SPECIAL EDITION

SCIENTIFIC AMERICAN

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Becoming Human

Evolution and the Rise of Intelligence

BRAINPOWER Dawn of the Modern Mind

BODY SHAPE Food and Physique

MIGRATION The First Explorers

LANGUAGE Ancient Roots of Speech

CULTURE The Art of Survival

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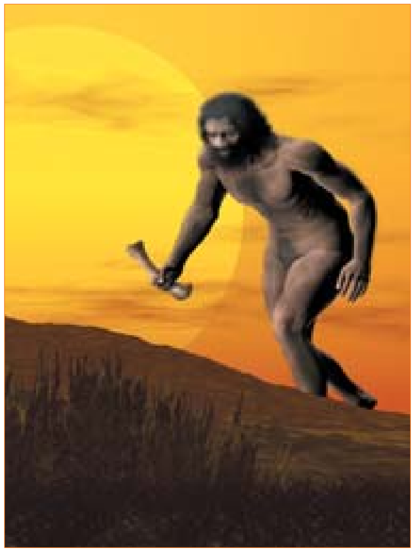
letter from the editor

An Unlikely Ascendancy



PHIL SAUNDERS *Space Channel Ltd.*

A SAVVY HANDICAPPER would never have put money on the continued existence of this evolutionary dark horse. Nearly hairless, weak—no sharp claws or slicing teeth here—and slow, with a bumpy bipedal gait, humans might initially appear to be one of the unlikeliest survivors on earth. Except for the oversize brains.

As the articles in this special edition collectively underscore, so much of the rise of our ancestors from humble beginnings to today's world-dominant swell of humanity tracked the stunning growth of all that furrowed cortex. From roughly two million years to 250,000 years ago, the brain's total volume expanded by a tablespoonful every 100,000 years, estimates Harvard University biologist E. O. Wilson. If we could stretch a modern person's cortex flat, it would occupy an area the size of four sheets of standard letter-size paper. In contrast, a chimp's would cover one sheet; a monkey's, a postcard; and a rat's, a stamp.

But size alone does not explain our matchless reasoning skills. One of the mysteries of human evolution is that other species with large brains (such as Neandertals) seemingly did not achieve comparable levels of cognition. Could a cultural innovation, perhaps driven by rapid environmental changes, have contributed to the rise of symbolic thought, language and cooperative group society? Ian Tattersall speculates along these lines in "How We Came to Be Human," starting on page 66, and William H. Calvin explores "The Emergence of Intelligence," beginning on page 84.

As our primate ancestors' intellects deepened, their bodies continued to morph. Their need to stoke the energy-consuming organ in their skulls with nutritious, calorie-rich fuel created selection pressure favoring features now characteristic of primates, such as grasping hands with opposable thumbs, relates Katharine Milton in "Diet and Primate Evolution," starting on page 22. "To a great extent," concludes Milton, "we are truly what we eat." Other articles in the issue explore how and when early humans and our ape cousins began to sprawl around the planet.

Even as recent discoveries answer some questions about our fascinating and complex history, they raise others. Alone among creatures alive today, we enjoy the ability to contemplate our species' odyssey through time. Food for thought.

Mariette DiChristina
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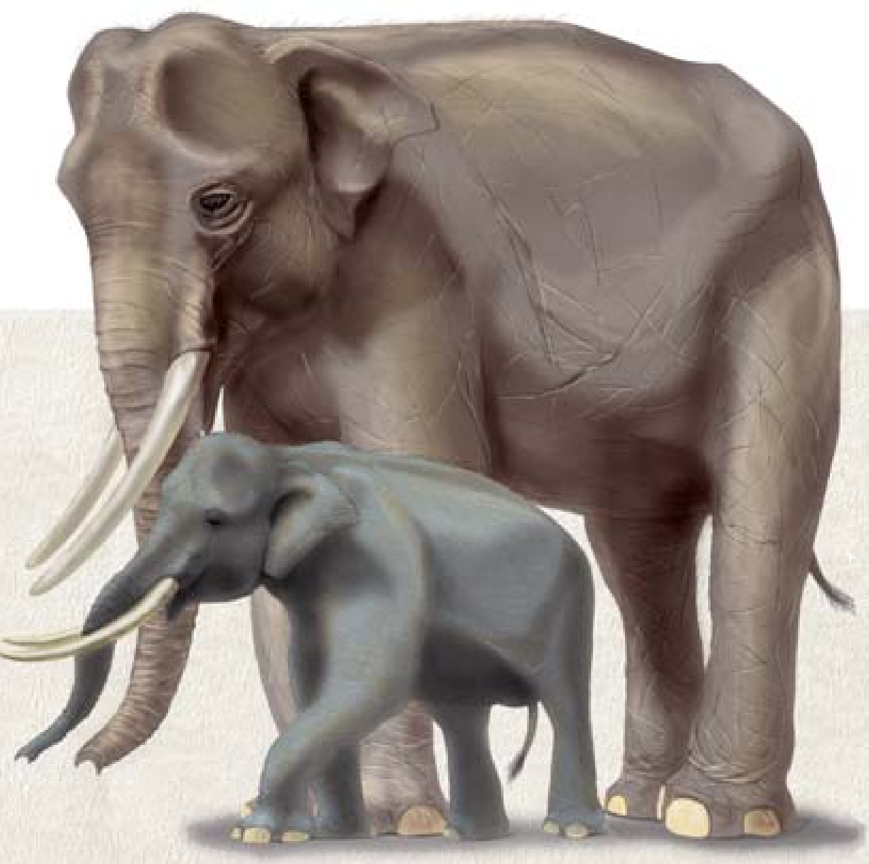

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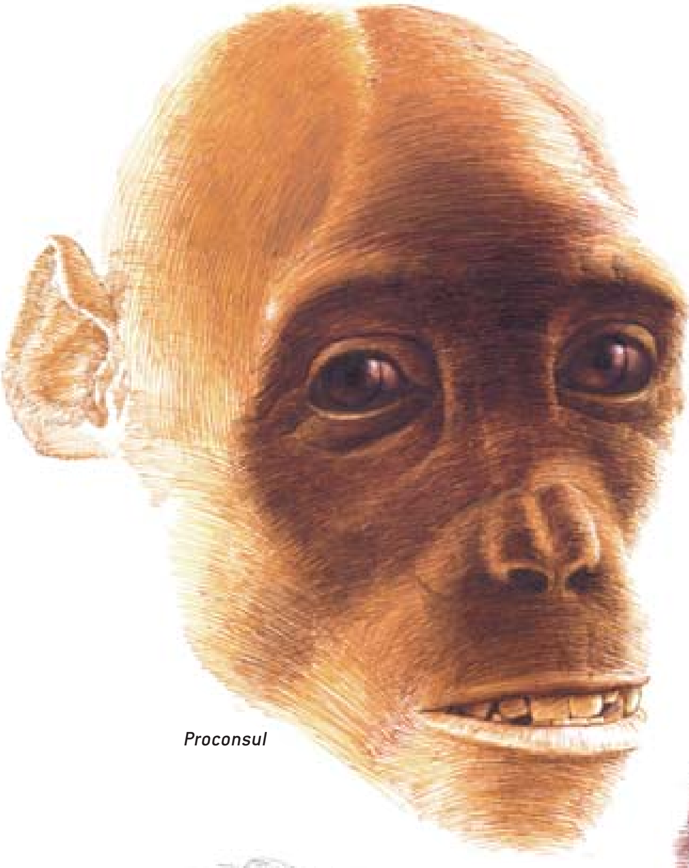
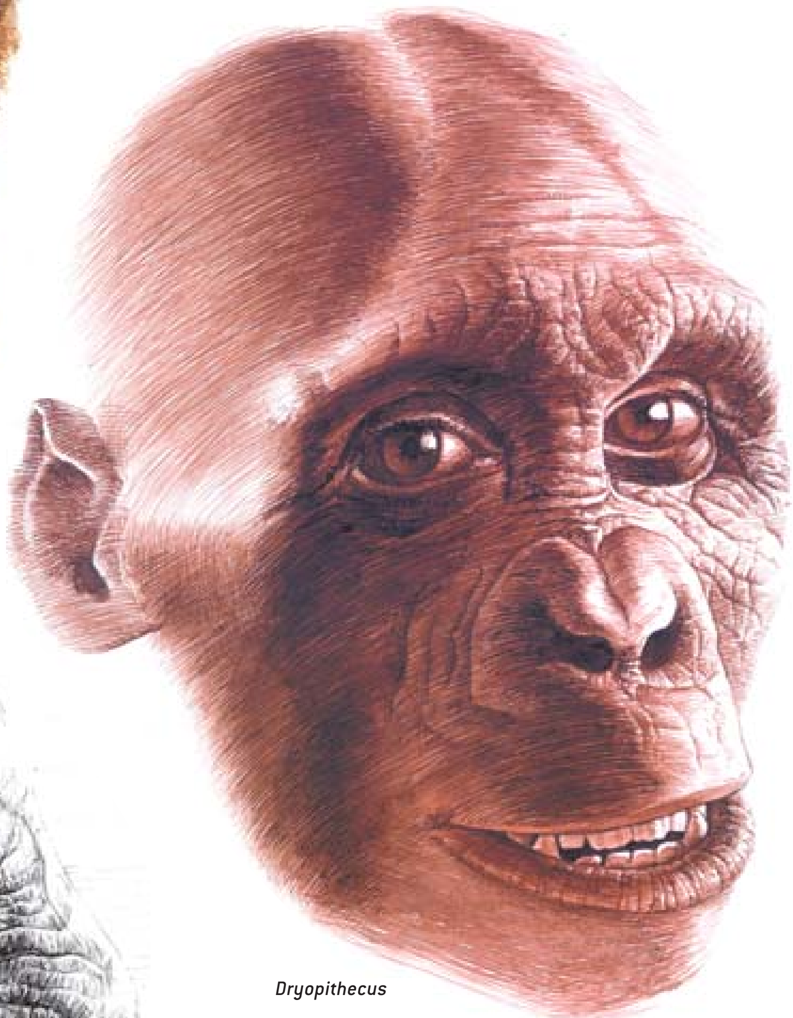
Planet of the



Proconsul



Dryopithecus

Sivapithecus

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.

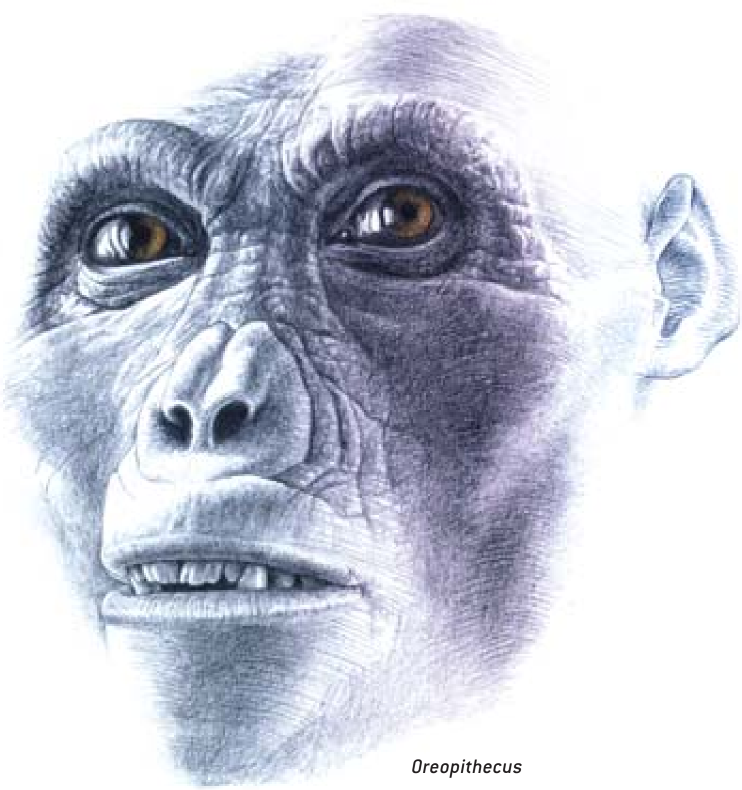
Apes

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

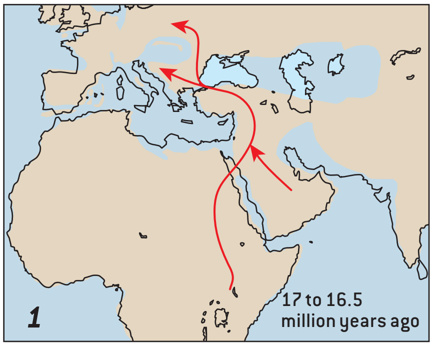


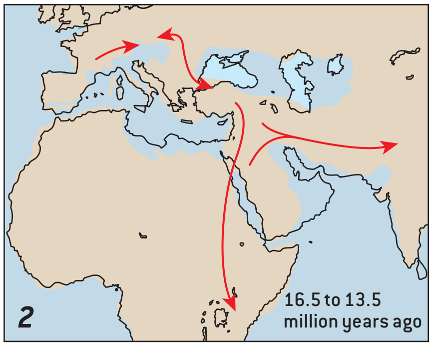
Oreopithecus

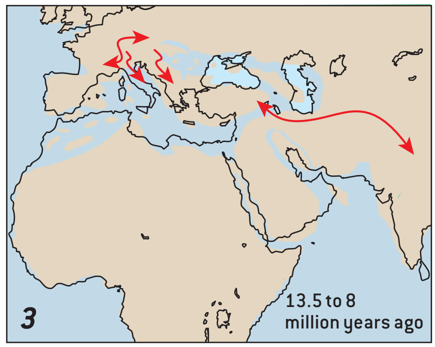
"It is therefore probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee; as these two species are now man's closest allies, it is somewhat more probable that our early progenitors lived on the African continent than elsewhere."

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







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

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 was not 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 western 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.

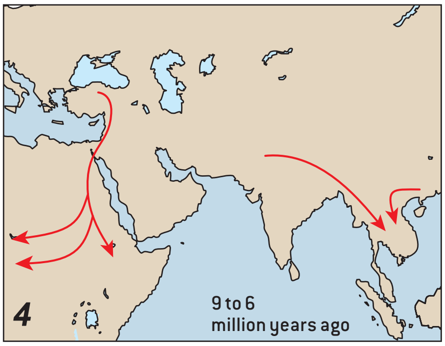
The First Apes

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

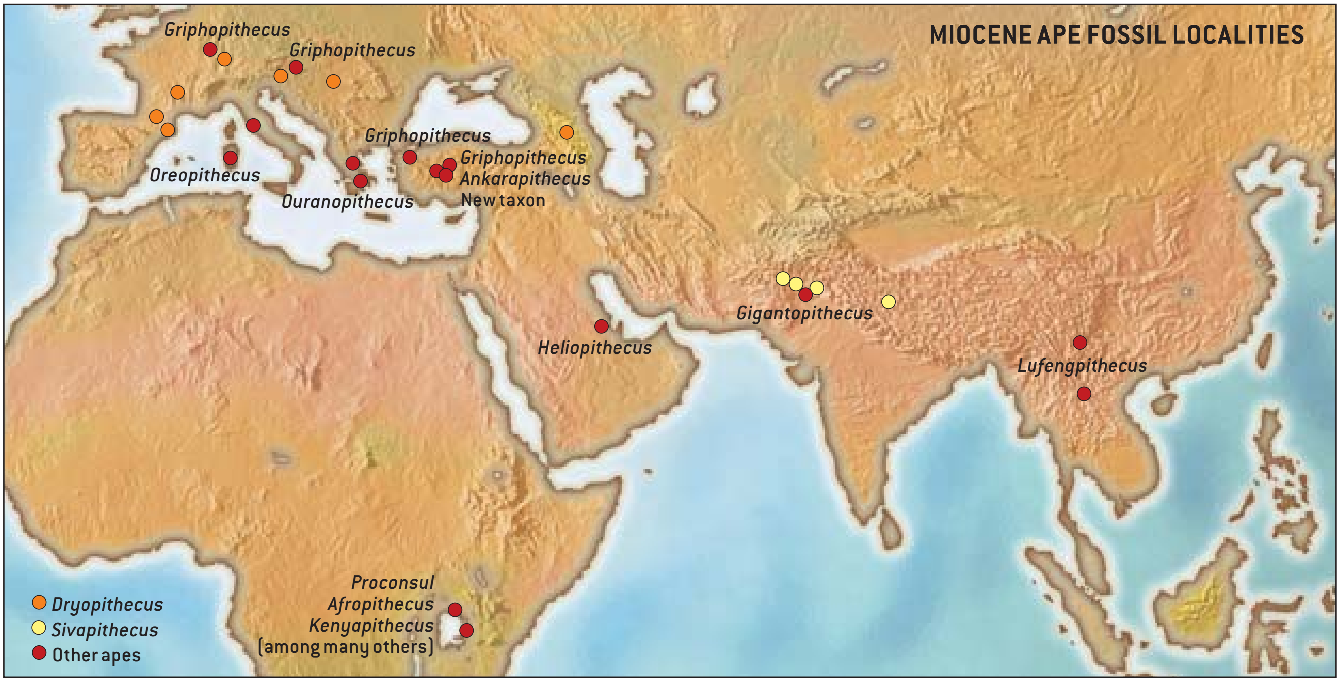
Like living apes, these creatures varied considerably in size. The smallest weighed in at a mere three kilograms, hardly more than a small housecat; the largest tipped the scales at a gorillalike

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).



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*).



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.

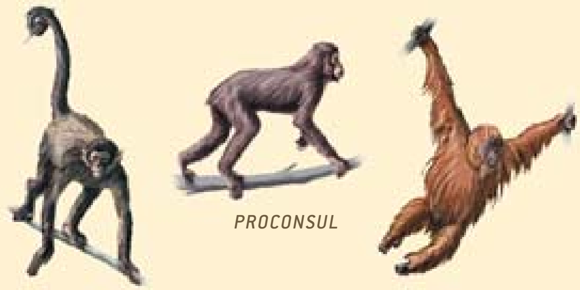
To understand why the first apes were restricted in this way, consider the body plan of the Early Miocene ape. The best-known ape from this period is *Proconsul*, exceptionally complete fossils of which have come from sites on Kenya's Rusinga Island. Specialists currently recognize four species of *Proconsul*, 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* 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.

THE AUTHOR

DAVID R. BEGUN is professor of anthropology at the University of Toronto. He received his Ph.D. in physical anthropology from the University of Pennsylvania in 1987. Focusing on Miocene hominoid evolution, Begun has excavated and surveyed fossil localities in Spain, Hungary, Turkey and Kenya. He is currently working with colleagues in Turkey and Hungary on several fossil ape sites and is trying to reconstruct the landscapes and mammalian dispersal patterns that characterized the Old World between 20 million and two million years ago.

What Is an Ape, Anyway?



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, massive arms compared with 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 because of 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.*

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 to Eurasia some 16.5 million years ago. 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 went 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.

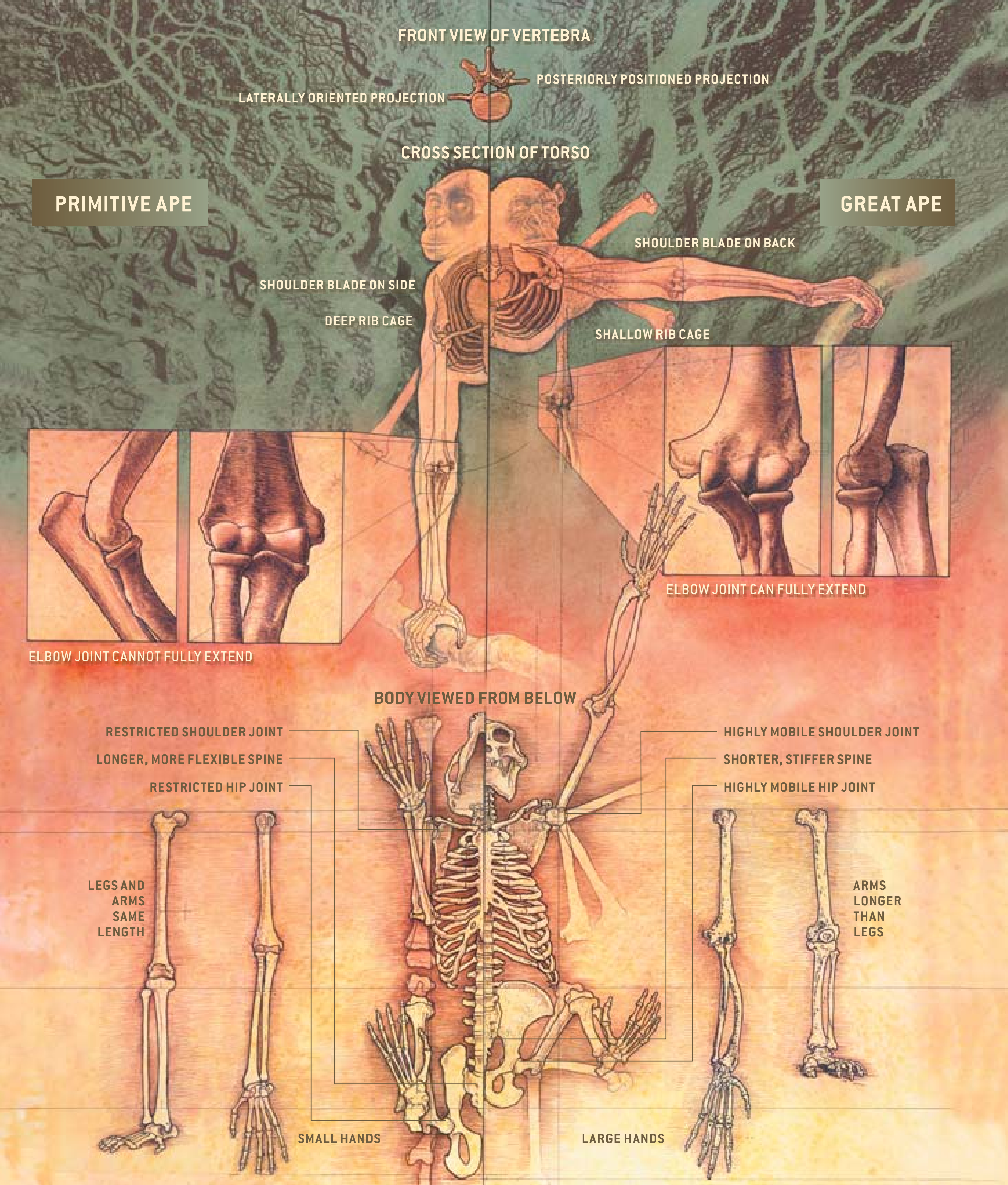
The movement of organisms into new environments drives speciation, and the arrival of apes in Eurasia was no exception. Indeed, within a geologic blink of an eye, these primates adapted to the novel ecological conditions and diversified into a plethora of forms—at least eight known in just 1.5 million years. This flurry of evolutionary activity laid the groundwork for the emergence of great apes and humans. Only within the past decade 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 like their Early Miocene predecessors from the neck down.)

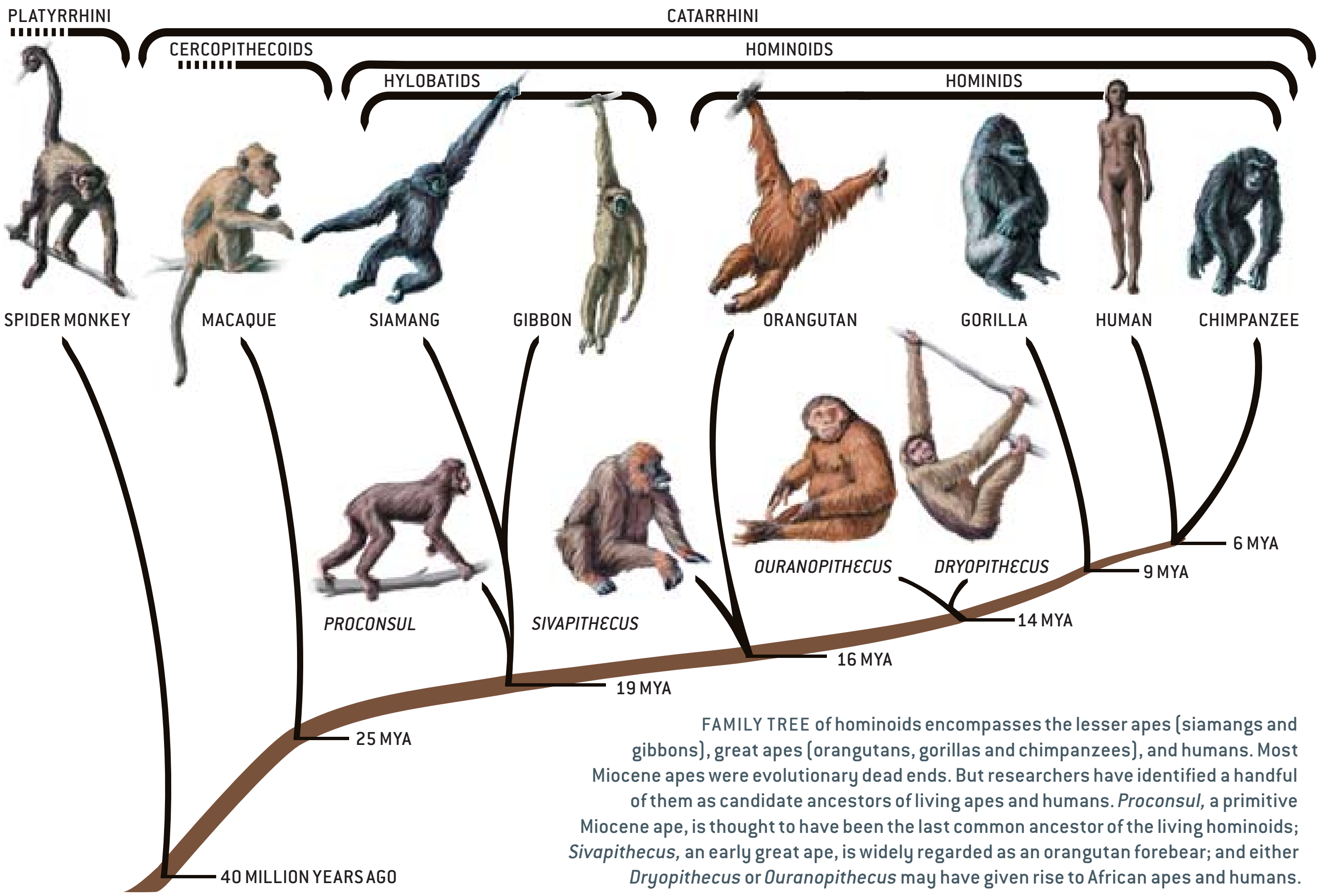
Rise of the Great Apes

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

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.

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. The recently discovered partial skeleton of *Pierolapithecus catalaunicus* in northeastern Spain documents the earliest appearance of the lineage that includes the modern African apes, humans and our fossil relatives (australopithecines). *Pierolapithecus* is closely related to *Dryopithecus fontani,* the ape found by Lartet, and may actually be the same animal. Over the next three million years or so, more specialized and modern-looking descendants would emerge. Within two million 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

PORTIA SLOAN

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 easily traversed arboreal habitat with several tree stories. Climate changes in the Late Miocene brought an end to this easy living. The combined effects

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, raksibombo, the abominable snowman—the list goes on).

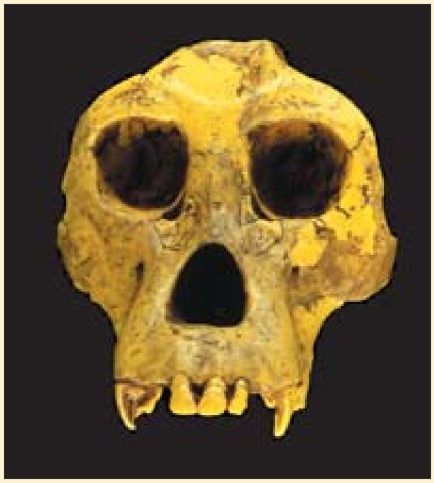
Those who believe in bigfoot (on the basis of suspicious hairs, feces, footprints and fuzzy videotape) usually point to the fossil great ape *Gigantopithecus* as its direct ancestor. *Gigantopithecus* was probably two to three times as large as a gorilla and is known to have lived until about 300,000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

ALLEGED BIGFOOT FOOTPRINT, photographed near Coos Bay, Ore., in 1976.

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.*

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

DAVID R. BEGUN

The next day we returned to the spot so 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* (*left*) 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 a dark layer of sediments suggestive of a high organic content often associated with

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 biogeographic 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 Africa, around nine million years ago. Thus, the lineage that produced African apes 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 (*right*).

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.*

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 recovered only a few teeth representing the 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, *Sahelanthropus tchadensis,* a six-million- to seven-million-year-old find unearthed in Chad a few years ago, 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 African ape–like 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 kadabba* from Ethiopia. Each of these taxa has been described by its discoverers as a human ancestor. 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,* 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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BONOBO Sex & Society

BY FRANS B. M. DE WAAL

The behavior of a close relative challenges assumptions about male supremacy in human evolution

At a juncture in history during which women are seeking equality with men, science arrives with a belated gift to the feminist movement. Male-biased evolutionary scenarios—Man the Hunter, Man the Toolmaker and so on—are being challenged by the discovery that females play a central, perhaps even dominant, role in the social life of one of our nearest relatives. In the past two decades many strands of knowledge have come together concerning a relatively unknown ape with an unorthodox repertoire of behavior: the bonobo.

The bonobo is one of the last large mammals to be found by science. The creature was discovered in 1929 in a Belgian colonial museum, far from its lush African habitat. A German anatomist, Ernst Schwarz, was scrutinizing a skull that had been ascribed to a juvenile chimpanzee because of its small size, when he realized that it belonged to an adult. Schwarz declared that he had stumbled on a new subspecies of chimpanzee. But soon the animal was assigned the status of an entirely distinct species within the same genus as the chimpanzee, *Pan*.

The bonobo was officially classified as *Pan paniscus,* or the diminutive *Pan*. But I believe a different label might have been selected had the discoverers known then what we know now. The old taxonomic name of the chimpanzee, *P. satyrus*—which refers to the myth of apes as lustful satyrs—would have been perfect for the bonobo.

The species is best characterized as female-centered and egalitarian and as one that substitutes sex for aggression. Whereas in most other species sexual behavior is a fairly distinct category, in the bonobo it is part and parcel of social relations—and not just between males and females. Bonobos engage in sex in virtually every partner combination (although such contact among close family members may be suppressed). And sexual interactions occur more often among bonobos than among other primates. Despite the frequency of sex, the bonobo's rate of reproduction in the wild is about the same as that of the chimpanzee. A female gives birth to a single infant at intervals of between five and six years. So bonobos share at least one very important characteristic with our own species, namely, a partial separation between sex and reproduction.

FRANS LANTING *Minden Pictures*

BONOBO FEMALE interacts with an infant. Juvenile bonobos depend on their mothers for milk and transport for up to five years. They are extremely well tolerated by adults, who have rarely been seen to attack or threaten them.

