakistan, India, Nepal, China and Southeast Asia. Most phylogenetic analyses concur that it is from *Sivapithecus* that the living orangutan, *Pongo pygmaeus,* is descended. Today this ape, which dwells in the rain forests of Borneo and Sumatra, is the sole survivor of that successful group.

In the west the radiation of great apes was similarly grand. From the earliest species of *Dryopithecus, D. fontani,* the one found by Lartet, several other species emerged over about three million years. More specialized descendants of this lineage followed suit. Within two million

Bigfoot Ballyhoo

A FEW INDIVIDUALS, including some serious researchers, have argued that the *Sivapithecus* lineage of great apes from which the orangutan arose has another living descendant. Details of the beast's anatomy vary from account to account, but it is consistently described as a large, hirsute, nonhuman primate that walks upright and has reportedly been spotted in locales across North America and Asia. Unfortunately, this creature has more names than evidence to support its existence (bigfoot, yeti, sasquatch, nyalmo, rimi, raksi-bombo, the abominable snowman—the list goes on).

Those who believe in bigfoot (on the basis of suspicious hairs, feces, footprints and fuzzy videotape) usually point to the fossil great ape *Gigantopithecus* as its direct ancestor. *Gigantopithecus* was probably two to three times as large as a gorilla and is known to have lived until about 300,000 years ago in China and Southeast Asia.

There is no reason that such a beast could not persist today. After all, we know from the subfossil record that gorilla-size lemurs lived on the island of Madagascar until they were driven to extinction by humans only 1,000 years ago. The problem is that whereas we have fossils of 20-million-year-old apes the size of very small cats, we do not have even a single bone of this putative half-ton, bipedal great ape living in, among other places, the continental U.S. Although every primatologist and primate paleontologist I know would love for bigfoot to be real, the complete absence of hard evidence for its existence makes that highly unlikely. —D.R.B.

ALLEGED bigfoot footprint, photographed near Coos Bay, Ore., in 1976.

BETTMANN/CORBIS

years four new species of *Dryopithecus* would evolve and span the region from northwestern Spain to the Republic of Georgia. But where *Dryopithecus* belongs on the hominoid family tree has proved controversial. Some studies link *Dryopithecus* to Asian apes; others position it as the ancestor of all living great apes. My own phylogenetic analysis of these animals—the most comprehensive in terms of the number of morphological characteristics considered—indicates that *Dryopithecus* is most closely related to an ape known as *Ouranopithecus* from Greece and that one of these two European genera was the likely ancestor of African apes and humans.

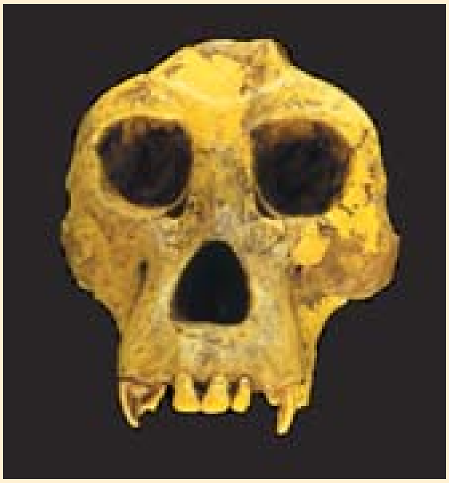
A *Dryopithecus* skull from Rudabánya, Hungary, that my colleagues and I discovered in 1999 bolsters that argument. Nicknamed "Gabi" after its discoverer, Hungarian geologist Gabor Hernyák, it is the first specimen to preserve a key piece of anatomy: the connection between the face and the braincase. Gabi shows that the cranium of *Dryopithecus,* like that of African apes and early fossil humans, had a long and low braincase, a flatter nasal region and an enlarged lower face. Perhaps most significant, it reveals that also like African apes and early humans, *Dryopithecus* was klinorhynch, meaning that viewed in profile its face tilts downward. Orangutans, in contrast—as well as *Proconsul,* gibbons and siamangs—have faces that tilt upward, a condition known as airorhinchy. That fundamental aspect of *Dryopithecus*'s cranial architecture speaks strongly to a close evolutionary relationship between this animal and the African apes and humans lineage. Additional support for that link comes from the observation that the *Dryopithecus* skull resembles that of an infant or juvenile chimpanzee—a common feature of ancestral morphology. It follows, then, that the unique aspects of adult cranial form in chimpanzees, gorillas and fossil humans evolved as modifications to the ground plan represented by *Dryopithecus* and living African ape youngsters.