A Near Relative

THIS FINDING commands attention because the bonobo shares more than 98 percent of our genetic profile, making it as close to a human as, say, a fox is to a dog. The split between the human line of ancestry and the line of the chimpanzee and the bonobo is believed to have occurred a mere eight million years ago. The subsequent divergence of the chimpanzee and the bonobo lines came much later, perhaps prompted by the chimpanzee's need to adapt to relatively open, dry habitats.

In contrast, bonobos probably never left the protection of the trees. Their present range lies in humid forests south of the Congo River, where perhaps fewer than 10,000 bonobos survive. (Given the species' slow rate of reproduction, the rapid destruction of its tropical habitat and the political instability of central Africa, there is reason for much concern about its future.)

If this evolutionary scenario of ecological continuity is true, the bonobo may have undergone less transformation than either humans or chimpanzees. It could most closely resemble the common ancestor of all three modern species. Indeed, in the 1930s Harold J. Coolidge—the American anatomist who gave the bonobo its eventual taxonomic status—suggested that the animal might be most similar to the primogenitor, because its anatomy is less specialized than is the chimpanzee's. Bonobo body proportions have been compared with those of the australopithecines, a form of prehuman. When the apes stand or walk upright, they look as if they stepped straight out of an artist's impression of early hominids.

Not too long ago the savanna baboon was regarded as the best living model of the human ancestor. That primate is adapted to the kinds of ecological conditions that prehumans may have faced after descending from the trees. But in the late 1970s chimpanzees, which are much more closely related to humans, became the model of choice. Traits that are observed in chimpanzees—including cooperative hunting, food sharing, tool use, power politics and primitive warfare—were absent or not as developed in baboons. In the laboratory the apes have been able to learn sign language and to recognize themselves in a mirror, a sign of self-awareness not yet demonstrated in monkeys.

Although selecting the chimpanzee as the touchstone of hominid evolution represented a great improvement, at least one aspect of the former model did not need to be revised: male superiority remained the natural state of affairs. In both baboons and chimpanzees, males are conspicuously dominant over females; they reign supremely and often brutally. It is highly unusual for a fully grown male chimpanzee to be dominated by any female.

Enter the bonobo. Despite their common name—the pygmy chimpanzee—bonobos cannot be distinguished from the chimpanzee by size. Adult males of the smallest subspecies of chimpanzee weigh some 43 kilograms (95 pounds) and females 33 kilograms (73 pounds), about the same as bonobos. Although female bonobos are much smaller than the males, they seem to rule.

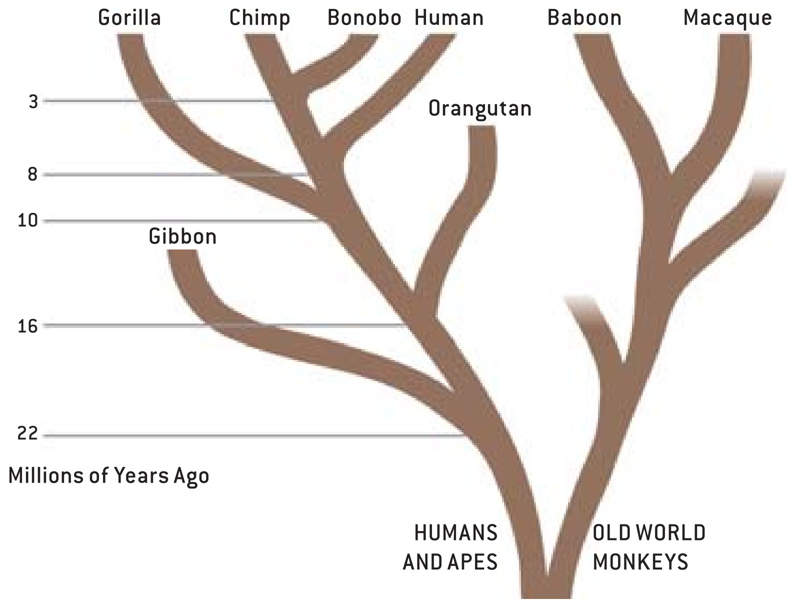
Graceful Apes

IN PHYSIQUE, a bonobo is as different from a chimpanzee as a Concorde is from a Boeing 747. I do not wish to offend any chimpanzees, but bonobos have more style. The bonobo, with its long legs and small head atop narrow shoulders, has a more gracile build than does a chimpanzee. Bonobo lips are reddish in a black face, the ears small and the nostrils almost as wide as a gorilla's. These primates also have a flatter, more open face with a higher forehead than the chimpanzee's and—to top it all off—an attractive coiffure with long, fine, black hair neatly parted in the middle.

Like chimpanzees, female bonobos nurse and carry around their young for up to five years. By the age of seven the offspring reach adolescence. Wild females give birth for the first time at 13 or 14 years of age, becoming full grown by about 15. A bonobo's longevity is unknown, but judging by the chimpanzee it may be older than 40 in the wild and close to 60 in captivity.

Fruit is central to the diets of both wild bonobos and chimpanzees. The former supplement with more pith from herbaceous plants, and the latter add meat. Although bonobos do eat invertebrates and occasionally capture and eat small vertebrates, including mammals, their diet seems to contain relatively little animal protein. Unlike chimpanzees, they have not been observed to hunt monkeys.

Whereas chimpanzees use a rich array of strategies to obtain foods—from cracking nuts with stone tools to fishing for ants and termites with sticks—tool use in wild bonobos seems undeveloped. (Captive bonobos use tools skillfully.) Apparently as intelligent as chimpanzees, bonobos have, however, a far more sensitive temperament. During World War II bombing of Hellabrunn, Germany, the bonobos in a nearby zoo all died of fright from the noise; the chimpanzees were unaffected.



EVOLUTIONARY TREE of primates, based on DNA analysis, shows that humans diverged from bonobos and chimpanzees a mere eight million years ago. The three species share more than 98 percent of their genetic makeup.

Bonobos are also imaginative in play. I have watched captive bonobos engage in "blindman's buff." A bonobo covers her eyes with a banana leaf or an arm or by sticking two fingers in her eyes. Thus handicapped, she stumbles around on a climbing frame, bumping into others or almost falling. She seems to be imposing a rule on herself: "I cannot look until I lose my balance." Other apes and monkeys also indulge in this game, but I have never seen it performed with such dedication and concentration as by bonobos.

Juvenile bonobos are incurably playful and like to make funny faces, sometimes in long solitary pantomimes and at other times while tickling one another. Bonobos are, however, more controlled in expressing their emotions—whether it be joy, sorrow, excitement or anger—than are the extroverted chimpanzees. Male chimpanzees often engage in spectacular charging displays in which they show off their strength: throwing rocks, breaking branches and uprooting small trees in the process. They keep up these noisy performances for many minutes, during which most other members of the group wisely stay out of their way. Male bonobos, on the other hand, usually limit displays to a brief run while dragging a few branches behind them.

Both primates signal emotions and intentions through facial expressions and hand gestures, many of which are also present in the nonverbal communication of humans. For example, bonobos will beg by stretching out an open hand (or, sometimes, a foot) to a possessor of food and will pout their lips and make whimpering sounds if the effort is unsuccessful. But bonobos make different sounds than chimpanzees do. The renowned low-pitched, extended "huuu-huuu" pant-hooting of the latter contrasts with the rather sharp, high-pitched barking sounds of the bonobo.

Love, Not War

MY OWN INTEREST in bonobos came not from an inherent fascination with their charms but from research on aggressive behavior in primates. I was particularly intrigued with the aftermath of conflict. After two chimpanzees have fought, for instance, they may come together for a hug and mouth-to-mouth kiss. Assuming that such reunions serve to restore peace and har-

THE AUTHOR

FRANS B. M. DE WAAL was trained as an ethologist in the European tradition, receiving his Ph.D. from the University of Utrecht in the Netherlands in 1977. After a six-year study of the chimpanzee colony at the Arnhem Zoo, he moved to the U.S. in 1981 to work on other primate species, including bonobos. He is now director of Living Links at the Yerkes National Primate Research Center in Atlanta and C. H. Candler Professor of Primate Behavior at Emory University.

LAURIE GRACE

mony, I labeled them reconciliations.

Any species that combines close bonds with a potential for conflict needs such conciliatory mechanisms. Thinking how much faster marriages would break up if people had no way of compensating for hurting one another, I set out to investigate such mechanisms in several primates, including bonobos. Although I expected to see peacemaking in these apes, too, I was little prepared for the form it would take.

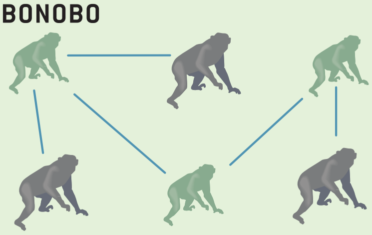
For my study, which began in 1983, I chose the San Diego Zoo. At the time, it housed the world's largest captive bonobo colony—10 members divided into three groups. I spent entire days in front of the enclosure with a video camera, which was switched on at feeding time. As soon as a caretaker approached the enclosure with food, the males would develop erections. Even before the food was thrown into the area, the bonobos would be inviting each other for sex: males would invite females, and females would invite males and other females.

Sex, it turned out, is the key to the social life of the bonobo. The first suggestion that the sexual behavior of bonobos is different had come from observations at European zoos. Wrapping their findings in Latin, primatologists Eduard Tratz and Heinz Heck reported in 1954 that the chimpanzees at Hellabrunn mated *more canum* (like dogs) and bonobos *more hominum* (like people). In those days, face-to-face copulation was considered uniquely human, a cultural innovation that needed to be taught to preliterate people (hence the term "missionary position"). These early studies, written in German, were ignored by the international scientific establishment. The bonobo's humanlike sexuality needed to be rediscovered in the 1970s before it became accepted as characteristic of the species.

Bonobos become sexually aroused remarkably easily, and they express this excitement in a variety of mounting positions and genital contacts. Al-

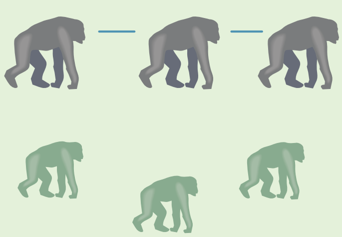
SOCIAL ORGANIZATION AMONG VARIOUS PRIMATES

BONOBO



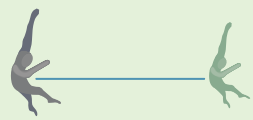
Bonobo communities are peace-loving and generally egalitarian. The strongest social bonds (*blue lines*) are those among females (*green*), although females also bond with males. The status of a male (*gray*) depends on the position of his mother, to whom he remains closely bonded for her entire life.

CHIMPANZEE



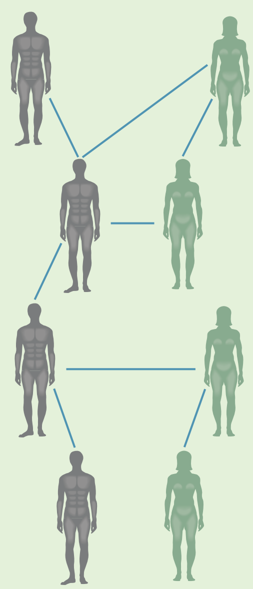
In chimpanzee groups the strongest bonds are established between the males in order to hunt and to protect their shared territory. The females live in overlapping home ranges within this territory but are not strongly bonded to other females or to any one male.

GIBBON



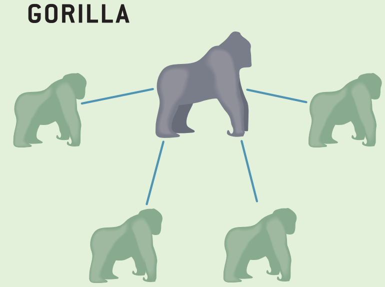
Gibbons establish monogamous, egalitarian relations, and one couple will maintain a territory to the exclusion of other pairs.

HUMAN



Human society is the most diverse among the primates. Males unite for cooperative ventures, whereas females also bond with those of their own sex. Monogamy, polygamy and polyandry are all in evidence.

GORILLA

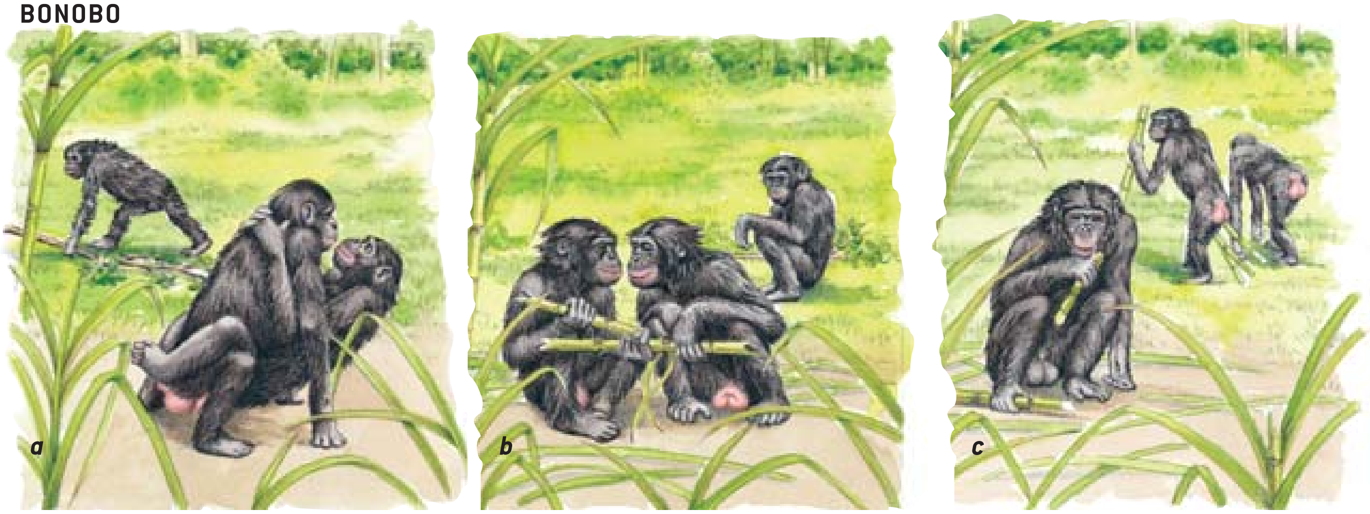


The social organization of gorillas provides a clear example of polygamy. Usually a single male maintains a range for his family unit, which contains several females. The strongest bonds are those between the male and his females.

ORANGUTAN

Orangutans live solitary lives with little bonding in evidence. Male orangutans are intolerant of one another. In his prime, a single male establishes a large territory, within which live several females. Each female has her own, separate home range.

LAURIE GRACE



DOMINANCE BY BONDING is evinced by female bonobos, who engage in genito-genital (GG) rubbing before eating sugarcane (*a*), while a bigger male displays to no avail. The females then share the food without competition (*b*). Only when they leave can the male get to the sugarcane (*c*). In male-dominated chimpanzee society the male eats first (*d*), while the females wait at a safe distance. After he leaves (*e*), carrying as many bananas as he can, the dominant female gets what is left (*f*). Small amounts of sugarcane and bananas are provided at some research sites in the Democratic Republic of the Congo (formerly Zaire).

though chimpanzees virtually never adopt face-to-face positions, bonobos do so in one out of three copulations in the wild. Furthermore, the frontal orientation of the bonobo vulva and clitoris strongly suggest that the female genitalia are adapted for this position.

Another similarity with humans is increased female sexual receptivity. The tumescent phase of the female's genitals, resulting in a pink swelling that signals willingness to mate, covers a much longer part of estrus in bonobos than in chimpanzees. Instead of a few days out of her cycle, the female bonobo is almost continuously sexually attractive and active [*see illustration on page 20*].

Perhaps the bonobo's most typical sexual pattern, undocumented in any other primate, is genito-genital rubbing (or GG rubbing) between adult females. One female facing another clings with arms and legs to a partner that, standing on both hands and feet, lifts her off the ground. The two females then rub their genital swellings laterally together, emitting grins and squeals that probably reflect orgasmic experiences. (Laboratory experiments on stump-tailed macaques have demonstrated that women are not the only female primates capable of physiological orgasm.)

Male bonobos, too, may engage in pseudocopulation but generally perform a variation. Standing back to back, one male briefly rubs his scrotum against the buttocks of another. They also practice so-called penis-fencing, in which two males hang face to face from a branch while rubbing their erect penises together.

The diversity of erotic contacts in bonobos includes sporadic oral sex, massage of another individual's genitals and intense tongue-kissing. Lest this leave the impression of a pathologically oversexed species, I must add, based on hundreds of hours of watching bonobos, that their sexual activity is rather casual and relaxed. It appears to be a completely natural part of their group life. Like people, bonobos engage in sex only occasionally, not continuously. Furthermore, with the average copulation lasting 13 seconds, sexual contact in bonobos is rather quick by human standards.

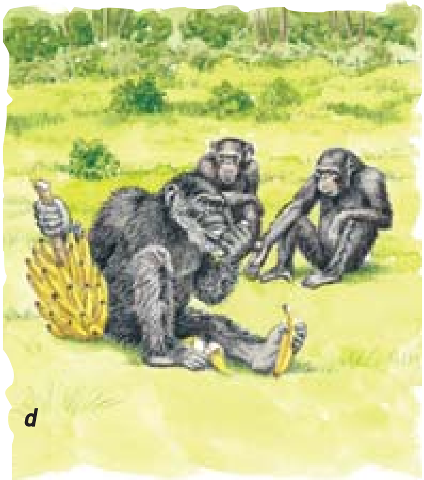
That sex is connected to feeding, and even appears to make food sharing possible, has been observed not only in zoos but also in the wild. Nancy Thompson-Handler, then at the State University of New York at Stony Brook, saw bonobos in the Lomako Forest of the Democratic Republic of the Congo (formerly Zaire) engage in sex after they had entered trees loaded with ripe figs or when one among them had captured a prey animal, such as a small forest duiker. The flurry of sexual contacts would last for five to 10 minutes, after which the apes would settle down to consume the food.

One explanation for the sexual activity at feeding time could be that excitement over food translates into sexual arousal. This idea may be partly true. Yet another motivation is probably the real cause: competition. There are two reasons to believe sexual activity is the bonobo's answer to avoiding conflict.

First, anything, not just food, that arouses the interest of more than one bonobo at a time tends to result in sexual contact. If two bonobos approach a cardboard box thrown into their enclosure, they will briefly mount each other before playing with the box. Such situations lead to squabbles in most other species. But bonobos are quite tolerant, perhaps because they use sex to divert attention and to diffuse tension.

Second, bonobo sex often occurs in aggressive contexts totally unrelated to food. A jealous male might chase another away from a female, after which the two males reunite and engage in scrotal rubbing. Or after a female hits a juvenile, the latter's mother may lunge at the aggressor, an action that is immediately followed by genital rubbing between the two adults.

I once observed a young male, Kako, inadvertently blocking an older, female juvenile, Leslie, from moving along a branch. First, Leslie pushed him; Kako, who was not very confident in trees, tightened his grip, grinning nervously. Next Leslie gnawed on one of his hands, presumably to loosen his grasp. Kako ut-



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tered a sharp peep and stayed put. Then Leslie rubbed her vulva against his shoulder. This gesture calmed Kako, and he moved along the branch. It seemed that Leslie had been very close to using force but instead had reassured both herself and Kako with sexual contact.

During reconciliations, bonobos use the same sexual repertoire as they do during feeding time. Based on an analysis of many such incidents, my study yielded the first solid evidence for sexual behavior as a mechanism to overcome aggression. Not that this function is absent in other animals—or in humans, for that matter—but the art of sexual reconciliation may well have reached its evolutionary peak in the bonobo. For these animals, sexual behavior is indistinguishable from social behavior. Given its peacemaking and appeasement functions, it is not surprising that sex among bonobos occurs in so many different partner combinations, including between juveniles and adults. The need for peaceful coexistence is obviously not restricted to adult heterosexual pairs.

Female Alliance

APART FROM maintaining harmony, sex is also involved in creating the singular social structure of the bonobo. This use of sex becomes clear when studying bonobos in the wild. Field research on bonobos started only in the mid-1970s, a decade after the most important studies on wild chimpanzees had been initiated. In terms of continuity and invested (wo)manpower, the chimpanzee projects of Jane Goodall and Toshisada Nishida, both in Tanzania, are unparalleled. But bonobo research by Takayoshi Kano and others of Kyoto University began to show the same payoffs after two decades at Wamba in the Democratic Republic of the Congo.

Both bonobos and chimpanzees live in so-called fission-fusion societies. The apes move alone or in small parties of a few individuals at a time, the composition of which changes constantly. Several bonobos traveling together in the morning might meet another group in the forest, whereupon one individual from the first group wanders off with others from the second group, while those left behind forage together. All associations, except the one between mother and dependent offspring, are of a temporary character.

Initially this flexibility baffled investigators, making them wonder if these apes formed any social groups with stable membership. After years of documenting the travels of chimpanzees in the Mahale Mountains, Nishida first reported that they form large communities: all members of one community mix freely in ever changing parties, but members of different communities never gather. Later, Goodall added territoriality to this picture. That is, not only do communities not mix, but males of different chimpanzee communities engage in lethal battles.

In both bonobos and chimpanzees, males stay in their natal group, whereas females tend to migrate during adolescence. As a result, the senior males of a chimpanzee or bonobo group have known all junior males since birth, and all junior males have grown up together. Females, on the other hand, transfer to an unfamiliar and often hostile group where they may know no one. A chief difference between chimpanzee and bonobo societies is the way in which young females integrate into their new community.

On arrival in another community, young bonobo females at Wamba single out one or two senior resident females for special attention, using frequent GG rubbing and grooming to establish a relation. If the residents reciprocate, close associations are set up, and the younger female gradually becomes accepted into the group. After producing her first offspring, the young female's position becomes more stable and central. Eventually the cycle repeats with younger immigrants, in turn, seeking a good relation with the now established female. Sex thus smooths the migrant's entrance into the community of females, which is much more close-knit in the bonobo than in the chimpanzee.

Bonobo males remain attached to their mothers all their lives, following them through the forest and being dependent on them for protection in aggressive encounters with other males. As a result, the highest-ranking males of a bonobo community tend to be sons of important females.

What a contrast with chimpanzees! Male chimpanzees fight their own battles, often relying on the support of other males. Furthermore, adult male chimpanzees travel together in same-sex parties, grooming one another frequently. Males form a distinct social hierarchy with high levels of both competition and association. Given the need to stick together against males of neighboring communities, their bonding is not surprising: failure to form a united front might result in the loss of lives and territory. The danger of being male is reflected in the adult sex ratio of chimpanzee populations, with considerably fewer males than females.

Serious conflict between bonobo groups has been witnessed in the field, but it seems quite rare. On the contrary, reports exist of peaceable mingling, including mutual sex and grooming, between what appear to be different communities. If intergroup combat is indeed unusual, it may explain the lower rate of all-male associations. Rather than being male-bonded, bonobo society gives the impression of being female-bonded, with even adult males relying on their mothers instead of on other males. No wonder Kano calls mothers the "core" of bonobo society.

The bonding among female bonobos violates a fairly general rule, outlined by Harvard University anthropologist Richard W. Wrangham, that the sex that stays in the natal group develops the strongest mutual bonds. Bonding among male chimpanzees follows naturally because they remain in the community of their birth. The same is true for female kinship bonding in Old World monkeys, such as macaques and baboons, where males are the migratory sex.

Bonobos are unique in that the migratory sex, females, strongly bond with same-sex strangers later in life. In setting up an artificial sisterhood, bonobos can be said to be secondarily bonded. (Kinship bonds are said to be primary.) Although we now know *how* this happens—through the use of sexual contact and grooming—we do not yet know *why* bonobos and chimpanzees differ in this respect. The answer may lie in the different ecological environments of bonobos and chimpanzees—such as the abundance and quality of food in the forest. But it is uncertain if such explanations will suffice.

Bonobo society is, however, not only female-centered but also appears to be female-dominated. Bonobo specialists, while long suspecting such a reality, had been reluctant to make the controversial claim. But in 1992, at the 14th Congress of the International Primatological Society in Strasbourg, investigators of both captive and wild bonobos presented data that left little doubt about the issue.

Amy R. Parish of the University of California, Davis, reported on food competition in identical groups (one adult male and two adult females) of chimpanzees and bonobos at the Stuttgart Zoo. Honey was provided in a "termite hill" from which it could be extracted by dipping sticks into a small hole. As soon as honey was made available, the male chimpanzee would make a charging display through the enclosure and claim everything for himself. Only when his appetite was satisfied would he let the females fish for honey.

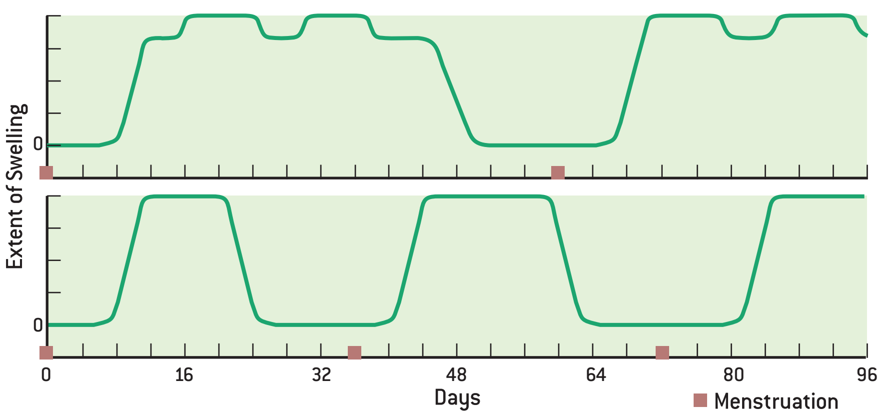
In the bonobo group, it was the females that approached the honey first. After having engaged in some GG rubbing, they would feed together, taking turns with virtually no competition between them. The male might make as many charging displays as he wanted; the females were not intimidated and ignored the commotion.

Observers at the Belgian animal park of Planckendael, which currently has the most naturalistic bonobo colony, reported similar findings. If a male bonobo tried to harass a female, all females would band together to chase him off. Because females appeared more successful in dominating males when they were together than on their own, their close association and frequent genital rubbing may represent an alliance. Females may bond so as to outcompete members of the individually stronger sex.

The fact that they manage to do so not only in captivity is evident from zoologist Takeshi Furuichi's summary of the relation between the sexes at Wamba, where bonobos are enticed out of the forest with sugarcane. "Males usually appeared at the feeding site first, but they surrendered preferred positions when the females appeared. It seemed that males appeared first not because they were dominant, but because they had to feed before the arrival of females," Furuichi reported at Strasbourg.

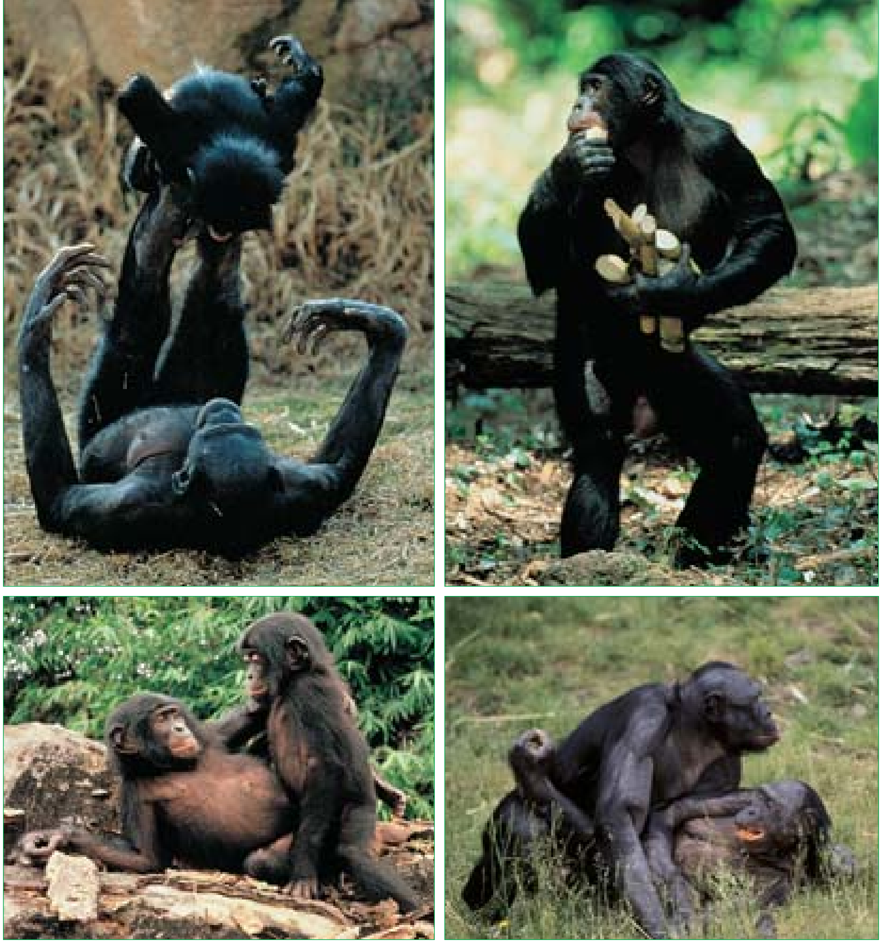
Sex for Food

OCCASIONALLY, the role of sex in relation to food is taken one step further, bringing bonobos very close to humans in their behavior. It has been speculated by anthropologists—including C. Owen Lovejoy of Kent State University and Helen Fisher of Rutgers University—that sex is partially separated from reproduction in our species because it serves to cement mutually profitable relationships between men and women. The human female's capacity to mate throughout her cycle and her strong sex drive



FEMALE RECEPTIVITY for sex, manifested by swollen genitals, occupies a much larger proportion of the estrus cycle of bonobos (*top*) than of chimpanzees (*bottom*). The receptivity of bonobos continues through lactation. (In chimpanzees, it disappears.) This circumstance allows sex to play a large part in the social relations of bonobos. The graph was provided by Jeremy Dahl of the Yerkes National Primate Research Center.

LAURIE GRACE



BEHAVIOR among bonobos is often reminiscent of that among humans. A female and an infant play (*top left*); a bonobo walks upright, using his hands to carry food (*top right*); two juveniles practice sex without penetration (*bottom left*); and a male and female have sex while facing each other (*bottom right*), a position once thought to be uniquely human.

FRANS LANTING *Minden Pictures* (*top left and top right; bottom left*); MARTIN HARVEY *Peter Arnold, Inc.* (*bottom right*)

allow her to exchange sex for male commitment and paternal care, thus giving rise to the nuclear family.

This arrangement is thought to be favored by natural selection because it allows women to raise more offspring than they could if they were on their own. Although bonobos clearly do not establish the exclusive heterosexual bonds characteristic of our species, their behavior does fit important elements of this model. A female bonobo shows extended receptivity and uses sex to obtain a male's favors when—usually because of youth—she is too low in social status to dominate him.

At the San Diego Zoo, I observed that if Loretta was in a sexually attractive state, she would not hesitate to approach the adult male, Vernon, if he had food. Presenting herself to Vernon, she would mate with him and make high-pitched food calls while taking over his entire bundle of branches and leaves. When Loretta had no genital swelling, she would wait until Vernon was ready to share. Primatologist Suehisa Kuroda reports similar exchanges at Wamba: "A young female approached a male, who was eating sugarcane. They copulated in short order, whereupon she took one of the two canes held by him and left."

Despite such quid pro quo between the sexes, there are no indications that bonobos form humanlike nuclear families. The burden of raising offspring appears to rest entirely on the female's shoulders. In fact, nuclear families are probably incompatible with the diverse use of sex found in bonobos. If our ancestors started out with a sex life similar to that of bonobos, the evolution of the family would have required dramatic change.

Human family life implies paternal investment, which is unlikely to develop unless males can be reasonably certain that they are caring for their own, not someone else's, offspring. Bonobo society lacks any such guarantee, but humans protect the integrity of their family units through all kinds of moral restrictions and taboos. Thus, although our species is characterized by an extraordinary interest in sex, there are no societies in which people engage in it at the drop of a hat (or a cardboard box, as the case may be). A sense of shame and a desire for domestic privacy are typical human concepts related to the evolution and cultural bolstering of the family.

Yet no degree of moralizing can make sex disappear from every realm of human life that does not relate to the nuclear family. The bonobo's behavioral peculiarities may help us understand the role of sex and may have serious implications for models of human society. Just imagine that we had never heard of chimpanzees or baboons and had known bonobos first. We would at present most likely believe that early hominids lived in female-centered societies, in which sex served important social functions and in which warfare was rare or absent. In the end, perhaps the most successful reconstruction of our past will be based not on chimpanzees or even on bonobos but on a three-way comparison of chimpanzees, bonobos and humans. SA

MORE TO EXPLORE

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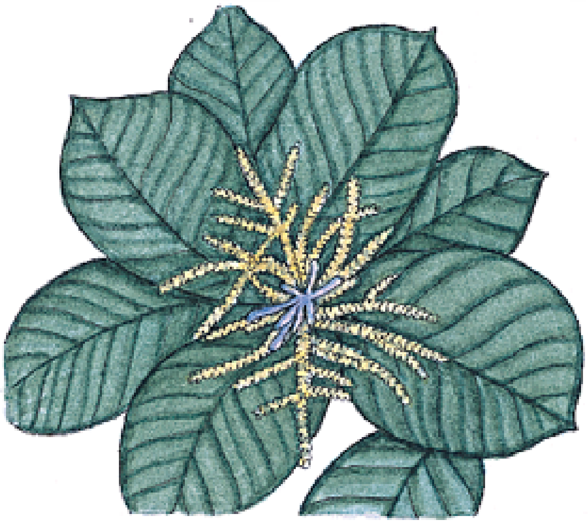
Diet and Primate Evolution



Many characteristics of modern primates, including our own species, derive from an early ancestor's practice of taking most of its food from the tropical canopy

BY KATHARINE MILTON

As recently as 30 years ago, the canopy of the tropical forest was regarded as an easy place for apes, monkeys and prosimians to find food. Extending an arm, it seemed, was virtually all our primate relatives had to do to acquire a ready supply of edibles in the form of leaves, flowers, fruits, and other components of trees and vines. Since then, efforts to understand the reality of life for tree dwellers have helped overturn that misconception.

My own field studies have provided considerable evidence that obtaining adequate nutrition in the canopy—where primates evolved—is, in fact, quite difficult. This research, combined with complementary work by others, has led to another realization as well: the strategies that early primates adopted to cope with the dietary challenges of the arboreal environment profoundly influenced the evolutionary trajectory of the primate order, particularly that of the anthropoids (monkeys, apes and humans).

Follow-up investigations indicate as well that foods eaten by humans today, especially those consumed in industrially advanced nations, bear little resemblance to the plant-based diets anthropoids have favored since their emergence. Such findings lend support to the suspicion that many health problems common in technologically advanced nations may result, at least in part, from a mismatch between the diets we now eat and those to which our bodies became adapted over millions of years. Overall, I would say that the collected evidence justifiably casts the evolutionary history of primates in largely dietary terms.

The story begins over 55 million years ago, after angiosperm forests spread across the earth during the late Cretaceous (94 million to 64 million years ago). At that time, some small, insect-eating mammal, which may have resembled a tree shrew, climbed into the trees, presumably in search of pollen-distributing insects. But its descendants came to rely substantially on edible plant parts from the canopy, a change that set the stage for the emergence of the primate order.

Natural selection strongly favors traits that enhance the efficiency of foraging. Hence, as plant foods assumed increasing importance over evolutionary time (thousands, indeed millions, of years), selection gradually gave rise to the suite of traits now regarded as characteristic of primates. Most of these traits facilitate movement and foraging in trees. For instance, selection yielded hands well suited for grasping slender branches and manipulating found delicacies.

Selective pressures also favored considerable enhancement

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of the visual apparatus (including depth perception, sharpened acuity and color vision), thereby helping primates travel rapidly through the three-dimensional space of the forest canopy and easily discern the presence of ripe fruits or tiny, young leaves. And such pressures favored increased behavioral flexibility as well as the ability to learn and remember the identity and locations of edible plant parts. Foraging benefits conferred by the enhancement of visual and cognitive skills, in turn, promoted development of an unusually large brain, a characteristic of primates since their inception.

As time passed, primates diverged into various lineages: first prosimians, most of which later went extinct, and then monkeys and apes. Each lineage arose initially in response to the pressures of a somewhat different dietary niche; distinct skills are required to become an efficient forager on a particular subset of foods in the forest canopy. Then new dietary pressures placed on some precursor of humans paved the way for the development of modern humans. To a great extent, then, we are truly what we eat.

No Easy Living

MY INTEREST IN THE ROLE of diet in primate evolution grew out of research I began in 1974. While trying to decide on a topic for my doctoral dissertation, I visited the tropical forest on Barro Colorado Island in the Republic of Panama. Studies done on mantled howler monkeys (*Alouatta palliata*) in the 1930s at that very locale had inadvertently helped foster the impression that primates enjoyed the "life of Riley" in the canopy.

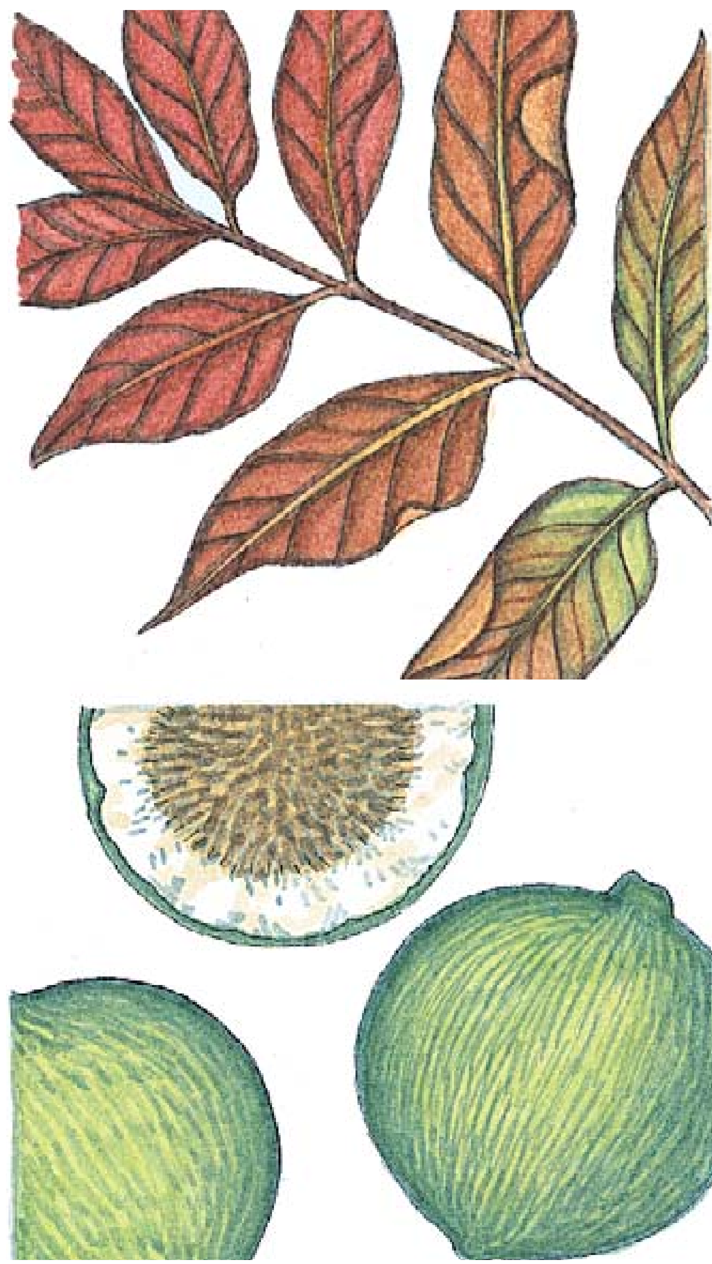
Yet, during my early weeks of following howlers, I realized they were not behaving as expected. Instead of sitting in a tree and eating whatever happened to be growing nearby, they went out of their way to seek specific foods, meanwhile rejecting any number of seemingly promising candidates. Having found a preferred food, they did not sate themselves. Instead they seemed driven to obtain a mixture of leaves and fruits, drawn from many plant species.

The old easy-living dogma was clearly far too simplistic. I decided on the spot to learn more about the problems howlers and other anthropoids face meeting their nutritional needs in the tropical forest. I hoped, too, to discern some of the strategies they had evolved to cope with these dietary difficulties.

The challenges take many forms. Because plants cannot run from hungry predators, they have developed other defenses to avoid the loss of their edible components. These protections include a vast array of chemicals known as secondary compounds (such as phenolics, alkaloids and terpenoids). At best, these chemicals taste awful; at worst, they are lethal.

Also, plant cells are encased by walls made up of materials collectively referred to as fiber or roughage: substances that resist breakdown by mammalian digestive enzymes. Among the fibrous constituents of the cell wall are the structural carbohydrates—cellulose and hemicellulose—and a substance called lignin; together these materials give plant cell walls their shape, hardness and strength. Excessive intake of fiber is troublesome, because when fiber goes undigested, it provides no energy for the feeder. It also takes up space in the gut. Hence, until it can be excreted, it prevents intake of more nourishing items. As will be seen, many primates, including humans, manage to extract a certain amount of energy, or calories, from fiber despite their lack of fiber-degrading enzymes. But the process is time-consuming and thus potentially problematic.

The dietary challenges that trees and vines pose do not end there. Many plant foods lack one or more nutrients required by animals, such as particular vitamins or amino acids (the building blocks of protein), or else they are low in readily digestible carbohydrates (starch and sugar), which provide glucose and therefore energy. Usually, then, animals that depend primarily on plants for meeting their daily nutritional requirements must seek out a variety of complementary nutri-



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ent sources, a demand that greatly complicates food gathering.

For instance, most arboreal primates focus on ripe fruits and young leaves, often supplementing their mostly herbivorous intake with insects and other animal matter. Fruits tend to be of high quality (rich in easily digested forms of carbohydrate and relatively low in fiber), but they provide little protein. Because all animals need a minimal amount of protein to function, fruit eaters must find additional sources of amino acids. Furthermore, the highest-quality items in the forest tend to be the most scarce. Leaves offer more protein and are more plentiful than fruit, but they are of lower quality (lower in energy and higher in fiber) and are more likely to include undesirable chemicals.

The need to mix and match plant foods is further exacerbated by the large distance between trees of the same species in tropical forests, which include hundreds of tree species. An animal that concentrated on eating food from a single species would have to exert great effort going from one individual of that species to another. What is more, trees exhibit seasonal peaks and valleys in the production of the fruits and young leaves primates like to eat, again making reliance on a single food species untenable.

From an evolutionary perspective, two basic strategies for coping with these many problems are open to a nascent plant eater. In one, morphology reigns supreme: over long time spans, natural selection may favor the acquisition of anatomic specializations—especially of the digestive tract—that ease the need to invest time and energy searching for only the highest-quality dietary items. That is, morphological adaptations enable animals to depend on plant parts that are ubiquitous, such as on mature leaves (which are readily available but not of particularly high quality).

Colobine monkeys, one of the Old World primate groups in Africa and Asia, offer an excellent example of this strategy. Unlike the typical primate digestive tract (including that of humans), with its simple acid stomach, that of colobines includes a compartmentalized, or sacculated, stomach functionally analogous to that of cows and other ruminants. This anatomic specialization enables colobines to process fiber extremely efficiently.

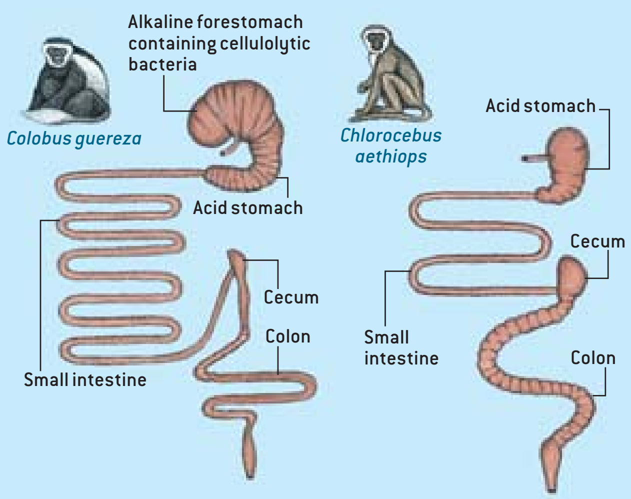
Chewed leaves flow through the esophagus into the forestomach, one of the two stomach compartments in colobines. In this alkaline forestomach, microbes known as cellulolytic bacteria do what digestive enzymes of the monkeys cannot do: degrade fiber. In a process known as fermentation, the bacteria break down the cellulose and hemicellulose in plant cell walls, using those substances as an energy source to fuel their own activities. As the bacteria consume the fiber, they release gases called volatile fatty acids. These gases pass through the stomach wall into the colobine bloodstream, where they provide energy for body tissues or are delivered to the liver for conversion into glucose. Some researchers think the colobine forestomach may also aid in the detoxification of harmful secondary compounds in plant foods.

Efficiency of nutrient extraction from fibrous foods is enhanced in another way in colobine monkeys. As cellulolytic bacteria die, they pass out of the forestomach into the second compartment, a simple acid stomach similar to our own. Here special enzymes (lysozymes) cleave the bacterial cell walls. In consequence, protein and other nutritious materials that compose the cellulolytic bacteria become available for digestion by the monkeys. (In a sense, then, once leaves are chewed and swallowed, colobine monkeys do not interact directly with most of their food; they live largely on products of the fermentation process and on the nutrients provided by the fermenters.)

In contrast to colobines, humans and most other primates pass fiber basically unchanged through their acid stomach and their small intestine (where most nutrients are absorbed) and into the hindgut (the cecum and colon). Once fiber reaches the hindgut, cellulolytic bacteria may be able to degrade some of it. But, for most primates, eating copious amounts of fiber does not confer the same benefits as it does for the digestively specialized colobines.

Another morphological change that can facilitate survival on lower-quality plant parts is to grow larger over time. Compared with small animals, big ones must consume greater absolute amounts of food to nourish their more extensive tissue mass. But, for reasons that are imperfectly understood, the bigger animals can actually attain adequate nourishment by taking in less energy per unit of body mass. This relatively lower energy demand means larger animals can meet their energy requirements with lower-quality foods. Growing bigger has been only a limited option for most primates, however.

FIBER FERMENTER



The digestive tract of colobine monkeys, such as that in *Colobus guereza* (*left*), is specialized: the stomach consists of two distinct compartments instead of the single chamber found in vervet monkeys (*right*) and most other primates. The forestomach is designed to extract more energy from fiber than would typically be obtainable. Colobine monkeys can thus survive on a more fibrous diet than other primates of similar size can.

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YOUNG CHIMPANZEES SEEK FRUIT as part of a diet that consists primarily of ripe fruits supplemented by leaves and some animal prey. Obtaining the foods needed for adequate nutrition in the tropical forest turns out to be significantly more difficult for primates than was once believed. The author contends that the solutions adopted by primates millions of years ago strongly influenced the subsequent evolution of the primate order. The drawings on the opening pages depict some typical plant foods available to arboreal animals in the tropical forest.

STEVE ROBINSON *Natural History Photographic Agency*

If arboreal animals grow too massive, they risk breaking the branches underneath their feet and falling to the ground.

Fruitful Memory

THE SECOND BASIC STRATEGY open to plant eaters is more behavioral than morphological. Species can opt to feed selectively on only the highest-quality plant foods. But because quality items are rare and very patchily distributed in tropical forests, this strategy requires the adoption of behaviors that help to minimize the costs of procuring these resources. The strategy would be greatly enhanced by a good memory. For example, an ability to remember the exact locations of trees that produce desirable fruits and to recall the shortest routes to those trees would enhance foraging efficiency by lowering search and travel costs. So would knowledge of when these trees were likely to bear ripe fruits. Reliance on memory, with its attendant benefits, might then select for bigger brains having more area for storing information.

Of course, these two basic evolutionary strategies—the morphological and behavioral—are not mutually exclusive, and species vary in the extent to which they favor one or the other. As a group, however, primates have generally depended most strongly on selective feeding and on having the brain size, and thus the wit, to carry off this strategy successfully. Other plant-eating orders, in contrast, have tended to focus heavily on morphological adaptations.

I gained my first insights into the evolutionary consequences of selective feeding in primates in the mid-1970s, when I noticed that howler monkeys and black-handed spider monkeys (*Ateles geoffroyi*)—two New World primate species—favored markedly different diets. Howler and spider monkeys, which diverged from a common ancestor, are alike in that they are about the same size, have a simple, unsacculated stomach, are totally arboreal and eat an almost exclusively plant-based diet, consisting for the most part of fruits and leaves. But my fieldwork showed that the foundation of the howler diet in the Barro Colorado forest was immature leaves, whereas the foundation of the spider monkey diet was ripe fruits.

Most of the year howlers divided their daily feeding time about equally between new leaves and fruits. But during seasonal low points in overall fruit availability, they ate virtually nothing but leaves. In contrast, spider monkeys consumed ripe fruits most of the year, eating only small amounts of leaves. When fruits became scarce, spider monkeys did not simply fill up on leaves as the howlers did. Their leaf intake did increase, but they nonetheless managed to include considerable quantities of fruit in the diet. They succeeded by carefully seeking out all fruit sources in the forest; they even resorted to consuming palm nuts that had not yet ripened.

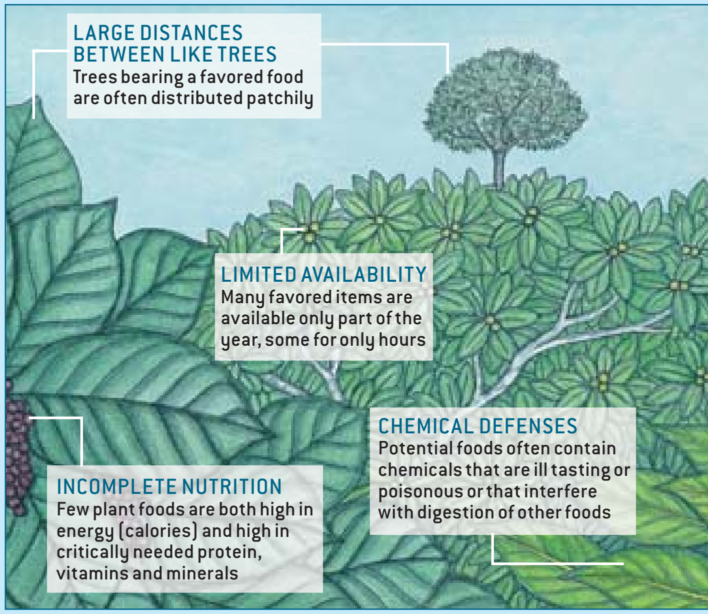
These observations raised a number of questions. I wanted to know how howlers obtained enough energy during months when they lived exclusively on leaves. As already discussed, much of the energy in leaves is bound up in fiber that is inaccessible to the digestive enzymes of primates. Further, why did howlers eat considerable foliage even when they had abundant access to ripe fruits? By the same token, why did spider monkeys go out of their way to find fruit during periods of scarcity; what stopped them from simply switching to leaves, as howlers did? And how did spider monkeys meet daily protein needs with their fruit-rich diet? (Recall that fruits are a poor source of protein.)

Because howler and spider monkeys are much alike externally, I speculated that some internal feature of the two species—perhaps the structure of the gut or the efficiency of digestion—might be influencing these behaviors. And, indeed, studies in which I fed fruits and leaves to temporarily caged subjects revealed that howler monkeys digested food more slowly than did spider monkeys. Howlers began eliminating colored plastic markers embedded in foods an average of 20 hours after eating. In contrast, spider monkeys began eliminating these harmless markers after only four hours. Examining the size of the digestive tract in the two species then revealed how these different passage rates were attained. In howler monkeys the colon was considerably wider and longer than in spider monkeys, which meant food had a longer distance to travel and that significantly more bulk could be retained.

Collectively, these results implied that howlers could survive on leaves because they were more adept at fermenting fiber in the cecum and colon. They processed food slowly, which gave bacteria in the capacious hindgut a chance to produce volatile fatty acids in quantity. Experiments I later carried out with Richard H. McBee, then at Montana State

A BALANCED DIET

	Readily accessible calories	Protein	Fiber	Chemical defenses	Availability on a given tree
Flowers	Moderate	Moderate to high	Low to moderate	Variable	Fewer than three months
Fruits	High	Low	Moderate	Low	Fewer than three months
Young leaves	Low	High	Moderate	Moderate	Fewer than three months
Mature leaves	Low	Moderate	High	Moderate	Almost year-round



Many challenges can deter primates in the tropical forest from obtaining the calories and mix of nutrients they need from plant foods (*right*). Because most such foods are inadequate in one way or another, animals must choose a variety of items each day. The chart above loosely reflects the relative abundance of desirable (*green*) and problematic (*yellow*) components in a mouthful of common foods. It also indicates the typical availability of these foods on any given tree.

PATRICIA J. WYNNE

University, confirmed that howlers may obtain as much as 31 percent of their required daily energy from volatile fatty acids produced during fermentation.

In contrast, spider monkeys, by passing food more quickly through their shorter, narrower colons, were less efficient at extracting energy from the fiber in their diet. This speed, however, enabled them to move masses of food through the gastrointestinal tract each day. By choosing fruits, which are highly digestible and rich in energy, they attained all the calories they needed and some of the protein. They then supplemented their basic fruit-pulp diet with a few very select young leaves that supplied the rest of the protein they required, without an excess of fiber.

Hence, howler monkeys never devote themselves exclusively to fruit, in part because their slow passage rates would probably prevent them from processing all the fruit they would need to meet their daily energy requirement. And the amount of fruit they could consume certainly would not provide enough protein. Conversely, spider monkeys must eat fruit because their digestive tract is ill equipped to provide great amounts of energy from fermenting leaves; efficient fermentation requires that plant matter be held in the gut for some time.

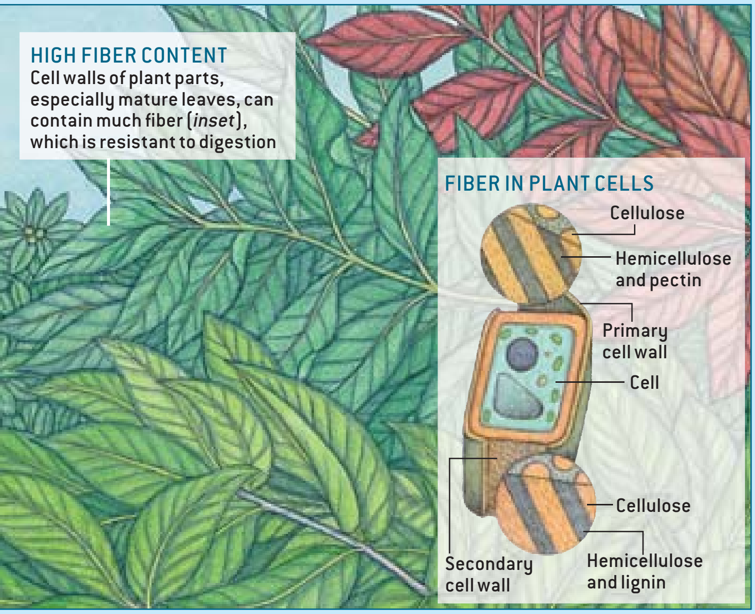
A Tale of Two Monkeys

BY LUCK, I had chosen to study two species that fell at opposite ends of the continuum between slow and rapid passage of food. It is now clear that most primate species can be ranked somewhere along this continuum, depending on whether they tend to maximize the efficiency with which they digest a given meal or maximize the volume of food processed in a day. This research further shows that even without major changes in the design of the digestive tract, subtle adjustments in the size of different segments of the gut can help compensate for nutritional problems posed by an animal's dietary choices. Morphological compensations in the digestive tract can have their drawbacks, however, because they may make it difficult for a species to alter its dietary habits should environmental conditions change suddenly.

These digestive findings fascinated me, but a comparison of brain size in the two species yielded one of those "eurekas" of which every scientist dreams. I examined information on the brain sizes of howler and spider monkeys because the spider monkeys in Panama seemed "smarter" than the howlers—almost human. Actually, some of them reminded me of my friends. I began to wonder whether spider monkeys behaved differently because their brains were more like our own. My investigations showed that, indeed, the brains of howler and spider monkeys do differ, even though the animals are about the same size. (Same-sized animals generally have like-sized brains.) The spider monkey brain weighs about twice that of howlers.

Now, the brain is an expensive organ to maintain; it usurps a disproportionate amount of the energy (glucose) extracted from food. So I knew natural selection would not have favored development of a large brain in spider monkeys unless the animals gained a rather pronounced benefit from the enlargement. Considering that the most striking difference between howler and spider monkeys is their diets, I proposed that the bigger brain of spider monkeys may have been favored because it facilitated the development of mental skills that enhanced success in maintaining a diet centered on ripe fruit.

A large brain would certainly have helped spider monkeys



to learn and, most important, to remember where certain patchily distributed fruit-bearing trees were located and when the fruit would be ready to eat. Also, spider monkeys comb the forest for fruit by dividing into small, changeable groups. Expanded mental capacity would have helped them to recognize members of their particular social unit and to learn the meaning of the different food-related calls through which troop members convey over large distances news of palatable items. Howler monkeys, in contrast, would not need such an extensive memory, nor would they need so complex a recognition and communication system. They generally forage for food as a cohesive social unit, following well-known arboreal pathways over a much smaller home range. Also, howlers tend to use only one or perhaps two large fruiting trees a day, whereas spider monkeys often visit five, 10 or more.

If I was correct that the pressure to obtain relatively difficult-to-find, high-quality plant foods encourages the development of mental complexity (which is paid for by greater foraging efficiency), I would expect to find similar differences in brain size in other primates. That is, monkeys and apes who concentrated on ripe fruits would have larger brains than those of their leaf-eating counterparts of equal body size. To pursue this idea, I turned to estimates of comparative brain sizes published by Harry J. Jerison of the University of California, Los Angeles. To my excitement, I found that those primate species that eat higher-quality, more widely dispersed foods generally have a larger brain than do their similar-sized counterparts that feed on lower-quality, more uniformly distributed resources.

As I noted earlier, primates typically have larger brains than do other mammals of their size. I believe the difference arose because all primates feed very selectively, favoring the highest-quality plant parts—for instance, even primates that eat leaves tend to choose very immature leaves or only the low-fiber tips of older leaves.

Bigger Brains

HAVING UNCOVERED these links between dietary pressures and evolution in nonhuman primates, I became curious about the role of such pressures in human evolution. A review of the fossil record for the hominid family—humans and their precursors—provided some intriguing clues.

Australopithecus, one important genus in our family, emerged in Africa more than 4.5 million years ago, during the Pliocene. As is true of later hominids, they were bipedal, but their brains were not appreciably larger than those of today's apes. Hence, selection had not yet begun to favor a greatly enlarged brain in our family. The fossil record also indicates *Australopithecus* had molar teeth that would have been well suited to a diet consisting largely of tough plant material. Toward the end of the Pliocene, climate conditions began to change. The next epoch, the Pleistocene (lasting from about two million to 10,000 years ago), was marked by repeated glaciations of the Northern Hemisphere. Over both epochs, tropical forests shrank and were replaced in many areas by savanna woodlands.

As the diversity of tree species decreased and the climate became more seasonal, primates in the expanding savanna areas must have faced many new dietary challenges. In the Pleistocene the last species of *Australopithecus*—which by then had truly massive jaws and molars—went extinct. Perhaps those species did so, as my colleague Montague W. Demment of the University of California, Davis, speculates, because they were outcompeted by the digestively specialized ungulates (hoofed animals).

The human, or *Homo,* genus emerged during the Pliocene. Early species of *Homo* were similar in body size to *Australopithecus* but had notably larger brains. These species were replaced by the even larger-brained *H. erectus* and then, in the Pleistocene, by *H. sapiens,* which has the biggest brain of all. In parallel with the increases in brain size in the *Homo* genus, other anatomic changes were also occurring. The molar and premolar teeth became smaller, and stature increased.

To me, the striking expansion of brain size in our genus indicates that we became so successful because selection amplified a tendency inherent in the primate order since its inception: that of using brainpower, or behavior, to solve dietary problems. Coupled with the anatomic changes—and

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HOWLER MONKEY
Alouatta palliata

TYPICAL DIET: Fruits: 42 percent
Leaves: 48 percent
Flowers: 10 percent

WEIGHT: Six to eight kilograms

BRAIN SIZE: 50.3 grams

DAY RANGE: 443 meters

DIGESTIVE FEATURES:
Large colon; slow passage of food through colon

SPIDER MONKEY
Ateles geoffroyi

TYPICAL DIET: Fruits: 72 percent
Leaves: 22 percent
Flowers: 6 percent

WEIGHT: Six to eight kilograms

BRAIN SIZE: 107 grams

DAY RANGE: 915 meters

DIGESTIVE FEATURES:
Small colon; fast passage of food through colon

HOWLER MONKEY (*left*) eats large quantities of leaves, whereas the spider monkey (*right*) is a fruit specialist. The author proposes that diet played a major role in shaping the different traits of the two like-sized species, which shared a common ancestor. Natural selection favored a larger brain in spider monkeys, in part because enhanced mental capacity helped them remember where ripe fruits could be found. And spider monkeys range farther each day because in any patch of forest, ripe fruits are less abundant than leaves. The digestive traits of howler and spider monkeys promote efficient extraction of nutrition from leaves and fruits, respectively.

RICHARD K. LAVAL *Animals Animals* (*left*); NATURAL HISTORY PHOTOGRAPHIC AGENCY (*right*)

with the associations in living primates between larger brains and a high-quality diet—this increase also points to the conclusion that the behavioral solution was to concentrate on high-quality foods. In fact, I suspect early humans not only maintained dietary quality in the face of changing environmental conditions but even improved it.

Expansion of the brain in combination with growth in body size and a reduction in the dentition supports the notion of a high-quality diet for a couple of reasons. When one examines present-day orangutans and gorillas, it becomes clear that in our superfamily, *Hominoidea* (apes and humans), an increase in body size combined with decreased dietary quality leads to a slow-moving, fairly sedentary and unsociable ape. Yet our *Homo* ancestors apparently were mobile and sociable—more resembling the lively, social and communicative chimpanzee. Unlike orangutans and gorillas, which eat quantities of leaves and other fibrous materials as well as ripe and unripe fruits, chimpanzees feed preferentially on large quantities of high-quality, energy-rich ripe fruits.