One more Miocene ape deserves special mention. The best-known Eurasian fossil ape, in terms of the percentage of the skeleton recovered, is seven-million-year-old *Oreopithecus* from Italy. First described in 1872 by renowned French paleontologist Paul Gervais, *Oreopithecus* was more specialized for dining on leaves than was any other Old World fossil monkey or ape. It survived very late into the Miocene in the dense and isolated forests of the islands of Tuscany, which would eventually be joined to one another and the rest of Europe by the retreat of the sea to form the backbone of the Italian peninsula. Large-bodied and small-brained, this creature is so unusual looking that it is not clear whether it is a primitive form that predates the divergence of gibbons and great apes or an early great ape or a close relative of *Dryopithecus*. Meike Köhler and Salvador Moyà-Solà of the Miquel Crusafont Institute of Paleontology in Barcelona have proposed that *Oreopithecus* walked bipedally along tree limbs and had a humanlike hand capable of a precision grip. Most paleoanthropologists, however, believe that it was instead a highly suspensory animal. Whatever *Oreopithecus* turns out to be, it is a striking reminder of how very diverse and successful at adapting to new surroundings the Eurasian apes were.

So what happened to the myriad species that did not evolve into the living great apes and humans, and why did the ancestors of extant species persevere? Clues have come from paleoclimatological studies. Throughout the middle Miocene, the great apes flourished in Eurasia, thanks to its then lush subtropical forest cover and consistently warm temperatures. These conditions assured a nearly continuous supply of ripe fruits and an

Lucky Strikes

FOSSIL FINDS often result from a combination of dumb luck and informed guessing. Such was the case with the discoveries of two of the most complete fossil great ape specimens on record. The first of these occurred at a site known as Can Llobateres in the Vallès Penedès region of Spain. Can Llobateres had been yielding fragments of jaws and teeth since the 1940s, and in the late 1980s I was invited by local researchers to renew excavations there. The first year I discovered little other than how much sunburn and gazpacho I could stand. Undaunted, I returned for a second season, accompanied by my then seven-year-old son, André. During a planning session the day before the work was to begin, André made it clear that, after enduring many hours in a stifling building without air-conditioning, he had had enough, so I took him to see the site. We went to the spots my team had excavated the year before and then wandered up the hillside to other exposures that had looked intriguing but that we had decided not to investigate at that time. After poking around up there with André over the course of our impromptu visit, I resolved to convince my collaborators to dig a test pit in that area at some point during the season.



STELLAR SPECIMENS of *Dryopithecus,* one of the earliest great apes, have come from sites in Spain (*left*) and Hungary (*right*).

The next day we returned to the spot so that I could show a colleague the sediments of interest, and as we worked to clear off some of the overlying dirt, a great ape premolar popped out. We watched in amazement as the tooth rolled down the hill, seemingly in slow motion, and landed at our feet. A few days later we had recovered the first nearly whole face of *Dryopithecus* (*top*) and the most complete great ape from Can Llobateres in the 50-year history of excavations at the site. We subsequently traced the same sedimentological layer across the site and found some limb fragments in another area, which, when excavated more completely in the following year, produced the most complete skeleton of *Dryopithecus* known to this day.

Nine years later in Hungary my Hungarian colleagues and I were starting a new field season at a locality called Rudabánya. Historically, Rudabánya had yielded numerous *Dryopithecus* fossils, mostly teeth and skeletal remains. Intensive excavation over the previous two years, however, failed to turn up any material. For the 1999 season I thought we should concentrate our efforts on

easily traversed arboreal habitat with several tree stories. Climate changes in the late Miocene brought an end to this easy living. The combined effects of Alpine, Himalayan and East African mountain building, shifting ocean currents, and the early stages of polar ice cap formation precipitated the birth of the modern Asian monsoon cycle, the desiccation of East Africa and the development of a temperate climate in Europe. Most of the Eurasian great apes went extinct as a result of this environmental overhaul. The two lineages that did persevere—those represented by *Sivapithecus* and *Dryopithecus*—did so by moving south of the Tropic of Cancer, into Southeast Asia from China and into the African tropics from Europe, both groups tracking the ecological settings to which they had adapted in Eurasia.

The biogeographical model outlined above provides an important perspective on a long-standing question in paleoanthropology concerning how and why humans came to walk on two legs. To address that issue, we need to know from what form of locomotion bipedalism evolved. Lacking unambiguous fossil evidence of the earliest biped and its ancestor, we cannot say with certainty what that ancestral condition was, but researchers generally fall into one of two theoretical camps: those who think two-legged walking arose from arboreal climbing and suspension and those who think it grew out of a terrestrial form of locomotion, perhaps knuckle walking.

Your Great, Great Grand Ape

THE EURASIAN FOREBEAR of African apes and humans moved south in response to a drying and cooling of its environs that led to the replacement of forests with woodlands and grasslands. I believe that adaptations to life on the ground—knuckle walking in particular—were critical in enabling this lineage to withstand that loss of arboreal habitat and make it to Africa. Once there, some apes returned to the forests, others settled into varied woodland environments, and one ape—the one from which humans descended—eventually invaded open territory by committing to life on the ground.