Likewise, the reduction in the molars and premolars shows that the texture of foods we ate had somehow been altered such that the dentition no longer had so much work to do. In other words, either these early humans were eating different (less fibrous, easier-to-chew) foods than was *Australopithecus,* or they were somehow processing foods to remove material that would be hard to chew and digest. Indeed, stone tools found with fossil remains of *H. habilis* indicate that even the earliest members of our genus were turning to technology to aid in the preparation of dietary items.

The probability that hominids persisted in seeking energy-rich foods throughout their evolution suggests an interesting scenario. As obtaining certain types of plant foods presumably became more problematic, early humans are thought to have turned increasingly to meat to satisfy their protein demands. One can readily envision their using sharp stone flakes to cut through tough hides and to break bones for marrow. To incorporate meat into the diet on a steady basis and also to amass energy-rich plant foods, our ancestors eventually developed a truly novel dietary approach. They adopted a division of labor, in which some individuals specialized in the acquisition of meat by hunting or scavenging and other individuals specialized in gathering plants. Many of the foods thus acquired were saved instead of being eaten on the spot; they were later shared among the entire social unit to assure all members of a balanced diet.

Survival of the individual thus came to depend on a number of technological and social skills. It demanded not only having a brain able to form and retain a mental map of plant food supplies but also having knowledge of how to procure or transform such supplies. In addition, survival now required an ability to recognize that a stone tool could be fashioned from a piece of a rock and a sense of how to implement that vision. And it required the capacity to cooperate with others (for instance, to communicate about who should run ahead of a hunted zebra and who behind), to defer gratification (to save food until it could be brought to an agreed site for all to share) and both to determine one's fair portion and to ensure that it was received. Such demands undoubtedly served as selective pressures favoring the evolution of even larger, more complex brains.

A New Type of Omnivore

IN OTHER WORDS, I see the emergence and evolution of the human line as stemming initially from pressures to acquire a steady and dependable supply of very high quality foods under environmental conditions in which new dietary challenges made former foraging behaviors somehow inadequate. Specialized carnivores and herbivores that abound in the African savannas were evolving at the same time as early humans, perhaps forcing them to become a new type of omnivore, one ultimately dependent on social and technological innovation and thus, to a great extent, on brainpower. Edward O. Wilson of Harvard University has estimated that for more than two million years (until about 250,000 years ago), the human brain grew by about a tablespoon every 100,000 years. Apparently each tablespoonful of brain matter added in the genus *Homo* brought rewards that favored intensification of the trend toward social and technological advancement.

Although the practice of adding some amount of meat to the regular daily intake became a pivotal force in the emergence of modern humans, this behavior does not mean that people today are biologically suited to the virtually fiber-free diet many of us now consume. In fact, in its general form, our digestive tract does not seem to be greatly modified from that of the common ancestor of apes and humans, which was undoubtedly a strongly herbivorous animal.

Yet as of the mid-1980s no studies had been done to find out whether the gut functions of modern humans were in fact similar to those of apes. It was possible that some functional differences existed, because anatomic evidence had shown that despite similarity in the overall form of the digestive tract, modern humans have a rather small tract for an animal of their size. They also differ from apes in that the small intestine accounts for the greatest fraction of the volume of the human digestive tract; in apes the colon accounts for the greatest volume.

To better understand the kind of diet for which the human gut was adapted, Demment and I decided to compare human digestive processes with those of chimpanzees, our closest living relatives. We hoped to determine whether, over the course of their respective evolutionary histories, humans and chimpanzees had diverged notably in their abilities to deal with fiber. (We were greatly encouraged in this effort by Glynn Isaac, who was then at the University of California, Berkeley.)

The feeding habits of chimpanzees are well known. Despite their skill in capturing live prey (particularly monkeys), these apes actually obtain an estimated 94 percent of their annual diet from plants, primarily ripe fruits. Even though the fruits chimpanzees eat tend to be rich in sugar, they contain less pulp and more fiber and seeds than do the cultivated fruits sold in our supermarkets. Hence, I calculated that wild chimpanzees take in hundreds of grams of fiber each day, much more than the 10 grams or less the average American is estimated to consume.

Various excellent studies, including a fiber project at Cornell University, had already provided much information about fiber digestion by humans. At one time, it was believed that the human digestive tract did not possess microbes capable of degrading fiber. Yet bacteria in the colons of 24 male college students at Cornell proved quite efficient at fermenting fiber found in a variety of fruits and vegetables. At their most effective, the microbial populations broke down as much as three quarters of the cell-wall material that the subjects ingested; about 90 percent of the volatile fatty acids that resulted were delivered to the bloodstream.

Following the example of the Cornell study, Demment and I assessed the efficiency of fiber breakdown in chimpanzees fed nutritious diets containing varying amounts of fiber. Demment handled the statistical analyses, and I collected raw data. How dry that sounds in comparison to the reality of the experience! At the Yerkes Primate Center in Atlanta, I whiled away the summer with six extremely cross chimpanzees that never missed an opportunity to pull my hair, throw fecal matter and generally let me know they were underwhelmed by our experimental cuisine.

Faster Food

OUR RESULTS SHOWED that the chimpanzee gut is strikingly similar to the human gut in the efficiency with which it processes fiber. Moreover, as the fraction of fiber in the diet rises (as would occur in the wild during seasonal lulls in the production of fruits or immature leaves), chimpanzees and humans speed the rate at which they pass food through the digestive tract.

These similarities indicate that as quality begins to decline in the natural environment, humans and chimpanzees are evolutionarily programmed to respond to this decrease by increasing the rate at which food moves through the tract. This response permits a greater quantity of food to be processed in a given unit of time; in so doing, it enables the feeder to make up for reduced quality by taking in a larger volume of food each day. (Medical research has uncovered another benefit of fast passage. By speeding the flow of food through the gut, fiber seems to prevent carcinogens from lurking in the colon so long that they cause problems.)

If the human digestive tract is indeed adapted to a plant-rich, fibrous diet, then this discovery lends added credence to the commonly heard assertion that people in highly technological societies eat too much refined carbohydrate and too few fresh fruits and vegetables. My work offers no prescription for how much fiber we need. But certainly the small amount many of us consume is far less than was ingested by our closest human ancestors.

More recently, my colleagues and I have analyzed plant parts routinely eaten by wild primates for their content of various constituents, including vitamin C, pectin and minerals. Pectin, a highly fermentable component of cell walls, is thought to have health benefits for humans. Our results suggest that diets eaten by early humans were extremely rich in vitamin C and pectin and contained notable amounts of some important minerals. Again, I do not know whether we need to take in the same proportions of these substances as wild primates do, but these discoveries are provocative.

To a major extent, the emergence of modern humans occurred because natural selection favored adaptations in our order that permitted primates to focus their feeding on the most energy-dense, low-fiber diets they could find. It seems ironic that our lineage, which in the past benefited from assiduously avoiding eating too much food high in fiber, may now be suffering because we do not eat enough of it. SA

MORE TO EXPLORE

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WHY ARE SOME ANIMALS

The unusual behavior of orangutans in a Sumatran swamp

PERRY VAN DUIJNHOVEN FROM *AMONG ORANGUTANS: RED APES AND THE RISE OF HUMAN CULTURE*, BY CAREL VAN SCHAIK. THE BELKNAP PRESS OF HARVARD UNIVERSITY PRESS,

SO SMART?

suggests a surprising answer

ORANGUTAN mother and infant in Sumatra.

BY CAREL VAN SCHAIK

Even though we humans write the textbooks and may justifiably be suspected of bias, few doubt that we are the smartest creatures on the planet. Many animals have special cognitive abilities that allow them to excel in their particular habitats, but they do not often solve novel problems. Some of course do, and we call them intelligent, but none are as quick-witted as we are.

What favored the evolution of such distinctive brainpower in humans or, more precisely, in our hominid ancestors? One approach to answering this question is to examine the factors that might have shaped other creatures that show high intelligence and to see whether the same forces might have operated in our forebears. Several birds and nonhuman mammals, for instance, are much better problem solvers than others: elephants, dolphins, parrots, crows. But research into our close relatives, the great apes, is surely likely to be illuminating.

Scholars have proposed many explanations for the evolution of intelligence in primates, the lineage to which humans and apes belong (along with monkeys, lemurs and lorises). Over the past 13 years, though, my group's studies of orangutans have unexpectedly turned up a new explanation that we think goes quite far in answering the question.

Incomplete Theories

ONE INFLUENTIAL ATTEMPT at explaining primate intelligence credits the complexity of social life with spurring the development of strong cognitive abilities. This Machiavellian intelligence hypothesis suggests that success in social life relies on cultivating the most profitable relationships and on rapidly reading the social situation—for instance, when deciding whether to come to the aid of an ally attacked by another animal. Hence, the demands of society foster intelligence because the most intelligent beings would be most successful at making self-protective choices and thus would survive to pass their genes to the next generation. Machiavellian traits may not be equally beneficial to other lineages, however, or even to all primates, and so this notion alone is unsatisfying.

One can easily envisage many other forces that would promote the evolution of intelligence, such as the need to work hard for one's food. In that situation, the ability to figure out how to skillfully extract hidden nourishment or the capacity to remember the perennially shifting locations of critical food items would be advantageous, and so such cleverness would be rewarded by passing more genes to the next generation.

My own explanation, which is not incompatible with these other forces, puts the emphasis on social learning. In humans, intelligence develops over time. A child learns primarily from the guidance of patient adults. Without strong social—that is, cultural—inputs, even a potential wunderkind will end up a bungling bumpkin as an adult. We now have evidence that this process of social learning also applies to great apes, and I will argue that, by and large, the animals that are intelligent are the ones that are cultural: they learn from one another innovative solutions to ecological or social problems. In short, I suggest that culture promotes intelligence.

I came to this proposition circuitously, by way of the swamps on the western coast of the Indonesian island of Sumatra, where my colleagues and I were observing orangutans. The orangutan is Asia's only great ape, confined to the islands of Borneo and Sumatra and known to be something of a loner. Compared with its more familiar relative, Africa's chimpanzee, the red ape is serene rather than hyperactive and reserved socially rather than convivial. Yet we discovered in them the conditions that allow culture to flourish.

KLUET SWAMP provides an unusually lush habitat for orangutans. The author and his colleagues discovered that in such a productive setting, the apes, generally known to live solitary lives, are surprisingly sociable.

Technology in the Swamp

WE WERE INITIALLY attracted to the swamp because it sheltered disproportionately high numbers of orangutans—unlike the islands' dryland forests, the moist swamp habitat supplies abundant food for the apes year-round and can thus support a large population. We worked in an area near Suaq Balimbing in the Kluet swamp [*see map below*], which may have been paradise for orangutans but, with its sticky mud, profusion of biting insects, and oppressive heat and humidity, was hell for researchers.

One of our first finds in this unlikely setting astonished us: the Suaq orangutans created and wielded a variety of tools. Although captive red apes are avid tool users, the most striking feature of tool use among the wild orangutans observed until then was its absence. The animals at Suaq ply their tools for two major purposes. First, they hunt for ants, termites and, especially, honey (mainly that of stingless bees)—more so than all their fellow orangutans elsewhere. They often cast discerning glances at tree trunks, looking for air traffic in and out of small holes. Once discovered, the holes become the focus of visual and then manual inspection by a poking and picking finger. Usually the

Overview/*The Orangutan Connection*

- The author has discovered extensive tool use among orangutans in a Sumatran swamp. No one has observed orangutans systematically using tools in the wild before.
- This unexpected finding suggests to the author a resolution to a long-standing puzzle: Why are some animals so smart?
- He proposes that culture is the key. Primatologists define culture as the ability to learn—by observation—skills invented by others. Culture can unleash ever increasing accomplishments and can bootstrap a species toward greater and greater intelligence.

finger is not long enough, and the orangutan prepares a stick tool. After carefully inserting the tool, the ape delicately moves it back and forth and then withdraws it, licks it off and sticks it back in. Most of this "manipulation" is done with the tool clenched between the teeth; only the largest tools, used primarily to hammer chunks off termite nests, are handled.

The second context in which the Suaq apes employ tools involves the fruit of the *Neesia*. This tree produces woody, five-angled capsules up to 10 inches long and four inches wide. The capsules are filled with brown seeds the size of lima beans, which, because they contain nearly 50 percent fat, are highly nutritious—a rare and sought-after treat in a natural habitat without fast food. The tree protects its seeds by growing a very tough husk. When the seeds are ripe, however, the husk begins to split open; the cracks gradually widen, exposing neat rows of seeds, which have grown nice red attachments (arils) that contain some 80 percent fat.

To discourage seed predators further, a mass of razor-sharp needles fills the husk. The orangutans at Suaq strip the bark off short, straight twigs, which they then hold in their mouths and insert into the cracks. By moving the tool up and down inside the crack, the ani-

JEN CHRISTIANSEN (*map*); PERRY VAN DUIJNHOVEN FROM *AMONG ORANGUTANS: RED APES AND THE RISE OF HUMAN CULTURE*, BY CAREL VAN SCHAIK. THE BELKNAP PRESS OF HARVARD UNIVERSITY PRESS, © 2004 BY THE PRESIDENT AND FELLOWS OF HARVARD COLLEGE (*photographs above and opposite page*)

MOST ORANGUTANS spend their lives without making or using tools. The red apes at Suaq are an exception; they create a variety of tools. One of the most common is a stick (*above*) they prepare for gathering ants, termites and, especially, honey. Without the tool (*left*), attempts to retrieve honey from a hole in a tree, by biting the hole, for example, often fail. The Suaq apes, in contrast, insert the tool into the hole and, holding it in their mouth (*arrow at right*), move it delicately back and forth. They then withdraw it to lick off the honey (*far right*).

mal detaches the seeds from their stalks. After this maneuver, it can drop the seeds straight into its mouth. Late in the season, the orangutans eat only the red arils, deploying the same technique to get at them without injury.

Both methods of fashioning sticks for foraging are ubiquitous at Suaq. In general, "fishing" in tree holes is occasional and lasts only a few minutes, but when *Neesia* fruits ripen, the apes devote most of their waking hours to ferreting out the seeds or arils, and we see them grow fatter and sleeker day by day.

Why the Tool Use Is Cultural

WHAT EXPLAINS this curious concentration of tool use when wild orangutans elsewhere show so little propensity? We doubt that the animals at Suaq are intrinsically smarter: the observation that most captive members of this species can learn to use tools suggests that the basic brain capacity to do so is present.

So we reasoned that their environment might hold the answer. The orangutans studied before mostly live in dry forest, and the swamp furnishes a uniquely lush habitat. More insects make their nests in the tree holes there than in forests on dry land, and *Neesia* grows only in wet places, usually near flowing water. Tempting as the environmental explanation sounds, however, it does not explain why orangutans in several populations outside Suaq ignore altogether these same rich food sources. Nor does it explain why some populations that do eat the seeds harvest them without tools (which results, of course, in their eating much less than the orangutans at Suaq do). The same holds for tree-hole tools. Occasionally, when the nearby hills—which have dryland forests—show massive fruiting, the Suaq orangutans go there to indulge, and while they are gathering fruit they use tools to exploit the contents of tree holes. The hill habitat is a dime a dozen throughout the orangutan's geographic range, so if tools can be used on the hillsides above Suaq, why not everywhere?

Another suggestion we considered, captured in the old adage that necessity is the mother of invention, is that the Suaq animals, living at such high density, have much more competition for provisions. Consequently, many would be left without food unless they could get at the hard-to-reach supplies—that is, they *need* tools in order to eat. The strongest argument against this possibility is that the sweet or fat foods that the tools make accessible sit very high on the orangutan preference list and should therefore be sought by these animals everywhere. For instance, red apes in all locations are willing to be stung many times by honeybees to get at their honey. So the necessity idea does not hold much water either.

A different possibility is that these behaviors are innovative techniques a couple of clever orangutans invented, which then spread and persisted in the population because other individuals learned by observing these experts. In other words, the tool use is cultural. A major obstacle to studying culture in nature is that, barring experimental introductions, we can never demonstrate convincingly that an animal we observe invents some new trick rather than simply applying a well-remembered but rarely practiced habit. Neither can we prove that one individual learned a new skill from another group member rather than figuring out what to do on its own. Although we can show that orangutans in the lab are capable of observing and learning socially, such studies tell us nothing about culture in nature—neither what it is generally about nor how much of it exists. So field-workers have had to develop a system of criteria to demonstrate that a certain behavior has a cultural basis.

First, the behavior must vary geographically, showing that it was invented somewhere, and it must be common where it is found, showing that it spread and persisted in a population. The tool

FRUIT OF THE *NEESIA* TREE (*below left*) has inspired another important tool in the repertoire of the orangutans at Suaq. The highly nutritious seeds are surrounded by razor-sharp needles that serve to keep out mammalian seed predators. To circumvent the painful needles, the Suaq apes strip the bark off short, straight twigs, which they then hold in their mouth and insert into cracks in the ripening fruit (*right*). By moving the tool up and down inside the crack, the ape detaches the seeds without getting injured. The photograph in the center shows a small fruit with the tool still sticking out.

uses at Suaq easily pass these first two tests. The second step is to eliminate simpler explanations that produce the same spatial pattern but without involving social learning. We have already excluded an ecological explanation, in which individuals exposed to a particular habitat independently converge on the same skill. We can also eliminate genetics because of the fact that most captive orangutans can learn to use tools.

The third and most stringent test is that we must be able to find geographic distributions of behavior that can be explained by culture and are not easily explained any other way. One key pattern would be the presence of a behavior in one place and its absence beyond some natural barrier to dispersal. In the case of the tool users at Suaq, the geographic distribution of *Neesia* gave us decisive clues. *Neesia* trees (and orangutans) occur on both sides of the wide Alas River. In the Singkil swamp, however, just south of Suaq and on the same side of the Alas River [*see map on opposite page*], tools littered the floor, whereas in Batu-Batu swamp across the river they were conspicuously absent, despite our numerous visits in different years. In Batu-Batu, we did find that many of the fruits were ripped apart, showing that these orangutans ate *Neesia* seeds in the same way as their colleagues did at a site called Gunung Palung in distant Borneo but in a way completely different from their cousins right across the river in Singkil.

Batu-Batu is a small swamp area, and it does not contain much of the best swamp forest; thus, it supports a limited number of orangutans. We do not know whether tool use was never invented there or whether it could not be maintained in the smaller population, but we do know that migrants from across the river never brought it in because the Alas is so wide there that it is absolutely impassable for an orangutan. Where it is passable, farther upriver, *Neesia* occasionally grows, but the orangutans in that area ignore it altogether, apparently unaware of its rich offerings. A cultural interpretation, then, most parsimoniously explains the unexpected juxtaposition of knowledgeable tool users and brute-force foragers living practically next door to one another, as well as the presence of ignoramuses farther upriver.

Tolerant Proximity

WHY DO WE SEE these fancy forms of tool use at Suaq and not elsewhere? To look into this question, we first made detailed comparisons among all the sites at which orangutans have been studied. We found that even when we excluded tool use, Suaq had the largest number of innovations that had spread throughout the population. This finding is probably not an artifact of our own interest in unusual behaviors, because some other sites have seen far more work by researchers eager to discover socially learned behavioral innovations.

We guessed that populations in which individuals had more chances to observe others in action would show a greater diversity of learned skills than would populations offering fewer learning opportunities. And indeed, we were able to confirm that sites in which individuals spend more time with others have greater repertoires of learned innovations—a relation, by the way, that also holds among chimpanzees [*see illustration on page 36*]. This link was strongest for

THE AUTHOR

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food-related behavior, which makes sense because acquiring feeding skills from somebody else requires more close-range observation than, say, picking up a conspicuous communication signal. Put another way, those animals exposed to the fewest educational opportunities have the smallest collection of cultural variants, exactly like the proverbial country bumpkin.

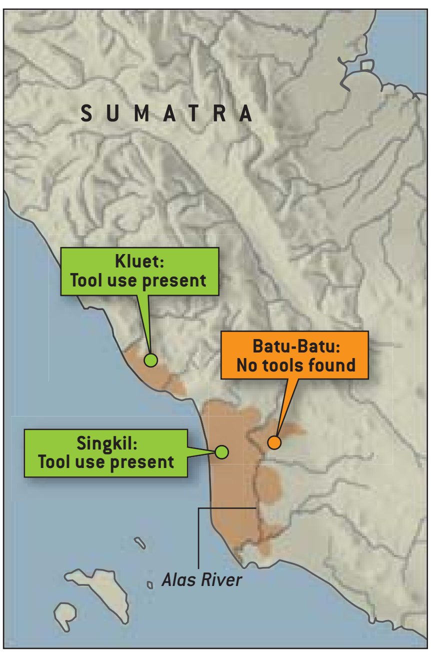
When we looked closely at the contrasts among sites, we noticed something else. Infant orangutans everywhere spend over 20,000 daylight hours in close contact with their mothers, acting as enthusiastic apprentices. Only at Suaq, however, did we also see adults spending considerable time together while foraging. Unlike any other orangutan population studied so far, they even regularly fed on the same food item, usually termite-riddled branches, and shared food—the meat of a slow loris, for example. This unorthodox proximity and tolerance allowed less skilled adults to come close enough to observe foraging methods, which they did as eagerly as kids.

Acquisition of the most cognitively demanding inventions, such as the tool uses found only at Suaq, probably requires face time with proficient individuals, as well as several cycles of observation and practice. The surprising implication of this need is that even though infants learn virtually all their skills from their mothers, a population will be able to perpetuate particular innovations only if tolerant role models other than the mother are around; if mom is not particularly skillful, knowledgeable experts will be close at hand, and a youngster will still be able to learn the fancy techniques that apparently do not come automatically. Thus, the more connected a social network, the more likely it is that the group will retain any skill that is invented, so that in the end tolerant populations support a greater number of such behaviors.

Our work in the wild shows us that most learning in nature, aside from simple conditioning, may have a social component, at least in primates. In contrast, most laboratory experiments that investigate how animals learn are aimed at revealing the subject's ability for individual learning. Indeed, if the lab psychologist's puzzle were presented under natural conditions, where myriad stimuli compete for attention, the subject might never realize that a problem was waiting to be solved. In the wild, the actions of knowledgeable members of the community serve to focus the attention of the naive animal.

The Cultural Roots of Intelligence

OUR ANALYSES of orangutans suggest that not only does culture—social learning of special skills—promote intelligence, it favors the evolution of greater and greater intelligence in a population over time. Different species vary greatly in the mechanisms that enable them to learn from others, but formal experiments confirm the strong impression one gets from observing great apes in the wild: they are capable of learning by watching what others do. Thus, when a wild orangutan, or an African great ape for that matter, pulls off a cognitively complex behavior, it has acquired the ability through a mix of observational learning and individual practice, much as a human child has garnered his or her skills. And when an orangutan in Suaq has acquired more of these tricks than its less fortunate cousins elsewhere, it has done so because it had greater opportunities for social learning through-



IMPASSABLE RIVERS may have halted the spread of tool use. *Neesia* trees and orangutans, for example, occur on both sides of the wide Alas River (*photograph*), but in the Singkil swamp (*map*), tools abound on the forest floor, whereas in Batu-Batu swamp across the river the resident orangutans use a simpler technique to detach *Neesia* seeds that does not involve tools. Migrants are not able to bring tool use to Batu-Batu, because the Alas is too wide there for an orangutan to cross.

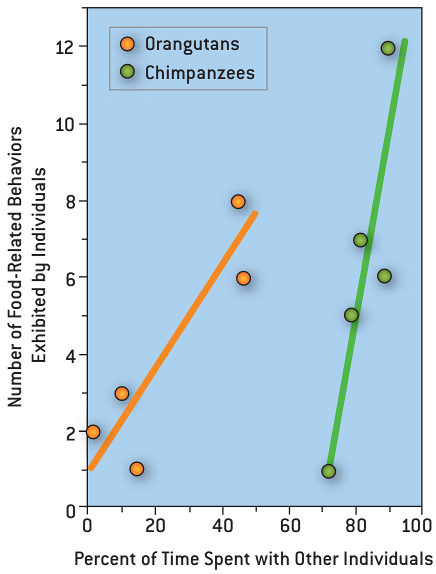
BASE MAP SOURCE: PERRY VAN DUIJNHOVEN; ADAPTED BY JEN CHRISTIANSEN; PERRY VAN DUIJNHOVEN (*photograph*) out its life. In brief, social learning may bootstrap an animal's intellectual performance onto a higher plane.

To appreciate the importance of social inputs to the evolution of ever higher intelligence, let us do a thought experiment. Imagine an individual that grows up without any social inputs yet is provided with all the shelter and nutrition it needs. This situation is equivalent to that in which no contact exists between the generations or in which young fend for themselves after they emerge from the nest. Now imagine that some female in this species invents a useful skill—for instance, how to open a nut to extract its nutritious meat. She will do well and perhaps have more offspring than others in the population. Unless the skill gets transferred to the next generation, however, it will disappear when she dies.

Now imagine a situation in which the offspring accompany their mother for a while before they strike out on their own. Most youngsters will learn the new technique from their mother and thus transfer it—and its attendant benefits—to the next generation. This process would generally take place in species with slow development and long association between at least one parent and offspring, but it would get a strong boost if several individuals form socially tolerant groups.

We can go one step further. For slowly developing animals that live in socially tolerant societies, natural selection will tend to reward a slight improvement in the ability to learn through observation more strongly than a similar increase in the ability to innovate, because in such a society, an individual can stand on the shoulders of those in both present and past generations. But because the cognitive processes underlying social learning overlap with those producing innovations, improvements in social learning techniques should also bring improvements in innovation abilities. Hence, being cultural predisposes species with some innovative capacities to evolve toward higher intelligence. This, then, brings us to the new explanation for cognitive evolution.

This new hypothesis makes sense of an otherwise puzzling phenomenon. Many times during the past century people reared great ape infants as they would human children. These so-called enculturated apes acquired a surprising set of skills, effortlessly imitating complex behavior—understanding pointing, for example, and even some human language, becoming humorous pranksters and creating drawings. More recently,



POPULATIONS in which individuals have more chances to observe others in action show a greater diversity of learned skills than populations offering fewer learning opportunities. The relation holds for both chimpanzees and orangutans.

JEN CHRISTIANSEN; SOURCE: CAREL VAN SCHAIK

formal experiments such as those performed by Sue Savage-Rumbaugh of the Great Ape Trust of Iowa, involving the bonobo Kanzi, have revealed startling language abilities [see "The Emergence of Intelligence," by William H. Calvin, on page 84]. Though often dismissed as lacking in scientific rigor, these consistently replicated cases reveal the astonishing cognitive potential that lies dormant in great apes. We may not fully appreciate the complexity of life in the jungle, but I guess that these enculturated apes have truly become overqualified. In a process that encapsulates the story of human evolution, an ape growing up like a human can be bootstrapped to cognitive peaks higher than any of its wild counterparts.

The same line of thinking solves the long-standing puzzle of why many primates in captivity readily use—and sometimes even make—tools, when their counterparts in the wild seem to lack any such urges. The often-heard suggestion that they do not need tools is belied by observations of orangutans, chimpanzees and capuchin monkeys showing that some of this tool use makes available the richest food in the animals' natural habitats or tides the creatures over during lean periods. The conundrum is resolved if we realize that two individuals of the same species can differ dramatically in their intellectual performance, depending on the social environment in which they grew up.

Orangutans epitomize this phenomenon. They are known as the escape artists of the zoo world, cleverly unlocking the doors of their cages. But the available observations from the wild, despite decades of painstaking monitoring by dedicated field-workers, have uncovered precious few technological accomplishments outside Suaq. Wild-caught individuals generally never take to being locked up, always retaining their deeply ingrained shyness and suspicion of humans. But zoo-born apes happily consider their keepers valuable role models and pay attention to their activities and to the objects strewn around the enclosures, learning to learn and thus accumulating numerous skills.

The critical prediction of the intelligence-through-culture theory is that the most intelligent animals are also likely to live in populations in which the entire group routinely adopts innovations introduced by members. This prediction is not easily tested. Animals from different lineages vary so much in their senses and in their ways of life that a single yardstick for intellectual performance has traditionally been hard to find. For now, we can merely ask whether lineages that show incontrovertible signs of intelligence also have innovation-based cultures, and vice versa. Recognizing oneself in a mirror, for example, is a poorly understood but unmistakable sign of self-awareness, which is taken as a sign of high intelligence. So far, despite widespread attempts in numerous lineages, the only mammalian groups to pass this test are great apes and dolphins, the same animals that can learn to understand many arbitrary symbols and that show the best evidence for imitation, the basis for innovation-based culture. Flexible, innovation-based tool use, another expression of intelligence, has a broader distribution in mammals: monkeys and apes, cetaceans, and elephants—all lineages in which social learning is common. Although so far only these very crude tests can be done, they support the intelligence-through-culture hypothesis.

Another important prediction is that the propensities for innovation and social learning must have coevolved. Indeed, Simon Reader, now at Utrecht University in the Netherlands, and Kevin N. Laland, currently at the University of St. Andrews in Scotland, found that primate species that show more evidence of innovation are also those that show the most evidence for social learning. Still more indirect tests rely on correlations among species between the relative size of the brain (after statistically correcting for body size) and social and developmental variables. The well-established correlations between gregariousness and relative brain size in various mammalian groups are also consistent with the idea.

Although this new hypothesis is not enough to explain why our ancestors, alone among great apes, evolved such extreme intelligence, the remarkable bootstrapping ability of the great apes in rich cultural settings makes the gap seem less formidable. The explanation for the historical trajectory of change involves many details that must be painstakingly pieced together from a sparse and confusing fossil and archaeological record.

Many researchers suspect that a key change was the invasion of the savanna by tool-wielding, striding early *Homo*. To dig up tubers and deflesh and defend carcasses of large mammals, they had to work collectively and create tools and strategies. These demands fostered ever more innovation and more interdependence, and intelligence snowballed.

ORANGUTANS near Sumatra's western coast are much more gregarious than red apes living elsewhere. Juveniles seek one another's company at every possible opportunity.

HERMAN D. RIJKSEN FROM *AMONG ORANGUTANS: RED APES AND THE RISE OF HUMAN CULTURE*, BY CAREL VAN SCHAIK. THE BELKNAP PRESS OF HARVARD UNIVERSITY PRESS, © 2004 BY THE PRESIDENT AND FELLOWS OF HARVARD COLLEGE

Once we were human, cultural history began to interact with innate ability to improve performance. Nearly 150,000 years after the origin of our own species, sophisticated expressions of human symbolism, such as finely worked nonfunctional artifacts (art, musical instruments and burial gifts), were widespread [see "The Morning of the Modern Mind," by Kate Wong, on page 74]. The explosion of technology in the past 10,000 years shows that cultural inputs can unleash limitless accomplishments, all with Stone Age brains. Culture can indeed build a new mind from an old brain. SA

MORE TO EXPLORE

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Conformity to Cultural Norms of Tool Use in Chimpanzees. Andrew Whiten, Victoria Horner and Frans B. M. de Waal in *Nature* online; August 2005.

Stranger in a New Land

BY KATE WONG

Stunning finds in the Republic of Georgia upend long-standing ideas about the first hominids to journey out of Africa

We shall not cease from exploration
And the end of all our exploring
Will be to arrive where we started
And know the place for the first time.
—*T. S. Eliot,* Four Quartets: "Little Gidding"

In an age of spacecraft and deep-sea submersibles, we take it for granted that humans are intrepid explorers. Yet from an evolutionary perspective, the propensity to colonize is one of the distinguishing characteristics of our kind: no other primate has ever ranged so far and wide. Humans have not always been such cosmopolitan creatures, however. For most of the seven million years or so over which hominids have been evolving, they remained within the confines of their birthplace, Africa. But at some point, our ancestors began pushing out of the motherland, marking the start of a new chapter in our family history.

JOHN GURCHE

PORTRAIT OF A PIONEER: With a brain half the size of a modern one and a brow reminiscent of *Homo habilis,* this hominid is one of the most primitive members of our genus on record. Paleoartist John Gurche reconstructed this 1.75-million-year-old explorer from a nearly complete teenage *H. erectus* skull and associated mandible found in Dmanisi in the Republic of Georgia. The background figures derive from two partial crania recovered at the site.

SKULL SURPRISES

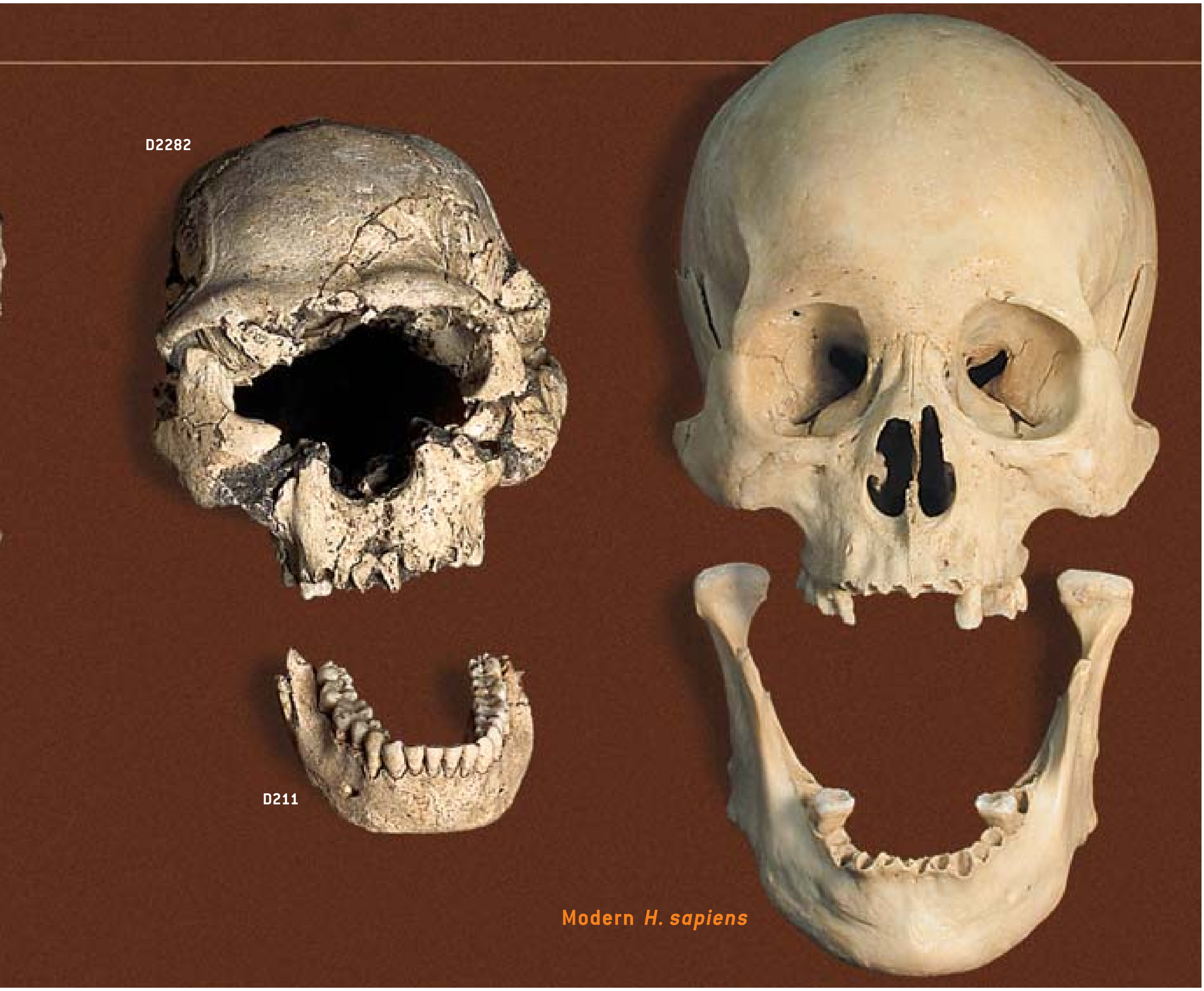
Fossil troika hints at a variable *H. erectus.* These specimens from Dmanisi exhibit characteristic *H. erectus* features, such as a heaping up of bone along the midline of the skull known as a sagittal keel and marked constriction of the skull behind the eyes. But they stop short of the classic morphology of that hominid in several ways—their small brain size, for example, which was about half that of a modern human (*far right*). Specimen D2700 (*near left*), from a teenager, is especially primitive, resembling *H. habilis* not only in size but in the thinness of its brow, the projection of its face and the rounded contour of the rear of the skull. Some researchers propose that these fossils might represent a new species of *Homo.* Others suggest that the remains belong to more than one species, pointing to the enormous lower jaw known as D2600 that was unearthed in 2000. Indeed, this mandible is far too large to fit comfortably with any of the crania yet described (only D2700 turned up with an associated mandible, D2735; the other fossils were isolated finds). For now, the Dmanisi team considers all the fossils as members of the same, mutable species, *H. erectus.*

GOURAM TSIBAKHASHVILI (*fossils*); CHRISTIAN SIDOR *New York College of Osteopathic Medicine (modern skull)*

It was, until recently, a chapter the fossil record had kept rather hidden from view. Based on the available evidence—a handful of human fossils from sites in China and Java—most paleoanthropologists concluded that the first intercontinental traveling was undertaken by an early member of our genus known as *Homo erectus* starting little more than a million years ago. Long of limb and large of brain, *H. erectus* had just the sort of stride and smarts befitting a trailblazer. Earlier hominids, *H. habilis* and the australopithecines among them, were mostly small-bodied, small-brained creatures, not much bigger than a modern chimpanzee. The *H. erectus* build, in contrast, presaged modern human body proportions.

Curiously, though, the first representatives of *H. erectus* in Africa, a group sometimes referred to as *H. ergaster,* had emerged as early as 1.9 million years ago. Why the lengthy departure delay? In explanation, researchers proposed that it was not until the advent of hand axes and other symmetrically shaped, standardized stone tools (a sophisticated technological culture known as the Acheulean) that *H. erectus* could penetrate the northern latitudes. Exactly what, if anything, these implements could accomplish that the simple Oldowan flakes, choppers and scrapers that preceded them could not is unknown, although perhaps they conferred a better means of butchering. In any event, the oldest accepted traces of humans outside Africa were Acheulean stone tools from a site called ‘Ubeidiya in Israel.

Brawny, brainy, armed with cutting-edge technology—this was the hominid hero Hollywood would have cast in the role, a picture-perfect pioneer. Too perfect, it turns out. Over the past few years, researchers working at a site called Dmanisi in the Republic of Georgia have unearthed a trove of spectacularly well preserved human fossils, stone tools and animal remains dated to around 1.75 million years ago—nearly half a million years older than the ‘Ubeidiya remains. It is by pa-



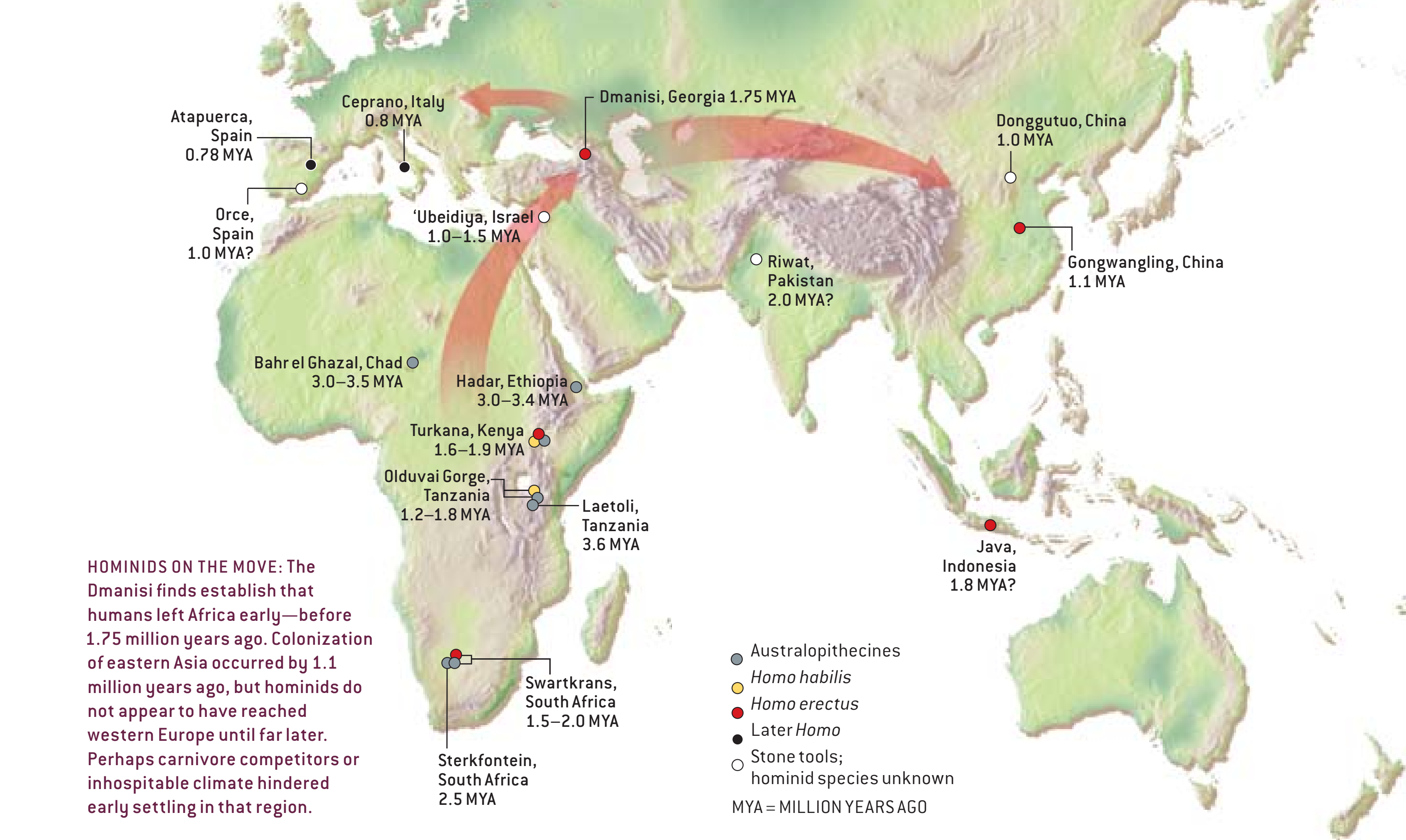
leoanthropological standards an embarrassment of riches. No other early *Homo* site in the world has yielded such a bounty of bones, presenting scientists with an unprecedented opportunity to peer into the life and times of our hominid forebears. The discoveries have already proved revolutionary: the Georgian hominids are far more primitive in both anatomy and technology than expected, leaving experts wondering not only why early humans first ventured out of Africa but how.

A Dubious Debut

AS THE CROW FLIES, the sleepy modern-day village of Dmanisi lies some 85 kilometers southwest of the Georgian capital of Tbilisi and 20 kilometers north of the country's border with Armenia, nestled in the lower Caucasus Mountains. During the Middle Ages, Dmanisi was one of the most prominent cities of the day and an important stop along the old Silk Road. The region has thus long intrigued archaeologists, who have been excavating the crumbling ruins of a medieval citadel there since the 1930s. The first hint that the site might also have a deeper significance came in 1983, when paleontologist Abesalom Vekua of the Georgian Academy of Sciences discovered in one of the grain storage pits the remains of a long-extinct rhinoceros. The holes dug by the citadel's inhabitants had apparently opened a window on prehistory.

The next year, during paleontological excavations, primitive stone tools came to light, bringing with them the tantalizing possibility that fossilized human remains might eventually follow. Finally, in 1991, on the last day of the field season, the crew found what they were looking for: a hominid bone, discovered underneath the skeleton of a saber-toothed cat.

Based on the estimated ages of the associated animal remains, the researchers judged the human fossil—a mandible, or lower jaw, that they attributed to *H. erectus*—to be around 1.6 million years old, which would have made it the



HOMINIDS ON THE MOVE: The Dmanisi finds establish that humans left Africa early—before 1.75 million years ago. Colonization of eastern Asia occurred by 1.1 million years ago, but hominids do not appear to have reached western Europe until far later. Perhaps carnivore competitors or inhospitable climate hindered early settling in that region.

LUCY READING-IKKANDA

oldest known hominid outside of Africa. But when David Lordkipanidze of the Georgian State Museum and the late Leo Gabunia showed the specimen to some of the biggest names in paleoanthropology at a meeting in Germany later that year, their claims were met with skepticism. Humans were not supposed to have made it out of Africa until a million years ago, and the beautifully preserved mandible—every tooth in place—looked too pristine to be as old as the Georgians said it was. Many scientists concluded that the fossil was not *H. erectus* but a later species. Thus, rather than receiving the imprimatur of paleoanthropology's elite, the jaw from Dmanisi came away with question marks.

Undaunted, team members continued work at the site, refining their understanding of its geology and searching for more hominid remains. Their perseverance eventually paid off: in 1999 workers found two skulls just a few feet away from where the mandible had turned up eight years prior. A paper describing the fossils appeared in *Science* the following spring. "That year the fanfare began," recollects Lordkipanidze, who now directs the excavation. The finds established a close relationship between the Dmanisi hominids and African *H. erectus*. Unlike the earliest humans on record from eastern Asia and western Europe, which exhibited regionally distinctive traits, the Dmanisi skulls bore explicit resemblances—in the form of the browridge, for example—to the early African material.

By this time, geologists had nailed down the age of the fossils, which come from deposits that sit directly atop a thick layer of volcanic rock radiometrically dated to 1.85 million years ago. The fresh, unweathered contours of the basalt indicate that little time passed before the fossil-bearing sediments blanketed it, explains C. Reid Ferring of the University of North Texas. And paleomagnetic analyses of the sediments signal that they were laid down close to 1.77 million years ago, when the earth's magnetic polarity reversed, the so-called Matuyama boundary. Furthermore, remains of animals of known antiquity accompany the hominid fossils—a rodent called *Mimomys*, for instance, which lived only between 1.6 and 2.0 million years ago—and a second, 1.76-million-year-old layer of basalt at a nearby site caps the same stratigraphy.

Together the new fossils and dating results clinched the case for Dmanisi being the oldest unequivocal hominid site outside

Overview/*The First Colonizers*

- Conventional paleoanthropological wisdom holds that the first humans to leave Africa were tall, large-brained people equipped with sophisticated stone tools who began migrating northward around a million years ago.
- New fossil discoveries in the Republic of Georgia are forcing scholars to rethink that scenario in its entirety. The remains are nearly half a million years older than hominid remains previously recognized as the most ancient outside of Africa. They are also smaller and accompanied by more primitive implements than expected.
- These finds raise the question of what prompted our ancestors to leave their natal land. They are also providing scientists with a rare opportunity to study not just a single representative of early *Homo* but a population.

of Africa, pushing the colonization of Eurasia back hundreds of thousands of years. They also toppled the theory that humans could not leave Africa until they had invented Acheulean technology. The Dmanisi tool kit contained only Oldowan-grade implements fashioned from local raw materials.

Pint-Size Pioneer

THE GREAT AGE of the Georgian hominids and the simplicity of their tools came as a shock to many paleoanthropologists. But Dmanisi had even more surprises in store. In July 2002 Lordkipanidze's team announced that it had recovered a third, virtually complete skull—including an associated mandible—that was one of the most primitive *Homo* specimens on record. Whereas the first two skulls had housed 770 cubic centimeters and 650 cubic centimeters of gray matter, the third had a cranial capacity of just 600 cubic centimeters—less than half the size of a modern brain and considerably smaller than expected for *H. erectus*. Neither was the form of the third skull entirely *erectus*-like. Rather the delicacy of the brow, the projection of the face and the curvature of the rear of the skull evoke *H. habilis,* the presumed forebear of *H. erectus*.

The discovery of the third skull has led to the startling revelation that contrary to the notion that big brains were part and parcel of the first transcontinental migration, some of these early wayfarers were hardly more cerebral than primitive *H. habilis*. Likewise, the Georgian hominids do not appear to have been much larger-bodied than *H. habilis*. Ribs, clavicles, vertebrae, as well as arm, leg, hand and foot bones—have also turned up, although most have yet to be formally described. But based on the femur, the Dmanisi people appear to have been only around four and a half feet tall.

"This is the first time we have an intermediate between *erectus* and *habilis,*" Lordkipanidze observes. Although the fossils have been provisionally categorized by the team as *H. erectus* based on the presence of certain defining characteristics, he thinks the population represented by the Dmanisi hominids may have been more specifically the rootstock of the species, a missing link between *erectus* and *habilis*.

Other scholars have proposed a more elaborate taxonomic scheme. Noting the anatomical variation evident in the skulls and mandibles recovered so far (including a behemoth jaw unearthed in 2000), Jeffrey Schwartz of the University of Pittsburgh suggested that the Dmanisi fossils might represent two or more early human species. "If that's the case, I'll eat one of them," retorts Milford H. Wolpoff of the University of Michigan at Ann Arbor. A more likely explanation, he offers, is that the rogue mandible comes from a male and the rest of the bones belong to females.

For his part, Lordkipanidze acknowledges that the massive mandible "is a bit of a headache," but given that the fossils all come from the same stratigraphic layer, he reasons, they are probably members of the same population of *H. erectus*. Indeed, one of the most important things about Dmanisi, he says, is that it "gives us an opportunity to think about what variation is." Perhaps some researchers have underestimated how variable *H. erectus* was—a notion that re-

STONE TOOL TRICK

Until recently, experts believed that humans could not leave Africa until they had developed an advanced technology known as the Acheulean, in which tools were symmetrically shaped and standardized (*see hand ax at right*). The tools found at Dmanisi, however, are simple flakes and choppers (*left* and *center*) manufactured according to much the same primitive Oldowan tradition that hominids in Africa were practicing nearly a million years earlier.

GOURAM TSIBAKHASHVILI

DIGGING DMANISI

DMANISI, REPUBLIC OF GEORGIA, JULY 2003—From the Republic of Georgia's capital, Tbilisi, the village of Dmanisi is just a two-hour drive, yet it seems a world apart from the bustle of the diesel- and dust-choked city. Here in the foothills of the Caucasus Mountains, donkey-drawn carts outnumber cars and the air is fragrant with hay. The locals farm the rich soil and raise sheep, pigs and goats; children spend summer afternoons racing down a stretch of paved road on homemade scooters. Even the roosters appear to lose track of time, crowing not only at daybreak but in the afternoon and evening as well.

The leisurely pace of modern life belies the region's storied past, however. Centuries ago Dmanisi was a seat of great power, situated at a crossroads of Byzantine and Persian trading routes. Today the region is littered with reminders of that bygone era. Haystacklike mounds resolve into ancient Muslim tombs on closer inspection; medieval burials erode out of a hillside after heavy rains; and looming above it all are the imposing ruins of a citadel built on a promontory that once overlooked the Silk Road.

That much about Dmanisi's past has been known for decades. Only recently have scholars learned that long before the rise and fall of the city, this was the dominion of a primitive human ancestor, the first known to march out of Africa and begin colonizing the rest of the Old World some 1.75 million years ago—far earlier than previously thought. It is a realization that still gives David Lordkipanidze pause. Just a dozen years ago he helped to unearth the first hominid bone at Dmanisi. Four skulls and thousands of stone tools and ancient animal fossils later, the 40-year-old is deputy director of the Georgian State Museum and head of an excavation many paleoanthropologists regard as the most spectacular in recent memory. "It is big luck to have these beautiful fossils," he reflects. But it is also "a big responsibility." Indeed, equal parts paleontologist and

REMAINS OF THE DAY: Excavations of Dmanisi's medieval city led to the discovery of the much older fossils. So far paleoanthropologists have thoroughly probed only 100 square meters of the site, which is estimated to span 11,000 square meters.

GOURAM TSIBAKHASHVILI

politician, Lordkipanidze seems to work around the clock, talking on his cell phone late into the night with colleagues and prospective sponsors.

Largely as a result of those efforts, what started as a 10-person team of Georgians and Germans has mushroomed into a 30-strong collaboration of scientists and students from around the world, a number of whom have gathered here for the annual field season. For eight weeks every summer, the Dmanisi field crew surveys, digs and analyzes new finds. It is a shoestring operation. Team members live in a no-frills house a couple of kilometers from the site, typically sleeping four to a tiny room. Electricity is ephemeral at best, hot running water nonexistent.

Every morning at around 8:30, after a breakfast of bread and tea at the picnic tables on the porch, the groggy workers pile into a Russian army-issue lorry left over from the days of Soviet occupation and drive up to the site. In the main excavation area—the 20-by-20-meter square that in 2001 yielded an extraordinarily complete skull and associated lower jaw—each person tends a square-meter plot, meticulously recording the three-dimensional position of each recognizable bone and artifact uncovered during removal of the sediments. These items are then labeled and bagged for later study. Even nondescript pebbles and sediments are saved for further scrutiny: rinsing and sieving them may expose shells, minuscule mammal bones and other important environmental clues.

SCRAPING AND BRUSHING away the chalky sediments, crew members expose stone tools and animal remains—the work of hungry hominids.

MARC MEYER *University of Pennsylvania*

On this particular day the fossil hunters are in especially good spirits. A rare bout of soggy weather left them housebound yesterday (waterlogged bones are too fragile to extract), and this morning's skies threatened to do the same. But the mist draping the mountains has finally burned off, eliciting a chorus of Johnny Nash's "I Can See Clearly Now," sung over the taps and scrapes of trowels, hammers and spackle knives against the chalky sediments. They progress slowly. The excavators are now working in the dense upper layer, which does not yield its bones and stones easily. They must take care not to scratch the remains with their implements, lest the fresh marks be mistaken for ancient ones in later analyses. When noon arrives, the diggers break eagerly for lunch—tomatoes, cucumbers, bread, hard-boiled eggs and pungent, brine-soaked cheese (an acquired taste)—and a catnap on the grass before returning to their squares.

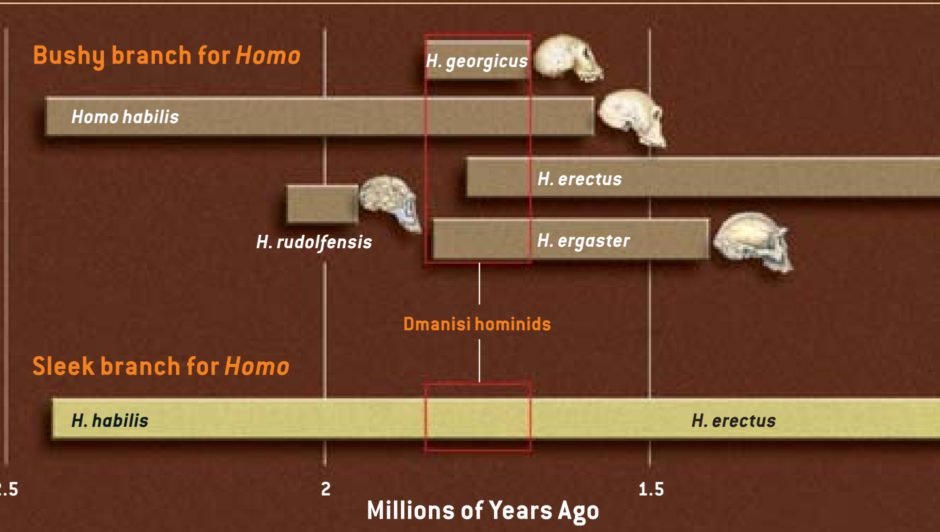
Meanwhile, in a makeshift lab back at camp, other crew members sort through remains brought back earlier by the excavators. Seated at metal-topped wooden tables and sharing an outmoded microscope, they identify the species to which each bone belongs and inspect it for telltale breaks, cut marks and tooth marks. Such data should eventually disclose how the bones accumulated. Preliminary findings from the main excavation suggest that denning saber-toothed cats may have collected them. In contrast, early data from another dig spot about 100 meters away, known as M6, hint that humans worked there—the abundance of smashed bone in this locale is more characteristic of hominid activity than carnivore activity. If so, M6 could provide critical insight into how the primitive Dmanisi hominids eked out an existence in this new land.

When the fossil hunters return with the day's haul at around 4:00, camp is once again the center of activity. An early dinner leaves time for a shower, a game of chess or a trip down the road to visit the enterprising village woman who vends candy, soda, cigarettes and other luxury goods from a small whitewashed building affectionately dubbed the Mall, before a final hour of lab work and the evening tea.

For Lordkipanidze, the work has come full circle. Here at the site where he cut his teeth on paleoanthropology, he hopes to establish a preeminent field school to train aspiring young archaeologists and anthropologists. In the meantime, he and his colleagues have plans to test promising spots elsewhere in the region for hominid fossils. Perhaps Georgia's biggest surprises are yet to come. *—K.W.*

TRIMMING THE FAMILY TREE

Experts vigorously debate just how many species our genus, *Homo,* comprises. The bushiest representations of the *Homo* branch of the family tree contain up to eight species, a number of which were evolutionary dead ends (*top*). Other renditions appear as a streamlined succession of just a few forms (*bottom*). The fossils from Dmanisi—categorized variously as *H. habilis, H. erectus, H. ergaster* and a new species, *H. georgicus*—could be compatible with scenarios of substantial hominid diversity. Alternatively, the anatomical range evident in the Georgian remains could just underscore how variable a species can be. Viewed that way, some pruning may be in order.



CORNELIA BLIK, PATRICIA J. WYNNE AND EDWARD BELL

cent discoveries from a site called Bouri in Ethiopia's Middle Awash region and another locality known as Ileret in Kenya support. Lordkipanidze suspects that as the Georgian picture becomes clearer, the sex and species of more than a few African fossils will need reassessing, as will the question of who the founding members of our lineage were. "Maybe *habilis* is not *Homo,*" he muses. In fact, a number of experts wonder whether this hominid may have been a species of *Australopithecus* rather than a member of our own genus.

"It is not cladistically compelling to place *habilis* in *Homo,*" comments Bernard Wood of George Washington University. Considering its brain and body proportions, characteristics of its jaws and teeth, and features related to locomotion, "*habilis* is more australopithlike than it has been made out to be." If so, the emergence of *H. erectus* may well have marked the birth of our genus. What is unclear thus far, Wood says, is whether the Dmanisi hominids fall on the *Homo* side of the divide or the *Australopithecus* one.

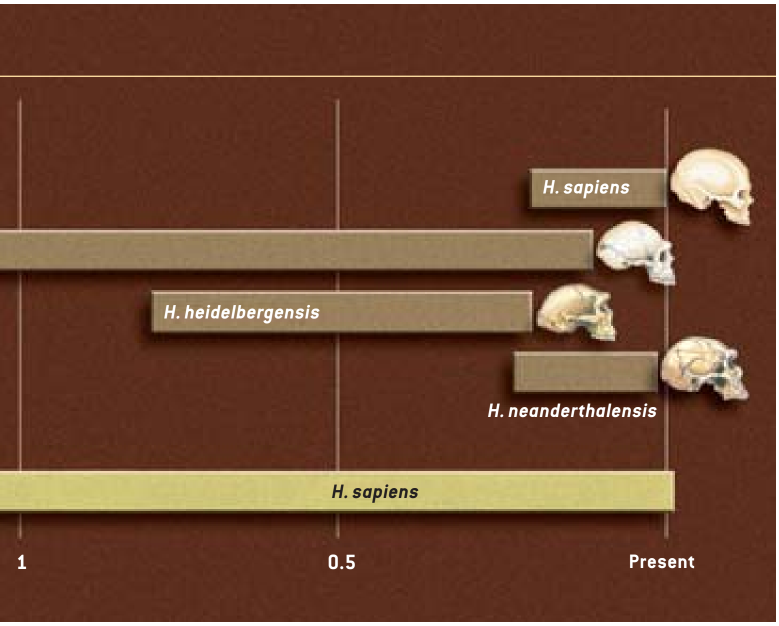
Taxonomic particulars aside, the apparently small stature of the Dmanisi people could pose further difficulty for paleoanthropologists. Another popular theory of why humans left Africa, put forth in the 1980s by Alan Walker and Pat Shipman of Pennsylvania State University and elaborated on more recently by William R. Leonard of Northwestern University and his colleagues, proposes that *H. erectus*'s large body size necessitated a higher-quality diet—one that included meat—than that of its smaller predecessors to meet its increased energy needs. Adopting such a regimen would have forced this species to broaden its horizon to find sufficient food—an expansion that might have led it into Eurasia. The discovery of individuals considerably smaller than classic *H. erectus* outside of Africa could force experts to rethink that scenario.

Perhaps it was language that enabled hominids to finally break free from the confines of Africa. Received wisdom holds that *H. erectus* lacked the ability to speak because it possessed a spinal cord that was too small to control with sufficient precision the muscles involved in speech production. This conclusion is based on what were long the only known *H. erectus* vertebrae, from the spectacular Kenyan fossil known as the Turkana Boy. But analysis of the Dmanisi vertebrae and the Turkana ones, conducted by Marc Meyer of the University of Pennsylvania, has shown that the Dmanisi people had modern spinal cords—and thus no neural constraint on language. The Turkana Boy, it turns out, had a disease that constricted his spinal cord and is therefore not representative of the normal *H. erectus* condition. Although the new work does not establish that the Dmanisi people had the gift of gab, it raises the possibility that they could have.

Georgia on Their Minds

HOWEVER EARLY HOMINIDS got out of Africa, it is not hard to see why they settled down in southern Georgia. For one, the presence of the Black Sea to the west and the Caspian Sea to the east would have ensured a relatively mild, perhaps even Mediterranean-like, climate. For another, the region appears to have been incredibly diverse ecologically: remains of woodland creatures, such as deer, and grassland animals, such as horses, have all turned up at the site, suggesting a mosaic of forest and savanna habitats. Thus, in practical terms, if the going got tough in one spot, the hominids would not have had to move far to get to a better situation. "The heterogeneity of the environment may have promoted occupation," Ferring says. The Dmanisi site in particular, located on a promontory formed by the confluence of two rivers, may have attracted hominids with its proximity to water, which would have not only quenched their thirst but lured potential prey as well.

"Biologically this was a happening place," remarks Martha Tappen of the University of Minnesota. Of the thousands of mammal fossils that workers have unearthed along with the hominid remains, many come from large carnivores such



as saber-toothed cats, panthers, bears, hyenas and wolves. Tappen, whose work centers on figuring out what led to the accumulation of bones at the site, suspects that the carnivores may have been using the water-lined promontory as a trap. "The question," she says, "is whether hominids were, too."