Flexibility in adaptation is the consistent message in ape and human evolution. Early Miocene apes left Africa because of a new adaptation in their jaws and teeth that allowed them to exploit a diversity of ecological settings. Eurasian great apes evolved an array of skeletal adaptations that permitted them to live in varied environments as well as large brains to grapple with complex social and ecological challenges. These modifications made it possible for a few of them to survive the dramatic climate changes that took place at the end of the Miocene and return to

DAVID R. BEGUN

a dark layer of sediments suggestive of a high organic content often associated with abundant fossils. That layer was visible in a north-south cross section of the site, becoming lighter and, I thought, less likely to have fossils, toward the north. I asked Hungarian geologist and longtime amateur excavator Gabor Hernyák to start on the north end and work his way south toward the presumed pay dirt. But within less than a minute, Gabor excitedly summoned me back to the spot where I had left him. There, in what appeared to be the fossil-poor sediment, he had uncovered a tiny piece of the upper jaw of *Dryopithecus*. By the time we finished extracting the fossil, we had the most complete cranium of *Dryopithecus* ever found and the first one with the face still attached to the braincase (*bottom*).

This skull from Rudabánya—dubbed "Gabi" after its discoverer—illustrates more clearly than any other specimen the close relation between *Dryopithecus* and the African apes. I will always remember the look on my friend and co-director László Kordos's face when I went back to the village. (I made the 15-minute car trip in five minutes at most.) He was in the middle of e-mailing someone and looked up, quite bored, asking, "What's new?" "Oh, nothing much," I replied. "We just found a *Dryopithecus* skull." —*D.R.B.*

Africa, around nine million years ago. Thus, the lineage that produced African apes and humans was preadapted to coping with the problems of a radically changing environment. It is therefore not surprising that one of these species eventually evolved very large brains and sophisticated forms of technology.

As an undergraduate more than 20 years ago, I began to look at fossil apes out of the conviction that to understand why humans evolved we have to know when, where, how and from what we arose. Scientists commonly look to living apes for anatomical and behavioral insights into the earliest humans. There is much to be gained from this approach. But living great apes have also evolved since their origins. The study of fossil great apes gives us both a unique view of the ancestors of living great apes and humans and a starting point for understanding the processes and circumstances that led to the emergence of this group. For example, having established the connection between European great apes and living African apes and humans, we can now reconstruct the last common ancestor of chimps and humans: it was a knuckle-walking, fruit-eating, forest-living chimplike primate that used tools, hunted animals, and lived in highly complex and dynamic social groups, as do living chimps and humans.

Tangled Branches

WE STILL HAVE MUCH to learn. Many fossil apes are represented only by jaws and teeth, leaving us with little or no idea about their posture and locomotion, brain size or body mass. Moreover, paleontologists have yet to recover any remains of ancient African great apes. Indeed, there is a substantial geographic and temporal gap in the fossil record between representatives of the early members of the African hominid lineage in Europe (*Dryopithecus* and *Ouranopithecus*) and the earliest African fossil hominids.

Moving up the family tree (or, more accurately, family bush), we find more confusion in that the earliest putative members of the human family are not obviously human. For instance, the recently discovered *Sahelanthropus tchadensis,* a six-million- to seven-million-year-old find from Chad, is humanlike in having small canine teeth and perhaps a more centrally located foramen magnum (the hole at the base of the skull through which the spinal cord exits), which could indicate that the animal was bipedal. Yet *Sahelanthropus* also exhibits a number of chimplike characteristics, including a small brain, projecting face, sloped forehead and large neck muscles. Another creature, *Orrorin tugenensis,* fossils of which come from a Kenyan site dating to six million years ago, exhibits a comparable mosaic of chimp and human traits, as does 5.8-million-year-old *Ardipithecus ramidus kadabba* from Ethiopia. Each of these taxa has been described by its discoverers as a human ancestor [see "An Ancestor to Call Our Own," by Kate Wong; SCIENTIFIC AMERICAN, January]. But in truth, we do not yet know enough about any of these creatures to say whether they are protohumans, African ape ancestors or dead-end apes. The earliest unambiguously human fossil, in my view, is 4.4-million-year-old *Ardipithecus ramidus ramidus,* also from Ethiopia.

The idea that the ancestors of great apes and humans evolved in Eurasia is controversial, but not because there is inadequate evidence to support it. Skepticism comes from the legacy of Darwin, whose prediction noted at the beginning of this article is commonly interpreted to mean that humans and African apes must have evolved solely in Africa. Doubts also come from fans of the aphorism "absence of evidence is not evidence of absence." To wit, just because we have not found fossil great apes in Africa does not mean that they are not there. This is true. But there are many fossil sites in Africa dated to between 14 million and seven million years ago—some of which have yielded abundant remains of forest-dwelling animals—and not one contains great ape fossils. Although it is possible that Eurasian great apes, which bear strong resemblances to living great apes, evolved in parallel with as yet undiscovered African ancestors, this seems unlikely.

It would be helpful if we had a more complete fossil record from which to piece together the evolutionary history of our extended family. Ongoing fieldwork promises to fill some of the gaps in our knowledge. But until then, we must hypothesize based on what we know. The view expressed here is testable, as required of all scientific hypotheses, through the discovery of more fossils in new places. SA

MORE TO EXPLORE

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