So far Tappen has identified a few cut marks on the animal bones, indicating that, at least on occasion, the Dmanisi settlers ate meat. But whether they scavenged animals brought down by the local carnivores or hunted the beasts themselves is not known. The matter warrants investigation. One of the few remaining hypotheses for what allowed humans to expand their range into northern lands holds that making the transition from the mostly vegetarian diet of the australopithecines to a hunter-gatherer subsistence strategy enabled them to survive the colder winter months, during which plant resources were scarce, if not altogether unavailable. Only further analyses of the mammal bones at the site can elucidate how the Dmanisi humans acquired meat. But Tappen surmises that they were hunting. "When you're a scavenger, the distribution of animals is so unpredictable," she remarks. "I don't think it was their main strategy."

That does not mean that humans were the top carnivores, however. "They could have been both the hunters and the hunted," Tappen observes. Telltale puncture wounds on one of the skulls and gnaw marks on the large mandible reveal that some of the hominids at Dmanisi ended up as cat food.

Outward Bound

THE GEORGIAN REMAINS prove that humans left Africa shortly after *H. erectus* evolved around 1.9 million years ago. But where they went after that is a mystery. The next oldest undisputed fossils in Asia are still just a bit more than a million years old (although controversial sites in Java date to 1.8 million years ago), and those in Europe are only around 800,000 years of age. Anatomically, the Dmanisi people make reasonable ancestors for later *H. erectus* from Asia, but they could instead have been a dead-end group, the leading edge of a wave that washed only partway across Eurasia. There were, scientists concur, multiple migrations out of Africa as well as movements back in. "Dmanisi is just one moment," Lordkipanidze says. "We need to figure out what happened before and after."

Echoing what has become a common refrain in paleoanthropology, the Dmanisi discoveries in some ways raise more questions than they answer. "It's nice that everything's been shaken up," team member G. Philip Rightmire of Binghamton University reflects, "but frustrating that some of the ideas that seemed so promising eight to 10 years ago don't hold up anymore." A shift toward meat eating might yet explain how humans managed to survive outside of Africa, but what prompted them to push into new territories remains unknown. Perhaps they were following herd animals north. Or maybe it was as simple and familiar as a need to know what lay beyond that hill, or river, or tall savanna grass—a case of prehistoric wanderlust.

The good news is that scientists have only begun plumbing Dmanisi's depths. The fossils recovered thus far come from just a fraction of the site's estimated extent, and new material is emerging from the ground faster than the researchers can formally describe it. Team members reported last year that a fourth skull unearthed in 2002 turned out to come from an elderly male who had lost all his teeth, indicating that he would have to have been cared for by other members of the group—possibly the oldest known evidence of compassion for the infirm. And just last summer a fifth skull was found. It is still undergoing analysis.

Topping the fossil hunters' wish list are pelvises, which will help reveal how these early colonizers efficiently covered long distances. There is every reason to expect they will find them. "They've got the potential to have truckloads of fossils," Wolpoff says enthusiastically. "There is work for generations here," Lordkipanidze agrees, noting that he can envision his grandchildren working at the site decades from now. Who knows what new frontiers humans will have explored by then? SA

Kate Wong is editorial director of ScientificAmerican.com

MORE TO EXPLORE

Earliest Pleistocene Hominid Cranial Remains from Dmanisi, Republic of Georgia: Taxonomy, Geological Setting, and Age. Leo Gabunia, Abesalom Vekua, David Lordkipanidze et al. in *Science,* Vol. 288, pages 1019–1025; May 12, 2000.

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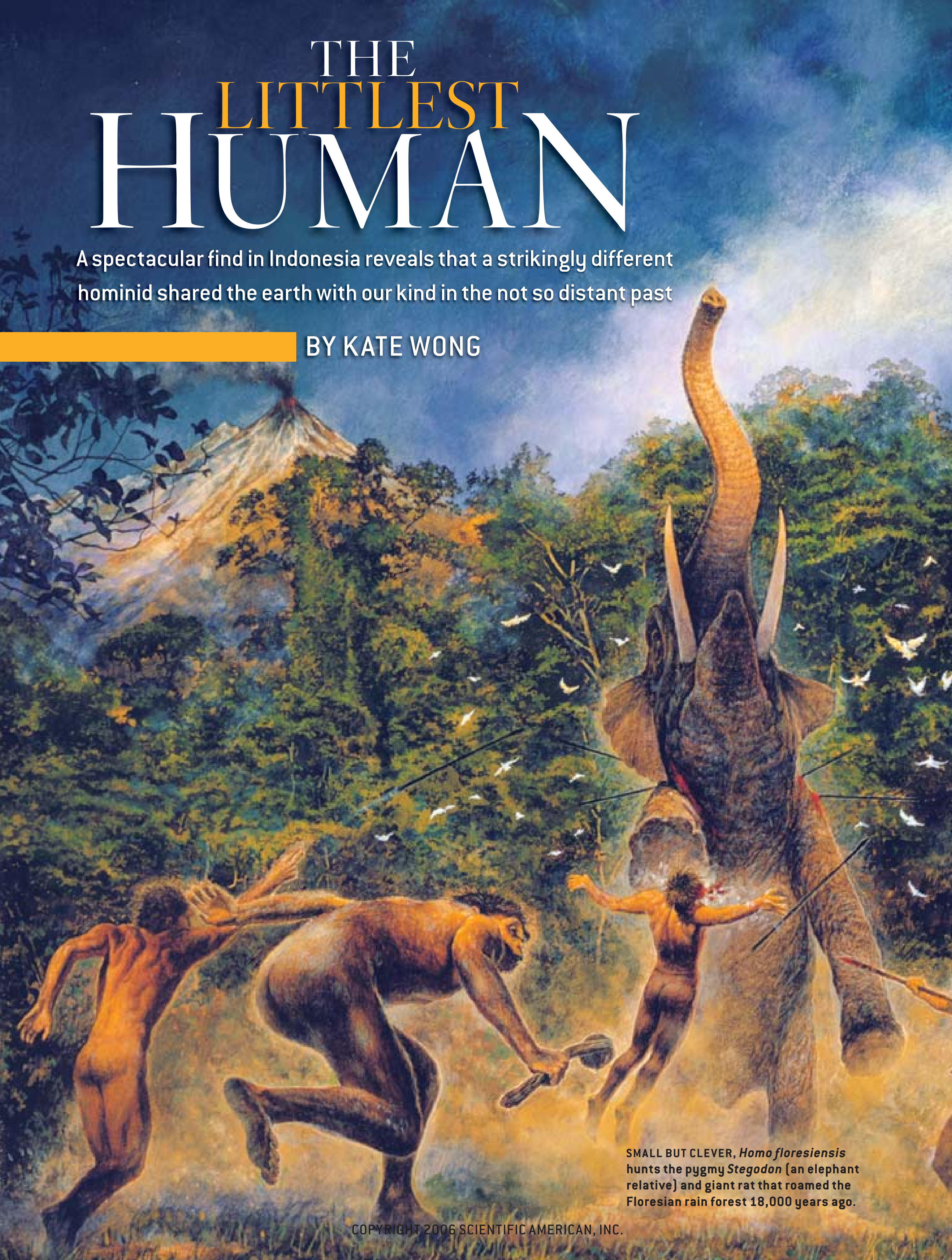
THE LITTLEST HUMAN

A spectacular find in Indonesia reveals that a strikingly different hominid shared the earth with our kind in the not so distant past

BY KATE WONG



SMALL BUT CLEVER, *Homo floresiensis* hunts the pygmy *Stegodon* (an elephant relative) and giant rat that roamed the Floresian rain forest 18,000 years ago.

On the island of Flores in Indonesia, villagers have long told tales of a diminutive, upright-walking creature with a lopsided gait, a voracious appetite, and soft, murmuring speech.

They call it *ebu gogo,* "the grandmother who eats anything." Scientists' best guess was that macaque monkeys inspired the *ebu gogo* lore. But in October 2004 an alluring alternative came to light. A team of Australian and Indonesian researchers excavating a cave on Flores unveiled the remains of a lilliputian human—one that stood barely a meter tall—whose kind lived as recently as 12,000 years ago.

The announcement electrified the paleoanthropology community. *Homo sapiens* was supposed to have had the planet to itself for the past 25 millennia, free from the company of other humans following the apparent demise of the Neandertals in Europe and *Homo erectus* in Asia. Furthermore, hominids this tiny were known only from fossils of australopithecines (Lucy and the like) that lived nearly three million years ago—long before the emergence of *H. sapiens*. No one would have predicted that our own species had a contemporary as small and primitive-looking as the little Floresian. Neither would anyone have guessed that a creature with a skull the size of a grapefruit might have possessed cognitive capabilities comparable to those of anatomically modern humans.

Isle of Intrigue

THIS IS NOT THE FIRST TIME Flores has yielded surprises. In 1998 archaeologists led by Michael J. Morwood of the University of New England in Armidale, Australia, reported having discovered crude stone artifacts some 840,000 years old in the Soa Basin of central Flores. Although no human remains turned up with the tools, the implication was that *H. erectus,* the only hominid known to have lived in Southeast Asia during that time, had crossed the deep waters separating Flores from Java. To the team, the find showed *H. erectus* to be a seafarer, which was startling because elsewhere *H. erectus* had left behind little material culture to suggest that it was anywhere near capable of making watercraft. Indeed, the earliest accepted date for boat-building was 40,000 to 60,000 years ago, when modern humans colonized Australia. (The other early fauna on Flores probably got there by swimming or accidentally drifting over on flotsam.) Humans are not strong enough swimmers to have managed that voyage, but skeptics say they may have drifted across on natural rafts.

Overview/*Mini Humans*

- Conventional wisdom holds that *Homo sapiens* has been the sole human species on the earth for the past 25,000 years. Remains discovered on the Indonesian island of Flores have upended that view.
- The bones are said to belong to a dwarf species of *Homo* that lived as recently as 12,000 years ago.
- Although the hominid is as small in body and brain as the earliest humans, it appears to have made sophisticated stone tools, raising questions about the relation between brain size and intelligence.
- The find is controversial, however—some experts wonder whether the discoverers have correctly diagnosed the bones and whether anatomically modern humans might have made those advanced artifacts.

KAZUHIKO SANO (*preceding pages*)

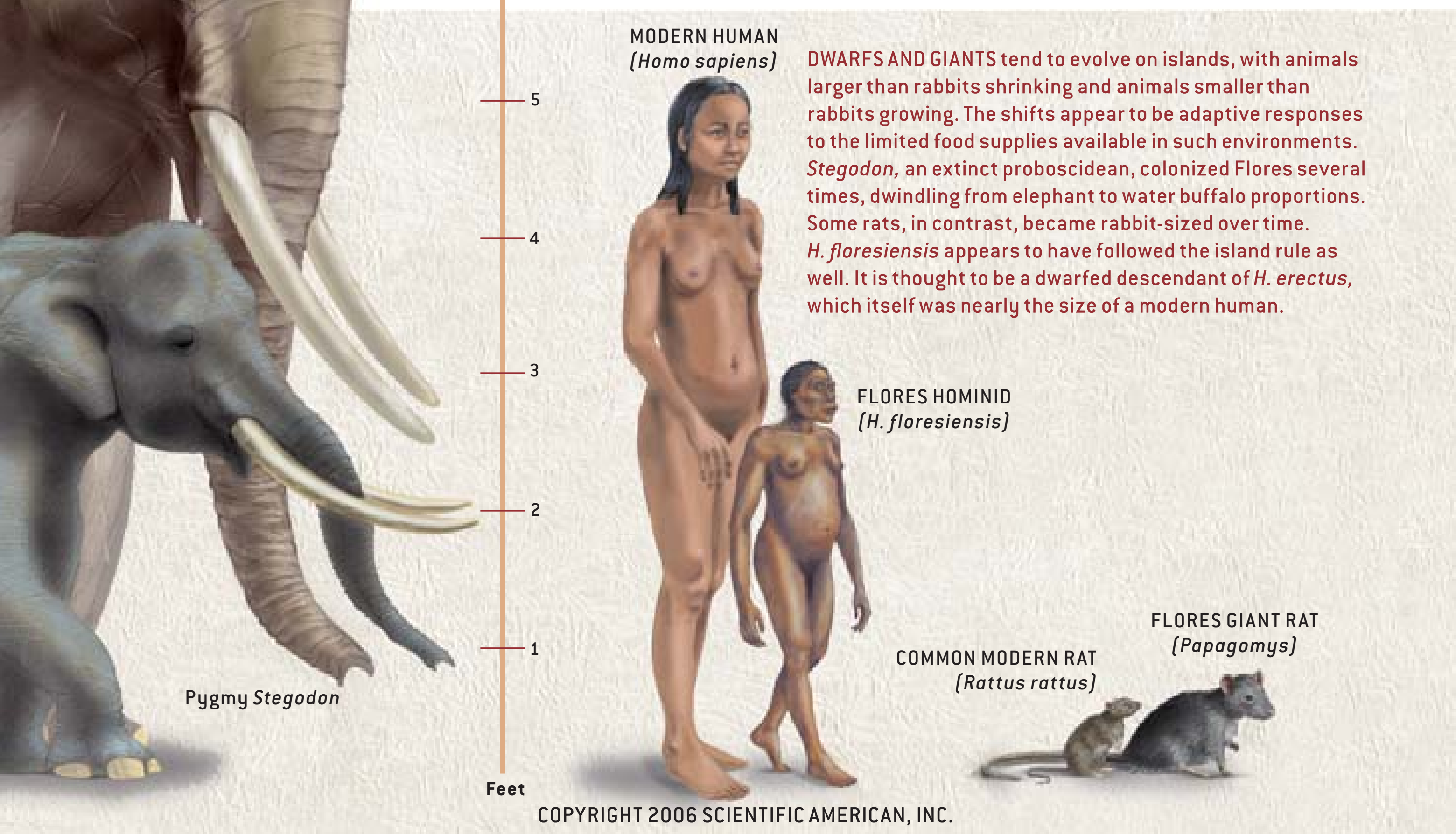
MODERN INDIAN ELEPHANT
(Elephas maximus)

Hoping to document subsequent chapters of human occupation of the island, Morwood and Radien P. Soejono of the Indonesian Center for Archaeology in Jakarta turned their attention to a large limestone cave called Liang Bua located in western Flores. Indonesian archaeologists had been excavating the cave intermittently since the 1970s, depending on funding availability, but workers had penetrated only the uppermost deposits. Morwood and Soejono set their sights on reaching bedrock and began digging in July 2001. Before long, their team's efforts turned up abundant stone tools and bones of a pygmy version of an extinct elephant relative known as *Stegodon*. But it was not until nearly the end of the third season of fieldwork that diagnostic hominid material in the form of an isolated tooth surfaced. Morwood brought a cast of the tooth back to Armidale to show to his department colleague Peter Brown. "It was clear that while the premolar was broadly humanlike, it wasn't from a modern human," Brown recollects. Seven days later Morwood received word that the Indonesians had recovered a skeleton. The Australians boarded the next plane to Jakarta.

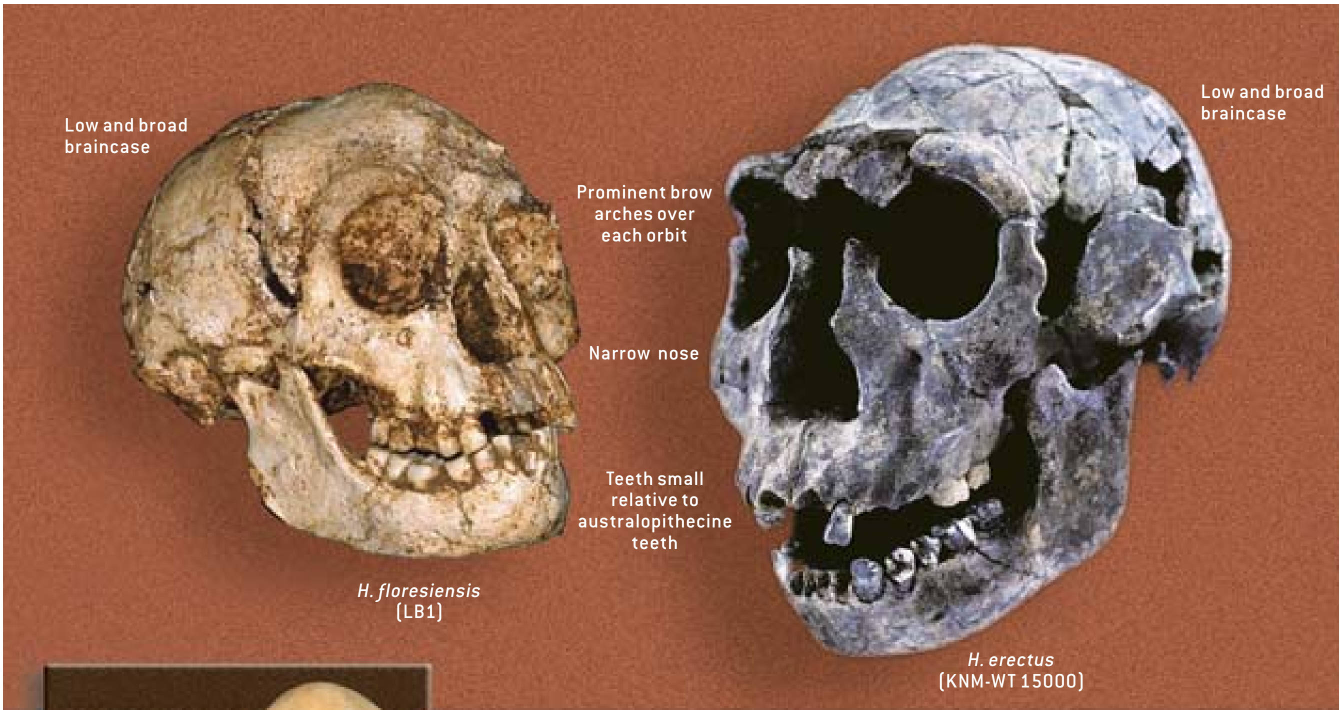
Peculiar though the premolar was, nothing could have prepared them for the skeleton, which apart from the missing arms was largely complete. The pelvis anatomy revealed that the individual was bipedal and probably a female, and the tooth eruption and wear indicated that it was an adult. Yet it was only as tall as a modern three-year-old, and its brain was as small as the smallest australopithecine brain known. There were other primitive traits as well, including the broad pelvis and the long neck of the femur. In other respects, however, the specimen looked familiar. Its small teeth and narrow nose, the overall shape of the braincase and the thickness of the cranial bones all evoked *Homo*.

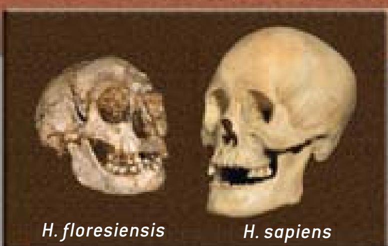
Brown spent the next three months analyzing the enigmatic skeleton, catalogued as LB1 and affectionately nicknamed the Hobbit by some of the team members, after the tiny beings in J.R.R. Tolkien's books. The decision about how to classify it did not come easily. Impressed with the characteristics LB1 shared with early hominids such as the australopithecines, he initially proposed that it represented a new genus of human. On further consideration, however, the similarities to *Homo* proved more persuasive. Based on the 18,000-year age of LB1, one might have reasonably expected the bones to belong to *H. sapiens,* albeit a very petite representative. But when Brown and his colleagues considered the morphological characteristics of small-bodied modern humans—including normal ones, such as pygmies, and abnormal ones, such as pitu-

PORTIA SLOAN

DWARFS AND GIANTS tend to evolve on islands, with animals larger than rabbits shrinking and animals smaller than rabbits growing. The shifts appear to be adaptive responses to the limited food supplies available in such environments. *Stegodon,* an extinct proboscidean, colonized Flores several times, dwindling from elephant to water buffalo proportions. Some rats, in contrast, became rabbit-sized over time. *H. floresiensis* appears to have followed the island rule as well. It is thought to be a dwarfed descendant of *H. erectus,* which itself was nearly the size of a modern human.





SHARED FEATURES between LB1 and members of our own genus led to the classification of the Flores hominid as *Homo,* despite its tiny brain size. Noting that the specimen most closely resembles *H. erectus,* the researchers posit that it is a new species, *H. floresiensis,* that dwarfed from a *H. erectus* ancestor. *H. floresiensis* differs from *H. sapiens* in having, among other characteristics, no chin, a relatively projecting face, a prominent brow and a low braincase.

itary dwarfs—LB1 did not seem to fit any of those descriptions. Pygmies have small bodies and large brains—the result of delayed growth during puberty, when the brain has already attained its full size. And individuals with genetic disorders that produce short stature and small brains have a range of distinctive features not seen in LB1 and rarely reach adulthood, Brown says. Conversely, he notes, the Flores skeleton exhibits archaic traits that have never been documented for abnormal small-bodied *H. sapiens*.

What LB1 looks like most, the researchers concluded, is a miniature *H. erectus*. Describing the find in the journal *Nature,* they assigned LB1 as well as the isolated tooth and an arm bone from older deposits to a new species of human, *Homo floresiensis*. They further argued that it was a descendant of *H. erectus* that had become marooned on Flores and evolved in isolation into a dwarf species, much as the elephantlike *Stegodon* did.

Biologists have long recognized that mammals larger than rabbits tend to shrink on small islands, presumably as an adaptive response to the limited food supply. They have little to lose by doing so, because these environments harbor few predators. On Flores, the only sizable predators were the Komodo dragon and another, even larger monitor lizard. Animals smaller than rabbits, on the other hand, tend to attain Brobdingnagian proportions—perhaps because bigger bodies are more energetically efficient than small ones. Liang Bua has yielded evidence of that as well, in the form of a rat as robust as a rabbit.

But attributing a hominid's bantam size to the so-called island rule was a first. Received paleoanthropological wisdom holds that culture has buffered us humans from many of the selective pressures that mold other creatures—we cope with cold, for example, by building fires and making clothes, rather than evolving a proper pelage. The discovery of a dwarf hominid species indicates that, under the right conditions, humans can in fact respond in the same, predictable way that other large mammals do when the going gets tough. Hints that *Homo* could deal with resource fluxes in this manner came earlier in 2004 from the discovery of a relatively petite *H. erectus* skull from Olorgesailie in Kenya, remarks Richard Potts of the Smithsonian Institution, whose team recovered the bones. "Getting small is one of the things *H. erectus* had in its biological tool kit," he says, and the Flores hominid seems to be an extreme instance of that.

Curiouser and Curiouser

H. FLORESIENSIS's teeny brain was perplexing. What the hominid reportedly managed to accomplish with such a modest organ was nothing less than astonishing. Big brains are a hallmark of human evolution. In the space of six million to seven million years, our ancestors more than tripled their cranial capacity, from some 360 cubic centimeters in *Sahelanthropus,* the earliest putative hominid, to a whopping 1,350 cubic centimeters on average in modern folks. Archaeological evidence indicates that behavioral complexity increased correspondingly. Experts were thus fairly certain that large

CHRISTIAN SIDOR *New York College of Osteopathic Medicine* (*H. sapiens*); PETER BROWN *University of New England, Armidale* AND TIMEFORKIDS/KRT (*H. floresiensis*); DAVID BRILL (*H. erectus*) brains are a prerequisite for advanced cultural practices. Yet whereas the pea-brained australopithecines left behind only crude stone tools at best (and most seem not to have done any stoneworking at all), the comparably gray-matter-impoverished *H. floresiensis* is said to have manufactured implements that exhibit a level of sophistication elsewhere associated exclusively with *H. sapiens*.

The bulk of the artifacts from Liang Bua are simple flake tools struck from volcanic rock and chert, no more advanced than the implements made by late australopithecines and early *Homo*. But mixed in among the pygmy *Stegodon* remains, excavators found a fancier set of tools, one that included finely worked points, large blades, awls and small blades that may have been hafted for use as spears. To the team, this association suggests that *H. floresiensis* regularly hunted *Stegodon*. Many of the *Stegodon* bones are those of young individuals that one *H. floresiensis* might have been able to bring down alone. But some belonged to adults that weighed up to half a ton, the hunting and transport of which must have been a coordinated group activity—one that probably required language, surmises team member Richard G. ("Bert") Roberts of the University of Wollongong in Australia.

The discovery of charred animal remains in the cave suggests that cooking, too, was part of the cultural repertoire of *H. floresiensis*. That a hominid as cerebrally limited as this one might have had control of fire gives pause. Humans are not thought to have tamed flame until relatively late in our collective cognitive development: the earliest unequivocal evidence of fire use comes from 200,000-year-old hearths in Europe that were the handiwork of the large-brained Neandertals.

If the *H. floresiensis* discoverers are correct in their interpretation, theirs is one of the most important paleoanthropological finds in decades. Not only does it mean that another species of human coexisted with our ancestors just yesterday in geologic terms and that our genus is far more variable than expected, it raises all sorts of questions about brain size and intelligence. Perhaps it should come as no surprise, then, that controversy has accompanied the claims.

Classification Clash

IT DID NOT TAKE LONG for alternative theories to surface. In a letter that ran in the October 31, 2004, edition of Australia's *Sunday Mail,* just three days after the publication of the *Nature* issue containing the initial reports, paleoanthropologist Maciej Henneberg of the University of Adelaide countered that a pathological condition known as microcephaly (from the Greek for "small brain") could explain LB1's unusual features. Individuals afflicted with the most severe congenital form of microcephaly, primordial microcephalic dwarfism, die in childhood. But those with milder forms, though mentally retarded, can survive into adulthood. Statistically comparing the head and face dimensions of LB1 with those of a 4,000-year-old skull from Crete that is known to have belonged to a microcephalic, Henneberg found no significant differences between the two. Furthermore, he argued,

COURTESY OF MARK MOORE

ADVANCED IMPLEMENTS appear to have been the handiwork of *H. floresiensis.* Earlier hominids with brains similar in size to that of *H. floresiensis* made only simple flake tools at most. But in the same stratigraphic levels as the hominid remains at Liang Bua, researchers found a suite of sophisticated artifacts—including awls, blades and points—exhibiting a level of complexity previously thought to be the sole purview of *H. sapiens.*

the isolated forearm bone found deeper in the deposit corresponds to a height of 151 to 162 centimeters—the stature of many modern women and some men, not that of a dwarf—suggesting that larger-bodied people, too, lived at Liang Bua. In Henneberg's view, these findings indicate that LB1 is more likely a microcephalic *H. sapiens* than a new branch of *Homo*.

Susan C. Antón of New York University disagrees with that assessment. "The facial morphology is completely different in microcephalic [modern] humans," she says. Antón questions whether LB1 warrants a new species, however. "There's little in the shape that differentiates it from *H. erectus,*" she notes. One can argue that it is a new species, Antón allows, but the difference in shape between LB1 and *H. erectus* is less striking than that between a Great Dane and a Chihuahua. The possibility exists that the LB1 specimen is a *H. erectus* individual with a pathological growth condition stemming from microcephaly or nutritional deprivation, she observes.

But some specialists say the Flores hominid's anatomy exhibits a more primitive pattern. According to Colin P. Groves of the Australian National University and David W. Cameron of the University of Sydney, the small brain, the long neck of the femur and other characteristics suggest an ancestor along the lines of *H. habilis,* the earliest member of our genus, rather than the more advanced *H. erectus*. Milford H. Wolpoff of the University of Michigan at Ann Arbor wonders whether the Flores find might even represent an offshoot of *Australopithecus*. If LB1 is a descendant of *H. sapiens* or *H. erectus,* it is hard to imagine how natural selection left her with a brain that is even smaller than expected for her height, Wolpoff says. Granted, if she descended from *Australopithecus,* which had massive jaws and teeth, one has to account for her relatively delicate jaws and dainty dentition. That, however, is a lesser evolutionary conundrum than the one posed by her tiny brain, he asserts. After all, a shift in diet could explain the reduced chewing apparatus, but why would selection downsize intelligence?

Finding an australopithecine that lived outside of Africa—not to mention all the way over in Southeast Asia—18,000 years ago would be a first. Members of this group were thought to have died out in Africa one and a half million years ago, never having left their mother continent. Perhaps, researchers reasoned, hominids needed long, striding limbs, large brains and better technology before they could venture out into the rest of the Old World. But the recent discovery of 1.8-million-year-old *Homo* fossils at a site called Dmanisi in the Republic of Georgia refuted that explanation—the Georgian hominids were primitive and small and utilized tools like those australopithecines had made a million years before. Taking that into consideration, there is no a priori reason why australopithecines (or habilines, for that matter) could not have colonized other continents.

Troubling Tools

YET IF *AUSTRALOPITHECUS* made it out of Africa and survived on Flores until quite recently, that would raise the question of why no other remains supporting that scenario have turned up in the region. According to Wolpoff, they may have: a handful of poorly studied Indonesian fossils discovered in the 1940s have been variously classified as *Australopithecus*, *Meganthropus* and, most recently, *H. erectus*. In light of the Flores find, he says, those remains deserve reexamination.

Many experts not involved in the discovery back Brown and Morwood's taxonomic decision, however. "Most of the differences [between the Flores hominid and known members of *Homo*], including apparent similarities to australopithecines, are almost certainly related to very small body mass," declares David R. Begun of the University of Toronto. That is, as the Flores people dwarfed from *H. erectus*, some of their anatomy simply converged on that of the likewise little australopithecines. Because LB1 shares some key derived features with *H. erectus* and some with other members of *Homo*, "the most straightforward option is to call it a new species of *Homo*," he remarks. "It's a fair and reasonable interpretation," agrees *H. erectus* expert G. Philip Rightmire of Binghamton University. "That was quite a little experiment in Indonesia."

Even more controversial than the position of the half-pint human on the family tree is the notion that it made those advanced-looking tools. Stanford University paleoanthropologist Richard Klein notes that the artifacts found near LB1 appear to include few, if any, of the sophisticated types found elsewhere in the cave. This brings up the possibility that the modern-looking tools were produced by modern humans, who could have occupied the cave at a different time. Further excavations are necessary to determine the stratigraphic relation between the implements and the hominid remains, Klein opines. Such efforts may turn up modern humans like us. The question then, he says, will be whether there were two species at the site or whether modern humans alone occupied Liang Bua—in which case LB1 was simply a modern who experienced a growth anomaly.

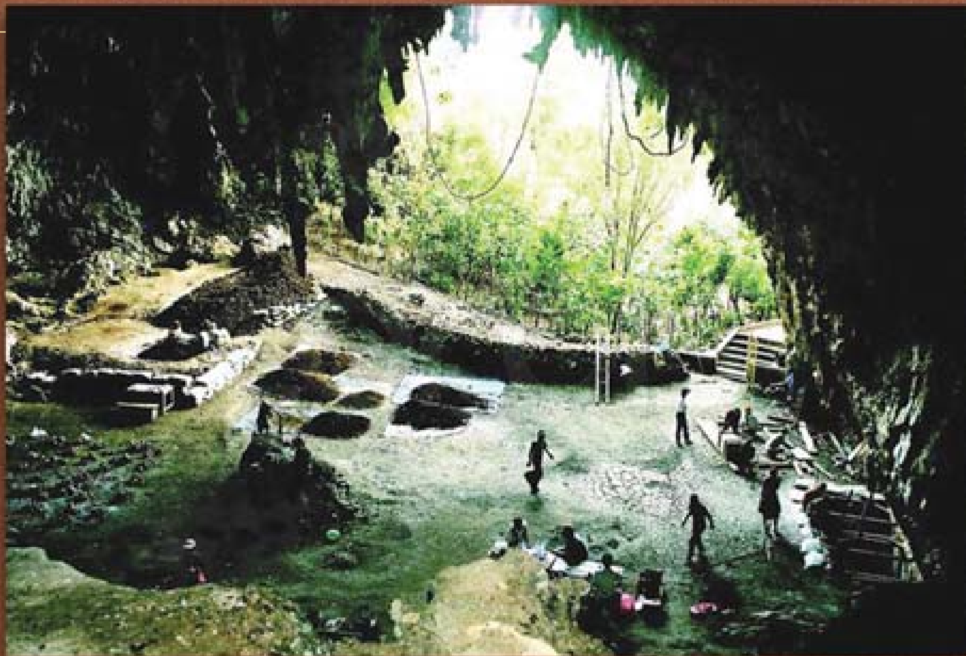
Stratigraphic concerns aside, the tools are too advanced and too large to make manufacture by a primitive, diminutive hominid likely, Groves contends. Although the Liang Bua implements allegedly date back as far as 94,000 years ago, which the team argues makes them too early to be the handi-

HOME OF THE HOBBIT

Scholars were stunned a decade ago to learn that *H. erectus* might have survived on the island of Java in Indonesia until 25,000 years ago, well after the arrival of *H. sapiens* in the region and even after the disappearance of Europe's Neandertals. The recent revelation that a third hominid, dubbed *H. floresiensis*, lived in the area until just 12,000 years ago has proved even more provocative.

Archaeologists recovered the remains from a large limestone cave known as Liang Bua located in western Flores. No one knows exactly how humans first reached the island—they may have made the requisite sea crossings by boat, or they may have drifted over on natural rafts quite by accident.

Geographically, Javan *H. erectus* is a good candidate for the ancestor of *H. floresiensis*. But resemblances to specimens from Africa and the Republic of Georgia raise the question of whether *H. floresiensis* stemmed from a different hominid migration into Southeast Asia from the one that gave rise to Javan *H. erectus*. Future excavations on Flores and other Indonesian islands (*detail*) may cast light on these mysteries.


Liang Bua cave

HANDOUT/REUTERS/CORBIS (*cave*); LAURIE GRACE AND EDWARD BELL (*maps*)

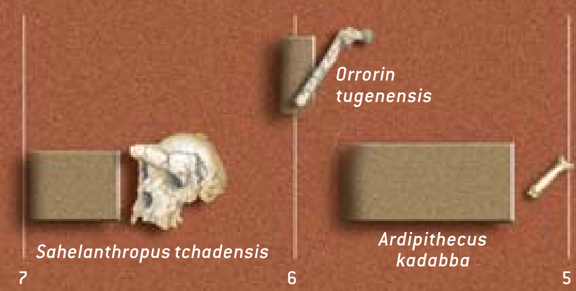
work of *H. sapiens,* Groves points out that 67,000-year-old tools have turned up in Liujiang, China, and older indications of a modern human presence in the Far East might yet emerge. "*H. sapiens,* once it was out of Africa, didn't take long to spread into eastern Asia," he comments.

"At the moment there isn't enough evidence" to establish that *H. floresiensis* created the advanced tools, concurs Bernard Wood of George Washington University. But as a thought experiment, he says, "let's pretend that they did." In that case, "I don't have a clue about brain size and ability," he confesses. If a hominid with no more gray matter than a chimp has can create a material culture like this one, Wood contemplates, "why did it take people such a bloody long time to make tools" in the first place?

"If *Homo floresiensis* was capable of producing sophisticated tools, we have to say that brain size doesn't add up to much," Rightmire concludes. Of course, humans today exhibit considerable variation in gray matter volume, and great

THE TIMES OF THEIR LIVES

Adding a twig to the family tree of humans, Peter Brown of the University of New England in Armidale, Australia, and his colleagues diagnosed the hominid remains from Flores as a new species of Homo, *H. floresiensis*. This brings the number of hominid forms alive at the time of early *H. sapiens* to four if Neandertals are considered a species separate from our own, as shown here. Brown believes that *H. floresiensis* descended from *H. erectus* (*inset*). Others hypothesize that it is an aberrant *H. sapiens* or *H. erectus* or an offshoot of the earlier and more primitive habilines or australopithecines.



PATRICIA J. WYNNE, CORNELIA BLIK AND EDWARD BELL

thinkers exist at both ends of the spectrum. French writer Jacques Anatole François Thibault (also known as Anatole France), who won the 1921 Nobel Prize for Literature, had a cranial capacity of only about 1,000 cubic centimeters; England's General Oliver Cromwell had more than twice that. "What that means is that once you get the brain to a certain size, size no longer matters, it's the organization of the brain," Potts states. At some point, he adds, "the internal wiring of the brain may allow competence even if the brain seems small."

LB1's brain is long gone, so how it was wired will remain a mystery. Clues to its organization reside on the interior of the braincase, however. Paleontologists can sometimes obtain latex molds of the insides of fossil skulls and then create plaster endocasts that reveal the morphology of the organ. Because LB1's bones are too fragile to withstand standard casting procedures, Brown created a virtual endocast based on CT scans of the skull he then used to generate a physical endocast via stereolithography, a rapid-prototyping technology.

A team led by Dean Falk of Florida State University compared LB1's endocast with those of great apes, *H. erectus*, australopithecines (the extinct hominid group to which Lucy belongs), full-sized modern humans, and pygmy and microcephalic modern humans. The results, published in *Science* in March 2005, were said to bolster the hypothesis that LB1 is representative of a new species of hominid, rather than a diseased modern. Falk's group reported that in terms of the size of the brain relative to the body, LB1 is most like an australopithecine. But her brain shape resembles that of *H. erectus*. Falk, who expected that LB1's brain would look like a chimp's, was surprised to find advanced features—including expanded frontal and temporal lobes, which in living humans are associated with higher cognitive processes, such as taking initiative and planning in advance.

The findings support the claim that *H. floresiensis* did indeed engage in the sophisticated cultural practices suggested by the archaeological remains at the site. But critics complain that Falk and her collaborators compared LB1 with only a single microcephalic in their study. Considering how variable that condition is, a larger comparative sample is warranted, in their view.

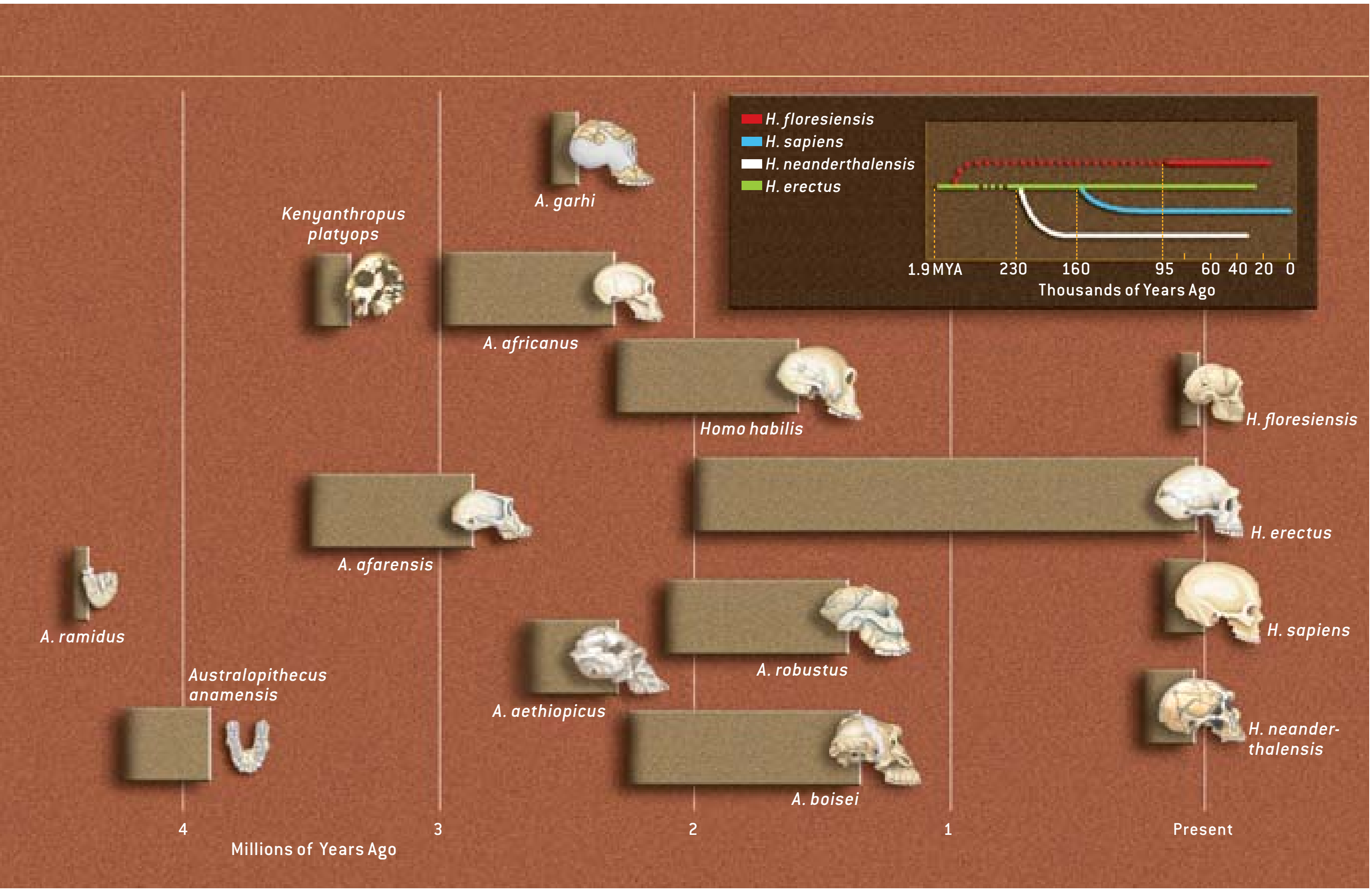
Return to the Lost World

SINCE SUBMITTING their initial papers to *Nature,* the Liang Bua excavators have recovered the remains of another seven or so individuals, all of which they say fit the *H. floresiensis* profile. None are nearly so complete as LB1, whose long arms turned up during the most recent field season. But they did unearth a second lower jaw that is reportedly identical in size and shape to LB1's. Such duplicate bones will be critical to their case that they have a population of these tiny humans (as opposed to a bunch of scattered bones from one person). They will need to find another comparably small skull to dispel concerns that LB1 was a diseased individual, however.

Additional evidence may come from DNA: hair samples possibly from *H. floresiensis* are undergoing analysis at the University of Oxford, and researchers at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, are working to extract DNA from a rib bone. "Tropical environments are not the best for long-term preservation of DNA, so we're not holding our breath," Roberts remarks, "but there's certainly no harm in looking."

The future of the Liang Bua excavation is grim. About a month after the discovery team published its initial report, Teuku Jacob of the Gadjah Mada University in Yogyakarta, Java, who was not involved in the discovery or the analyses, had the delicate specimens transported from their repository at the Indonesian Center for Archaeology to his own laboratory with Soejono's assistance. Jacob, the dean of Indonesian paleoanthropology, thinks LB1 was a microcephalic and allegedly ordered the transfer of it and the new, as yet undescribed finds for examination and safekeeping, despite strong objections from other staff members at the center. When the fossils arrived back in Jakarta—nearly two months later than promised—some of them had suffered extensive damage. The incident sparked a bitter dispute between the two sides. In response, the government mandated that the cave be closed to further excavation for the time being.

Still, efforts to piece together the *H. floresiensis* puzzle will proceed. For his part, Brown is eager to find the tiny hominid's large-bodied forebears. The possibilities are threefold, he notes. Either the ancestor dwarfed on Flores (and was pos-



sibly the maker of the 840,000-year-old Soa Basin tools), or it dwindled on another island and later reached Flores, or the ancestor was small before it even arrived in Southeast Asia. In fact, in many ways, LB1 more closely resembles African *H. erectus* and the Georgian hominids than the geographically closer Javan *H. erectus,* he observes. But whether these similarities indicate that *H. floresiensis* arose from an earlier *H. erectus* foray into Southeast Asia than the one that produced Javan *H. erectus* or are merely coincidental results of the dwarfing process remains to be determined. Future excavations, on Flores and other Indonesian islands, including Sulawesi to the north, may connect the dots.

The hominid bones from Liang Bua now span the period from 95,000 to 12,000 years ago, suggesting to the team that the little Floresians perished along with the pygmy *Stegodon* because of a massive volcanic eruption in the area around 12,000 years ago, although they may have survived later farther east. If *H. erectus* persisted on nearby Java until 25,000 years ago, as some evidence suggests, and *H. sapiens* had arrived in the region by 40,000 years ago, three human species lived cheek by jowl in Southeast Asia for at least 15,000 years. And the discoverers of *H. floresiensis* predict that more will be found. The islands of Lombok and Sumbawa would have been natural stepping-stones for hominids traveling from Java or mainland Asia to Flores. Those that put down roots on these islands may well have set off on their own evolutionary trajectories.

Perhaps, it has been proposed, some of these offshoots of the *Homo* lineage survived until historic times. Maybe they still live in remote pockets of Southeast Asia's dense rain forests, awaiting (or avoiding) discovery. On Flores, oral histories hold that the *ebu gogo* was still in existence when Dutch colonists settled there in the 19th century. And Malay folklore describes another small, humanlike being known as the *orang pendek* that supposedly dwells on Sumatra to this day.

"Every country seems to have myths about these things," Brown reflects. "We've excavated a lot of sites around the world, and we've never found them. But then [in September 2003] we found LB1." Scientists may never know whether tales of the *ebu gogo* and *orang pendek* do in fact recount actual sightings of other hominid species, but the newfound possibility will no doubt spur efforts to find such creatures for generations to come. SA

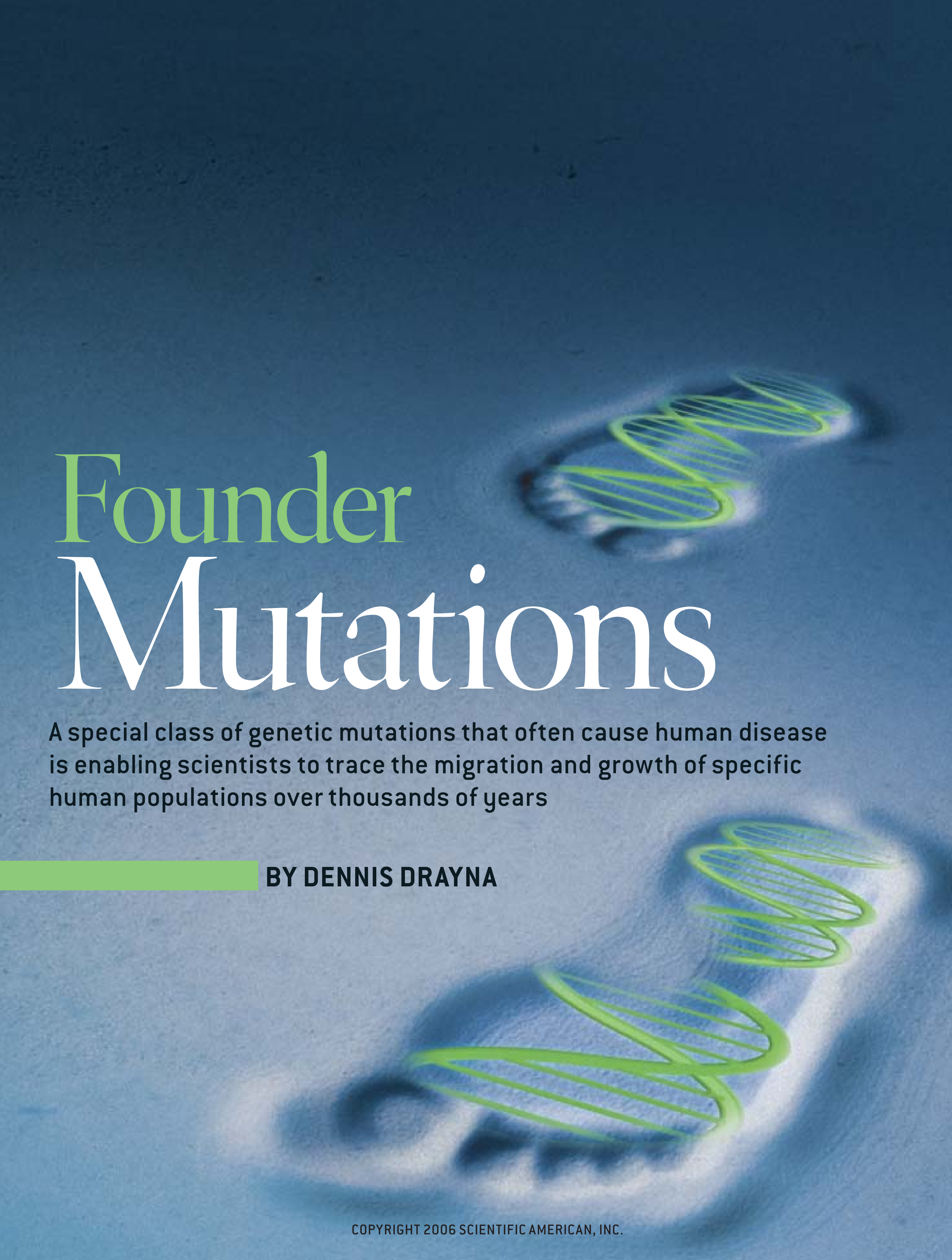
Kate Wong is editorial director of ScientificAmerican.com

MORE TO EXPLORE

Archaeology and Age of a New Hominin from Flores in Eastern Indonesia. M. J. Morwood et al. in *Nature,* Vol. 431, pages 1087–1091; October 28, 2004.

A New Small-Bodied Hominin from the Late Pleistocene of Flores, Indonesia. P. Brown et al. in *Nature,* Vol. 431, pages 1055–1061; October 28, 2004.

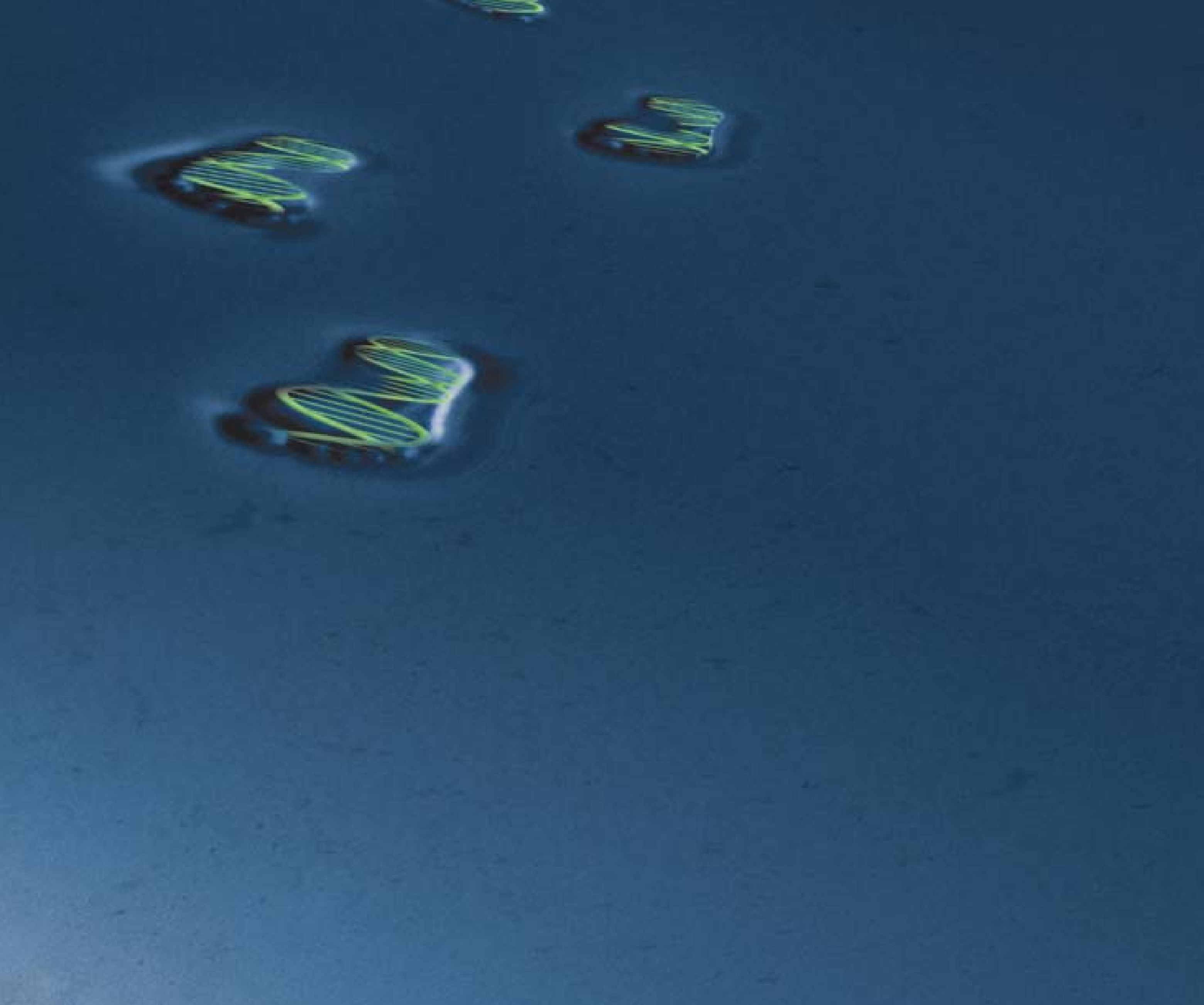
A Q&A with Peter Brown is at **www.sciam.com/**



Founder Mutations

A special class of genetic mutations that often cause human disease is enabling scientists to trace the migration and growth of specific human populations over thousands of years

BY DENNIS DRAYNA



Two middle-aged men who live thousands of miles apart in the U.S. and have never met each other may have a common trait: a propensity to absorb iron so well that this seeming benefit can actually become unhealthy, potentially causing multiple-organ damage and even death. Someone with this condition, called hereditary hemochromatosis, often has it because each of his parents passed on to him the same mutation in a specific gene, an error that originated long ago in a single individual in Europe. The mutation was then carried through time and space in that European's descendants, who now include some 22 million Americans possessing at least one copy of the gene—including the two men, who might be surprised to learn that they are related. The long-gone ancestor is known as the founder of this population, and his or her genetic legacy is called a founder mutation.

Geneticists have discovered thousands of mutations responsible for diseases in humans, but founder mutations stand apart. The victims of many genetic diseases die before reproducing, stopping the mutant genes from reaching future generations. But founder mutations often spare their carriers and therefore can spread from the original founder to his or her descendants. And some of the disorders resulting from these mutations are common, such as the hereditary hemochromatosis caused by the mutation mentioned above, as well as sickle cell anemia and cystic fibrosis. (Why does evolution preserve rather than weed out such seemingly detrimental mutations? Nature's logic will be illustrated presently.)

Medical researchers study disease mutations in the hope of finding simple ways to identify at-risk groups of people, as well as coming up with new ideas for preventing and treating the conditions related to these mutations [*see box on page 63*]. But in a remarkable by-product of such efforts, investigators have discovered that founder mutations can serve as the footprints humanity has left on the trail of time—these mutations provide a powerful way for anthropologists to trace the history of human populations and their migrations around the globe.

The Uniqueness of Founder Mutations

AN APPRECIATION of the unusual status of founder mutations and why they can provide so much information requires a brief examination of mutations in general. Mutations arise by random changes to our DNA. Most of this damage gets repaired or eliminated at birth and thus does not get passed down to subsequent generations. But some mutations, called germ-line mutations, are passed down, often with serious medical consequences to the offspring who inherit them—more than 1,000 different diseases arise from mutations in different human genes.

Founder mutations fit in the germ-line category but are atypical. Inherited diseases ordinarily follow two general rules. First, different mutations in the same gene generally cause the same disease. As a consequence, different families affected by the same disease usually have different mutations responsible for that disease. For example, the bleeding disorder hemophilia is caused by mutations in the gene encoding factor VIII, a component of the blood-clotting system. In general, each new case of hemophilia carries a discrete, single mutation in the factor VIII gene—researchers have spotted mutations at hundreds of locations in the gene.

In a few disorders, however, the same mutation is observed over and over. And there are two ways this identical mutation can arise—as a hot-spot mutation or a founder mutation. A hot spot is a DNA base pair (the individual units of DNA) that is especially prone to mutation. For example, achondroplasia, a common form of dwarfism, usually occurs as a result of a mutation at base pair 1138 in a gene called *FGFR3* on the short arm of human chromosome 4. Individuals who harbor hot-spot mutations are usually not related to one another, and thus the rest of their DNA will vary, as is typical of unrelated people. Founder mutations, which get passed down intact over the generations, are quite distinct from spontaneous hot-spot mutations.

In everyone with a founder mutation, the damaged DNA is embedded in a larger stretch of DNA identical to that of the founder. (Scientists refer to this phenomenon as "identical by descent.") This entire shared region of DNA—a whole cassette of genetic information—is called a haplotype. Share a haplotype, and you share an ancestor, the founder. Furthermore, study of these haplotypes makes it possible to trace the origins of founder mutations and to track human populations.

The age of a founder mutation can be estimated by determining the length of the haplotype—they get shorter over time [*see box on page 62*]. The original founder haplotype is actually the entire chromosome that includes the mutation. The founder passes on that chromosome to offspring, with the founder's mate contributing a clean chromosome. These two chromosomes, one from each parent, randomly exchange sections of DNA, like two sets of cards being crudely cut and mixed.

The mutation will still be embedded in a very long section of the founder's version of DNA after only one recombination, just as a marked card would still be accompanied by many of the same cards that were around it in its original deck after only one rough cut-and-mix. But a marked card will have fewer of its original companions after each new cut-and-mix. And the haplotype that includes the mutated gene will likewise get whittled down with each subsequent recombination.

A young founder mutation—say, only a few hundred years old—should thus be found in the midst of a long haplotype in people who have it today. An ancient founder mutation, perhaps tens of thousands of years old, rests in a short haplotype in current carriers.

Overview/*History in a Sequence*

- Founder mutations are a special class of genetic mutations embedded in stretches of DNA that are identical in all people who have the mutation. Everyone with a founder mutation has a common ancestor—the founder—in whom the mutation first appeared.
- By measuring the length of the stretch of DNA that includes the founder mutation and by determining who currently carries the founder mutation, scientists can calculate the approximate date at which that mutation first appeared and its route of dispersion. Both pieces of data provide information about the migrations of specific groups of people through history.
- As discrete populations mix, disease-causing mutations now associated with specific ethnic groups will be found more randomly. Future medicine will turn to DNA analysis to determine risks of diseases currently associated with ethnicity.

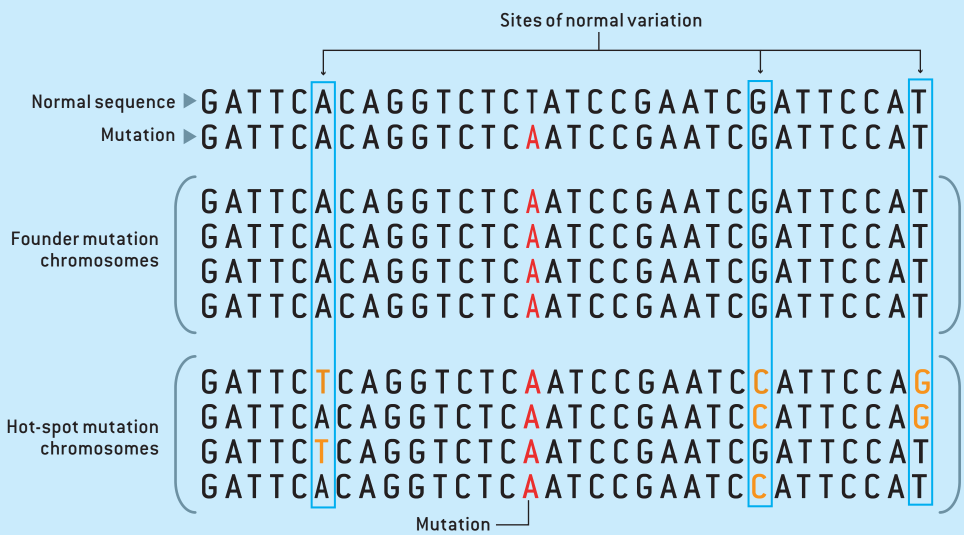
SLIM FILMS (*preceding pages*)

AN OLD ORIGINAL VS. NUMEROUS NEWCOMERS

If a group of patients with the same disease all had the same mutation at a given spot in their DNA, how could physicians know whether they were looking at a hot spot or a founder mutation? They could tell by analyzing the surrounding DNA sequences.

Suppose that in all patients the code at one spot changed from a T to an A (*red, below*). If A were a founder mutation, the surrounding sequences in all patients would be identical—the patients would have inherited the full sequence from the same distant ancestor. But if A were a hot-spot mutation, having occurred spontaneously at a place where DNA is prone to error, the surrounding sequences would also show other differences (*gold*) at sites where DNA codes normally tend to vary without causing disease.

Sickle cell disease, marked by misshapen red blood cells (*top photograph*), is usually caused by a founder mutation. Achondroplasia, a form of human dwarfism (*bottom photograph*), ordinarily results from a hot-spot mutation.



ALISON KENDALL (*illustration*); GOPAL MURTI *Photo Researchers, Inc.* (*top photograph*); WELLCOME PHOTO LIBRARY (*bottom photograph*)

The hemochromatosis gene aberration is just one of a rogue's gallery of founder mutations. A number of others are known and well studied in Europeans, and a few are now recognized in Native American, Asian and African populations [*see box on page 64*]. A striking fact is how common these mutations can be—hundreds or even thousands of times more frequent than typical mutations that cause disease. Most disease mutations exist at a frequency of one in a few thousand to one in a few million. But founder mutations can occur in as much as a few percent of the population.

This anomaly—shouldn't evolution get rid of these harmful genes rather than select for them?—offers an important clue as to why founder mutations persist and spread, over land and sea and across time.

The answer, perhaps not surprisingly, is that under some circumstances founder mutations prove beneficial. Most founder mutations are recessive: only a person with two copies of the affected gene, one from each parent, will suffer from the disease. The much larger percentage of people with only one copy are called carriers. They can pass on the gene to their children and have no symptoms of disease themselves, and the single copy of the founder mutation gives the carrier an advantage in the struggle for survival.

For example, carriers of the hereditary hemochromatosis mutation are thought to be protected from iron-deficiency anemia (a life-threatening condition in the past), because the protein encoded by that mutated gene makes

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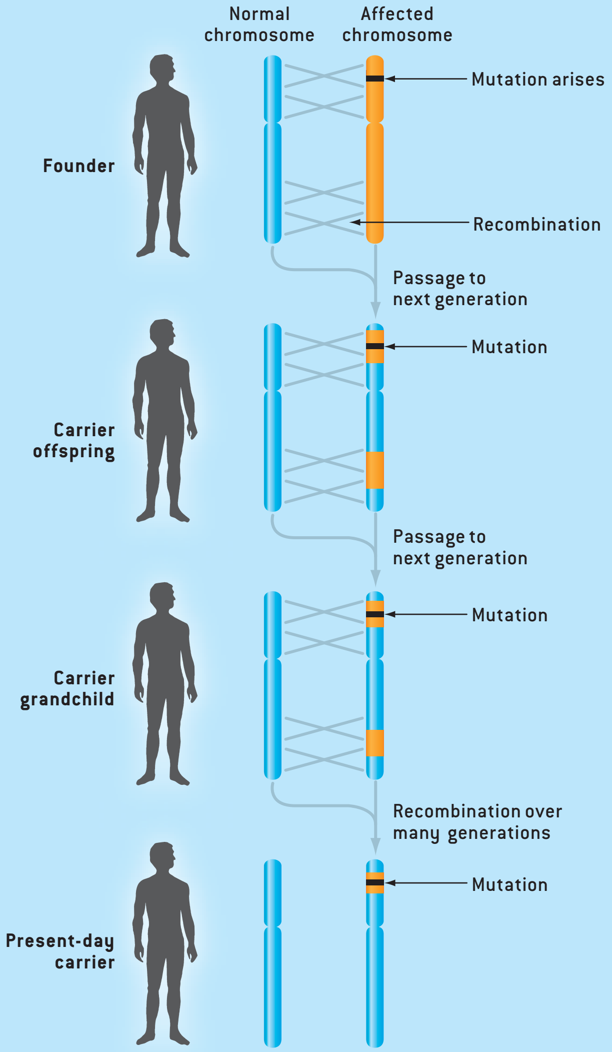
DENNIS DRAYNA received his bachelor's degree from the University of Wisconsin–Madison in 1975 and his Ph.D. from Harvard University in 1981. He did a postdoctoral fellowship at the Howard Hughes Medical Institute at the University of Utah and then spent 14 years in the biotechnology industry in the San Francisco Bay Area, where he identified a number of different human genes involved in cardiovascular and metabolic disorders. In 1996 he joined the National Institutes of Health, where he currently serves as a section chief in the National Institute on Deafness and Other Communication Disorders. His primary research interests are the genetics of human communication disorders, work that has taken him to eight different countries on four continents in pursuit of families with these disorders. In his spare time he enjoys technical rock and ice climbing in equally far-flung places.

GETTING SHORTER WITH AGE

The uniquely identifiable chromosome region—the haplotype—that surrounds a founder mutation gets shorter over generations as chromosomes mix in a process called recombination. In this example, the yellow chromosome in the founder holds the founder mutation, and the blue chromosome comes from a normal parent. When the founder produces sperm or eggs, the two chromosomes exchange sections. Carrier offspring inherit a newly mixed chromosome that includes the mutation and other parts of the founder haplotype (*orange region*). Chromosomal mixing over generations inevitably leads to a shortened haplotype.



ALISON KENDALL

the person absorb iron more effectively than can those who carry two normal copies of the gene. Carriers thus have an edge when dietary iron is scarce.

Perhaps the best-known example of a double-edged genetic mutation is the one responsible for sickle cell disease. The sickle cell mutation apparently arose repeatedly in regions riddled with malaria in Africa and the Middle East. A single copy of a sickle cell gene helps the carrier survive malarial infection. But two copies doom the bearer to pain and a shortened life span. The sickle cell mutation today can be found in five different haplotypes, leading to the conclusion that the mutation appeared independently five times in five different founders. (Although sickle cell disease usually results from a founder mutation, some cases do arise from other mutations.)

The frequency of a founder mutation in the population is governed by two competing forces—someone who has two copies will probably die before reproducing, but those who have only one copy will survive preferentially over those with no copies. This produces so-called balancing selection, in which the beneficial effects drive the frequency of the mutant gene up while the harmful effects damp down the frequency. Evolution giveth and evolution taketh away, so that over time the gene maintains a relatively steady level in the population.

Researchers still have not found the advantage conferred by some disease-related founder mutations, although a gene's continuing presence does point to such a benefit. One example is the persistence of factor V Leiden, a mutation in the factor V gene, which is responsible for another blood-clotting component. This founder mutation, present in 4 percent of Europeans, leads to thrombosis, a condition of pathological blood clots. In 2003 Bryce A. Kerlin and his colleagues at the Blood Center of Southeast Wisconsin and the Medical College of Wisconsin demonstrated that carriers of this mutation are resistant to the lethal effects of bacterial infections in the bloodstream, a huge threat to survival in the preantibiotics past and still a cause of death today.

A Gene Spread Round the World

LONG BEFORE modern transportation, founder mutations migrated great distances, journeys that in many cases took dozens or even hundreds of generations. The sickle cell trait migrated from Africa west to America on slave ships and north to Europe. A common founder mutation in a gene called *GJB2* causes deafness; this mutation has been traced from its ancient origins in the Middle East along two routes, one along the Mediterranean coast to Italy and Spain and the other along the Rhine and Danube River valleys to northern Europe. A founder mutation in a gene called

ABCA4 that causes blindness appears to have arisen in Sweden about 2,700 years ago and spread to the south and west across Europe.

The most extreme example of migration, however, is probably provided by a genetic variability in our sense of taste. About 75 percent of everyone on earth perceives a substance called phenylthiocarbamide (PTC) as very bitter. The remaining 25 percent do not experience PTC as bitter at all. My colleagues and I at the National Institutes of Health and other institutions recently discovered that the combination of three different changes brings about the form of the gene that codes for the nontaster PTC receptor. Virtually all nontasters worldwide are descended from a founder individual who had these specific alterations in this gene. (Our sense of bitter taste exists to protect us from ingesting toxic substances in plants, but what might be the advantage of the nontaster variant of the gene? We suspect that the nontaster form codes for a version of the PTC detector that has switched to sensing some other toxic substance not yet identified.)

The nontaster mutation is embedded in an exceedingly short stretch of ancestral DNA, only 30,000 base pairs in some carriers, which tells us that the founder mutation is extremely ancient—probably more than 100,000 years old. In the past few years, worldwide studies have shown that seven different forms of the PTC gene exist in sub-Saharan Africa. But only the major taster and the major nontaster forms have been found at significant frequency outside of African populations. Of the five remaining forms, one is found only occasionally in non-African populations (and never in New World natives), whereas the other four are exclusively African.

The PTC nontaster mutation provides a remarkable amount of information about early human migration. Its current distribution and frequency confirm anthropological and archaeological evidence that the original population of modern humans lived in Africa and that a small subgroup of those Africans emerged about 75,000 years ago and spread across five other continents—the Out of Africa hypothesis. All existing non-African populations descend from them. But in addition to confirming previous findings, the nontaster form helps to answer one of modern anthropology's most controversial questions: As our *Homo sapiens* ancestors spread across the world, did they interbreed with the more archaic hominids they met in Europe and Asia?

These archaic hominids would almost certainly have had their own forms of the PTC gene, selected for as a response to natural toxins in the local flora. If other hominids produced offspring with *H. sapiens* partners, we would then expect to find different forms of the PTC gene in European, East Asian or Southeast Asian populations. But there is a conspicuous absence of such variation. We therefore believe that

YESTERDAY'S GENES, TOMORROW'S MEDICINE

The ability to identify founder mutations has profound implications for the practice of medicine. Knowledge of such mutations can, for instance, help physicians identify patients who should be tested for certain diseases. Currently physicians may rely on an individual's ethnicity to assign some disease risks and perform further tests. For example, most sickle cell disease occurs in those of African ancestry. But as the world's peoples become more genetically mixed, it will become increasingly difficult to assign an ancestral geographic origin or specific ethnicity to any person. With ethnic background disappearing as a diagnostic clue, physicians will therefore rely on testing individuals' DNA more as they try to identify disease risks or the cause of patients' symptoms. And finding founder mutations now, while human populations remain genetically distinct, will help identify the specific genes responsible for numerous conditions.

In fact, known founder mutations may be viewed as special cases of a much larger group of disease-causing variants in our DNA. Although we do not yet know what many of these are, such variants are most likely to be ancient in origin. As the accompanying article notes, such disease-related variants were probably beneficial to humans in their ancestral homes and therefore became common in the population. But the meeting of our old genes from far-flung places with modern environments and behaviors can lead to illnesses, which have become major disorders.

Genetic evaluation will be important in the broad practice of medicine because these numerous variants probably predispose us to many common disorders, not just to rare inherited diseases. Examples of such genetic variants might be those that help us make cholesterol but now contribute to high cholesterol or those that help conserve salt but now lead to salt-sensitive high blood pressure. The recognition of specific genetic profiles tied to common deleterious conditions will mean that genetics will go from being a subspecialty of medicine, concerned with rare and obscure ailments, to center stage in the prevention, diagnosis and management of human disease. *—D.D.*

OBSERVING ETHNICITY is currently a quick way for physicians to estimate the risk of certain disorders. As humanity's DNA becomes ever more mixed, the DNA itself will inform doctors of an individual's predisposition for those diseases.

LARRY WILLIAMS *Corbis*

the examination of founder mutations in humans alive today shows that no successful interbreeding between *H. sapiens* and other human groups took place during this great out-migration tens of thousands of years ago.

Finding a Founder

A CLOSER LOOK at the haplotype at the root of hereditary hemochromatosis shows how the conjunction of historical records and genetic analysis of current populations can provide new insights into the causes and history of a particular condition. In the 1980s, before the gene for this disease was identified, medical geneticists found that almost everyone with the condition had a virtually identical stretch of DNA on one part of chromosome 6. This finding was stunning because most of these patients were apparently unrelated to one another and would thus have been expected to have random differences at any place in the sequence. Because of this unique stretch of DNA, researchers realized that patients with hereditary hemochromatosis most likely were all descendants of a common, long-lost ancestor and that the gene responsible for the condition probably sat within the shared area.

Operating on this hypothesis, our research group in the 1990s performed a detailed analysis in 101 patients of the genes we could find in the relevant region of chromosome 6. We also looked at the DNA of 64 control subjects who did not have hemochromatosis. Most patients shared a long region of several million base pairs. A few, however, matched in only a smaller fraction of this region. When we compared the part of chromosome 6 that matched in *all* the patients, we found that this region contained 16 genes. Thirteen of the genes coded for proteins known as histones, which bind to and wind up DNA into sausage-shaped structures visible under the microscope during cell divisions. Histones, and the genes for them, are virtually identical throughout living things, so we thought it was unlikely that they were involved in hemochromatosis. That left three genes of interest.

BALANCING SELECTION keeps a potentially deleterious gene circulating. In regions with malaria, which is spread by mosquitoes, having a single copy of a mutation in the hemoglobin gene is protective. Individuals with that mutation have higher survival rates. But those who inherit two copies of the mutation suffer from sickle cell disease and have lower survival rates. The competing forces lead to a stable level of the sickle cell mutation in the population.

Two of the genes were the same in the hemochromatosis patients and the healthy control subjects. But in one of those genes, now designated *HFE*, we discovered a mutation that was present in people who had the disease but conspicuously absent from those who did not have an iron problem. This gene thus had to be the one containing the founder mutation that causes hereditary hemochromatosis.

Our discovery of the hemochromatosis founder mutation immediately led to several questions, including, Who was this founder? When and where did this person live? Chasing the answers to these questions led medical geneticists to join forces with anthropologists and historians. Surveys showed that hereditary hemochromatosis occurs all across Europe but is somewhat more common in northern Europe. In addition, the founder mutation was present in virtually all patients in the north but appeared in less than two thirds of the eastern and southern European patients. That result meant that the other third had some other mutation in the *HFE* gene or perhaps actually had a different iron disorder altogether.

Focusing in on northwestern Europe,

NOTEWORTHY FOUNDER MUTATIONS

Affected gene	Condition	Mutation origin	Migration	Possible advantage of one copy
HFE	Iron overload	Far northwestern Europe	South and east across Europe	Protection from anemia
CFTR	Cystic fibrosis	Southeast Europe/Middle East	West and north across Europe	Protection from diarrhea
HbS	Sickle cell disease	Africa/Middle East	To New World	Protection from malaria
FV Leiden	Blood clots	Western Europe	Worldwide	Protection from sepsis
ALDH2	Alcohol toxicity	Far East Asia	North and west across Asia	Protection from alcoholism, possibly hepatitis B
LCT	Lactose tolerance	Asia	West and north across Eurasia	Allows consumption of milk from domesticated animals
GJB2	Deafness	Middle East	West and north across Europe	Unknown
ABCC11	Dry ear wax	Northeast Asia	Outward, including into Amerindian populations	Decreased perspiration (beneficial in cold, dry climates)

ALISON KENDALL

more detailed genetic surveys revealed that the highest frequency of the founder mutation occurs in Ireland, western Great Britain and across the English Channel in the French province of Brittany. This pattern almost perfectly overlaps the current distribution of a particular group of people: the Celts.

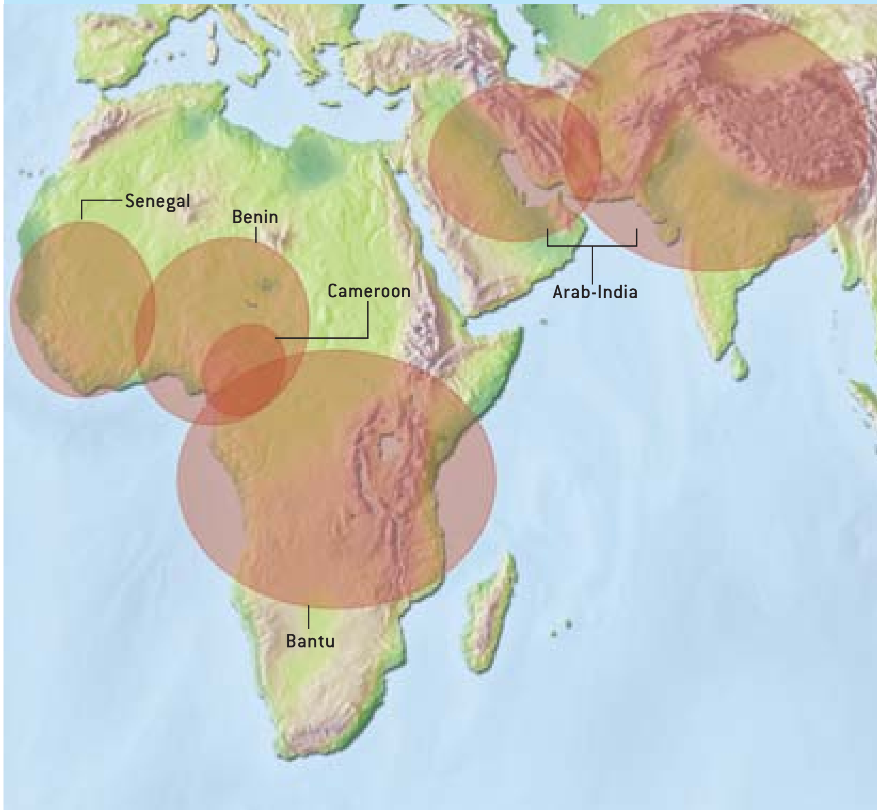
The Celts rose to power in central Europe more than 2,000 years ago. Some were displaced northward and westward by the expanding Roman Empire, whereas others intermixed with southern Europeans and remained in their original location. Did the hemochromatosis founder mutation arise in central Europe and move north with its migrating carriers? Or did it originate in the north? Additional studies of the surrounding DNA on chromosome 6 led to the probable answer.

The extensive length of the modern haplotype indicates that the founder mutation is quite young. Exactly how young has been a subject of much discussion among scientists. The methods for estimating the age of these mutations make a number of assumptions and give us an age range, rather than an exact age. In the case of the hemochromatosis mutation, the majority of the estimates suggest that it arose 60 to 70 generations ago, around A.D. 800 and long after the fall of the Roman Empire. Such a young age suggests that our founder mutation most likely originated in northwestern Europe and spread southward. Other evidence, including the mutation's high frequency in Norway, has led to an alternative hypothesis that it is older, perhaps even predating the Roman Empire. Further use of DNA markers in European populations is likely to settle this question.

Anthropologists, notably Luigi Luca Cavalli-Sforza of Stanford University, have previously studied other types of DNA variants to trace populations. Founder mutations now add a new dimension to DNA studies: calibrating the haplotype length dates the mutation, and calculating the frequency of the haplotype in the population measures the geographic spread of the founder's descendants.

UNCOMMON ORIGINS

People with sickle cell disease all have the same mutation. But that mutation can occur within five distinct haplotypes, indicating that the mutation arose independently five different times in human history, as indicated in areas on the map. Patients can have the Senegal, Benin, Bantu, Arab-India or recently discovered Cameroon haplotype. Eight percent of African-Americans carry at least one copy of the sickle cell mutation.



LUCY READING-IKKANDA

Each of us bears biochemical witness to the fact that all humans are indeed members of a single family, bound together by the shared inheritance of our genome. In addition to confirming the Out of Africa hypothesis, analyses of founder mutations have revealed the common ancestry of various other seemingly unrelated groups—research by David B. Goldstein of Duke University, for instance, has revealed an unexpected genetic connection between the Celts and the Basques. Further investigations of founder mutations and their haplotypes will no doubt reveal more of the genetic relationships that give us new insights into where we came from and how we arrived at our modern locations. Such study also reveals surprising kinships that may inspire a deeper appreciation for the shared roots of humanity's family tree. SA

MORE TO EXPLORE

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The National Human Genome Research Institute's overview of its International Haplotype Map Project can be found at **www.genome.gov/10001688**

How we came to be

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SOME 28,000 YEARS AGO this 60-year-old man was given an elaborate burial, rife with implications of ceremonial practices and of abstract belief. He was interred with rich grave goods and was wearing bracelets, necklaces, pendants, and a tunic on which hundreds of mammoth-ivory beads had been sewn. Along with two juvenile burials from the same site—Sungir in Russia—this is one of the earliest and most resplendent examples of human burials found in Europe.

HUMAN

The acquisition of language and the capacity for symbolic art may lie at the very heart of the extraordinary cognitive abilities that set us apart from the rest of creation

BY IAN TATTERSALL

When we contemplate the extraordinary abilities and accomplishments of *Homo sapiens,* it is certainly hard to avoid a first impression that there must somehow have been an element of inevitability in the process by which we came to be what we are. The product, it's easy to conclude, is so magnificent that it *must* stand as the ultimate expression of a lengthy and gradual process of amelioration and enhancement. How could we have got this way by accident? If we arrived at our exalted state through evolution, then evolution must have worked long and hard at burnishing and improving the breed, must it not? Yet that seems not to be how evolution works; for natural selection is not—it cannot be—in itself a creative process. Natural selection can only work to promote or eliminate novelties that are presented to it by the random genetic changes (influenced, of course, by what was there before) that lie behind all biological innovations. Evolution is best described as opportunistic, simply exploiting or rejecting possibilities as and when they arise, and in turn, the same possibility may be favorable or unfavorable, depending on environmental circumstances (in the broadest definition) at any given moment. There is nothing inherently directional or inevitable about this process, which can smartly reverse itself any time the fickle environment changes.

Indeed, as we'll see a little later, perhaps the most important lesson we can learn from what we know of our own origins involves the significance of what has in recent years increasingly been termed "exaptation." This is a useful name for characteristics that arise in one context before being exploited in another, or for the process by which such novelties are adopted in populations. The classic example of exaptation becoming adaptation is birds' feathers. These structures are essential nowadays to bird flight, but for millions of years before flight came along they were apparently used simply as insulators (and maybe for nothing much at all before that). For a long time, then, feathers were highly useful adaptations for maintaining body temperatures. As adjuncts to flight, on the other hand, they were simply exaptations until, much later, they began to assume an adaptive role in this new function, too. There are many other similar examples, enough that we can't ignore the possibility that maybe our vaunted cognitive capacities originated rather as feathers did: as a very much humbler feature than they became, perhaps only marginally useful, or even as a by-product of something else.

Let's look at this possibility a little more closely by starting at the beginning. When the first Cro-Magnons arrived in Europe some 40,000 years (kyr) ago, they evidently brought

Excerpted from *The Monkey in the Mirror,* by Ian Tattersall, © 2002 by Ian Tattersall, published by Harcourt, Inc.

with them more or less the entire panoply of behaviors that distinguishes modern humans from every other species that has ever existed. Sculpture, engraving, painting, body ornamentation, music, notation, subtle understanding of diverse materials, elaborate burial of the dead, painstaking decoration of utilitarian objects—all these and more were an integral part of the day-to-day experience of early *Homo sapiens,* and all are dramatically documented at European sites more than 30 kyr old.

What these behavioral accomplishments most clearly have in common is that all were evidently underwritten by the acquisition of symbolic cognitive processes. There can be little doubt that it was this generalized acquisition, rather than the invention of any one of the specific behaviors I've just listed—or any other—that lay behind the introduction of "modern" behavior patterns into our lineage's repertoire. This new capacity, what's more, stands in the starkest possible contrast to the more modest achievements of the Neandertals whom the Cro-Magnons so rapidly displaced from their homeland in Europe and western Asia. Indeed, Cro-Magnon behaviors—just like our own—evidently differed totally from those of any other kind of human that had ever previously existed. It is no denigration at all of the Neandertals and of other now extinct human species—whose attainments were entirely admirable in their own ways—to say that with the arrival on Earth of symbol-centered, behaviorally modern *Homo sapiens,* an entirely new order of being had materialized on the scene. And explaining just how this extraordinary new phenomenon came about is at the same time both the most intriguing question and the most baffling one in all of biology.

One complicating factor is that there appears to be no correlation whatever between the achievement in the human lineage of behavioral modernity and anatomical modernity. We have evidence of humans who looked exactly like us in the Levant at close to 100 kyr ago. But at the same time, in dramatic contrast to what happened in Europe, the Levantine Neandertals persisted in the area for some 60 kyr after the anatomical moderns appeared. What's more, throughout this long period of coexistence (whatever form it took, and frankly we have no idea how the different hominids contrived to share the landscape for all those millennia), as far as we can tell from the toolkits they made and the sites they left behind, the two kinds of hominid behaved in more or less identical ways. Suggestively, it was not until right around the time that Cro-Magnon-equivalent stoneworking techniques showed up in the Levant, at about 45 kyr ago, that the Neandertals finally yielded possession of the area. And it was almost certainly the adoption of symbolic cognitive processes that gave our kind the final—and, for the Neandertals, fatal—edge. The conclusion thus seems ineluctable that the emergence of anatomically modern *Homo sapiens* considerably predated the arrival of behaviorally modern humans. But while this might sound rather counterintuitive (for wouldn't it be most plausible to "explain" the arrival of a new kind of behavior by that of a new kind of hominid?), it actually makes considerable sense. For where else can any behavioral innovation become established, except within a preexisting species?

The Brain and Innovation

NOBODY WOULD DISPUTE that to understand cognitive processes in any vertebrate species, we have to look to the brain. In the case of our own family, *Homo neanderthalensis* was endowed with a brain as large as our own, albeit housed in a skull of remarkably different shape. And while we know from the very different archaeological records they left behind that Neandertals and Cro-Magnons behaved in highly distinctive ways, specialists on human brain evolution are hard put to identify any features on the external surface of the brain (as revealed in casts of the interior of the braincase) that would by themselves suggest any major functional difference between Neandertal and modern *sapiens* brains. The same is obviously true for the brains of those early *sapiens* whose material cultures and ways of life resembled those of the Neandertals. Clearly, then, we cannot attribute the advent of modern cognitive capacities simply to the culmination of a slow trend in brain improvement over time. Something happened other than a final physical buffing-up of the cognitive mechanism. Of course, by the time modern-looking humans came on the scene the necessary groundwork must have been laid for the adoption of modern cognitive processes, but this is not necessarily the same as saying that a specific neural mechanism had been acquired for them.

> Our VAUNTED COGNITIVE CAPACITIES may have originated rather as feathers did: as an "exaptation" that arose in one context before being exploited in another.

Let's look again, for a moment, at what our knowledge of the evolutionary process suggests may have occurred. First, it's important to remember that new structures do not arise *for* anything. They simply come about spontaneously, as byproducts of copying errors that routinely occur as genetic information is passed from one generation to the next. Natural selection is most certainly not a generative force that calls new structures into existence; it can only work on variations that are presented to it, whether to eliminate unfavorable variants or to promote successful ones. We like to speak in terms of "adaptations," since this helps us to make up stories about how and why particular innovations have arisen, or

ICE AGE ANIMAL images, such as this aurochs—a form of wild cattle—from the French cave of Lascaux, are frequently accompanied by a wealth of abstract symbols, as we glimpse here in the markings above the neck and back and on the haunches. Lascaux is dated to about 17,000 years ago.

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have been successful, in the course of evolution; but in reality, all new genetic variants must come into being as exaptations. The difference is that while adaptations are features that fulfill specific, identifiable functions (which they cannot do, of course, until they are in place), exaptations are simply features that have arisen and are potentially available to be co-opted into some new function. This is routine stuff, for many new structures stay around for no better reason than that they just don't get in the way.

This is the general context in which we are obliged to view both the evolution of the human brain as we are familiar with it today and the appearance of modern cognitive function. There was unquestionably an increase in average hominid brain size over the past two million years, although this doesn't tell us much about the actual events of human brain evolution. But the example of the Neandertals and, even more tellingly, of the anatomical-but-not-behavioral moderns shows us that the arrival of the modern cognitive capacity did not simply involve adding just a bit more neural material, that last little bit of extra brain size that pushed us over the brink. Still less did it involve adding any major new brain structures, for basic brain design remains remarkably uniform among all the higher primates. Instead an exapted brain, equipped since who knows when with a neglected potential for symbolic thought, was somehow put to use.

Unfortunately, exactly what it was that exapted the brain for modern cognitive purposes remains obscure. This is largely because, while we know a lot about brain structure and about which brain components are active during the performance of particular functions, we have no idea at all about how the brain converts a mass of electrical and chemical signals into what we are individually familiar with as consciousness and thought patterns. And it is this which it will be crucial to understand if we are ever to make the leap to comprehending exactly what it is that enables us to be (and I use the term advisedly) human.

Still, it is possible to talk in general terms about the evolution of modern cognition. It has, for example, been argued that at some time between, say, 60 and 50 kyr ago, a speciation event occurred in the human lineage that gave rise to a new, symbolically expressive entity. By implication, this new species would have possessed neural modifications that permitted modern behavior patterns. It would be nice to believe this, because on one level it would certainly simplify the story. The problem is, though, that the time frame doesn't appear to permit it. For this explanation to work, a new human species, physically identical but intellectually superior to one that already existed, would have had to appear and then to spread throughout the Old World in a remarkably short space of time, totally eliminating its predecessor species in the pro-

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cess. And there is no indication at all, in an admittedly imperfect record, that anything of this kind occurred. Which leaves us with only one evident alternative.

Instead of some anatomical innovation, perhaps we should be seeking some kind of cultural stimulus to our extraordinary cognition. If the modern human brain, with all its potential capacities, had been born along with modern human skull structure at some time around 150 to 100 kyr ago, it could have persisted for a substantial amount of time as exaptation, even as the neural mass continued to perform in the old ways. We have much less evidence than we would like that directly bears on the origin and spread of *Homo sapiens*; however, we do know that our species originated in this general time frame, probably in Africa. And we know as well that it quite rapidly spread Old World–wide from its center of origin, wherever that was.

Further, if at some point, say around 70 to 60 kyr ago, a cultural innovation occurred in one human population or another that activated a potential for symbolic cognitive processes that had resided in the human brain all along, we can readily explain the rapid spread of symbolic behaviors by a simple mechanism of cultural diffusion. It is much more convincing (and certainly more pleasant) to claim that the new form of behavioral expression spread rapidly among populations that already possessed the potential to absorb it than it is to contemplate the alternative: that the worldwide distribution of the unique human capacity came about through a process of wholesale population replacement. What carnage this latter would undoubtedly have involved! On the other hand, cultural interchange among human populations is a phenomenon that is widely documented throughout recorded history, and it must clearly be the preferred explanation for the rapid success of symbolically mediated human behaviors. It remains, though, to suggest what the new cultural stimulus might have been.

Cognition and Symbolism

WHEN WE SPEAK OF "symbolic processes" in the brain or in the mind, we are referring to our ability to abstract elements of our experience and to represent them with discrete mental symbols. Other species certainly possess consciousness in some sense, but as far as we know, they live in the world simply as it presents itself to them. Presumably, for them the environment seems very much like a continuum, rather than a place, like ours, that is divided into the huge number of separate elements to which we humans give individual names. By separating out its elements in this way, human beings are able constantly to re-create the world, and individual aspects of it, in their minds. And what makes this possible is the ability to form and to manipulate mental symbols that correspond to elements we perceive in the world within and beyond ourselves. Members of other species often display high levels of intuitive reasoning, reacting to stimuli from the environment in quite complex ways, but only human beings are able arbitrarily to combine and recombine mental symbols and to ask themselves questions such as "What if?" And it is the ability to do this, above everything else, that forms the foundation of our vaunted creativity.

Of course, intuitive reasoning still remains a fundamental component of our mental processes; what we have done is to add the capacity for symbolic manipulation to this basic ability. An intuitive appreciation of the relationships among objects and ideas is, for example, almost certainly as large a force in basic scientific creativity as is symbolic representation; but in the end it is the unique combination of the two that makes science—or art, or technology—possible. Certainly, intuitive reasoning can take you a long way just by itself, as I think it's justifiable to claim the example of the Neandertals shows. The Neandertals left behind precious few hints of symbolic abilities in the abundant record they bequeathed us of their lives, and it is clear that symbols were not generally an important factor in their existences. Still, their achievements were hardly less remarkable for that, and as far as we can tell, *Homo neanderthalensis* possessed a mastery of the natural world that had been unexceeded in all of earlier human history. Indeed, it seems fair to regard the Neandertals as exponents of the most complex—and in many ways admirable—lifestyle that it has ever proved possible to achieve with intuitive processes alone.

This inevitably brings up the question about the Neandertals that everyone wants answered: Could they talk? Many people, especially looking at the spectacularly beautiful stone tools that the Neandertals made with such skill, find it hard to believe that they couldn't. How, other than through the use of language, could such remarkable skills have been passed down over the generations? Well, not long ago a group of Japanese researchers made a preliminary stab at addressing this problem. They divided a group of undergraduates in two and taught one half how to make a typical Neandertal stone tool by using elaborate verbal explanations along with practical demonstrations. The other half they taught by silent example alone. One thing this experiment dramatically revealed was just how tough it is to make stone tools; some of the undergraduates never became proficient. But more re-

> Humans had a vocal tract that could produce the SOUNDS OF ARTICULATE SPEECH over half a million years before we have evidence our forebears used language.

markable still was that the two groups showed essentially no difference either in the speed at which they acquired tool-making skills or in the efficiency with which they did so. Apparently learning by silent example is just fine for passing along even sophisticated stone tool–making techniques.

Although this experiment involved modern humans, not Neandertals, it does show quite forcefully that, once again, we are making a fundamental mistake by assuming that our way is the only way of doing business in the world. None of this is to suggest, of course, that the Neandertals did not have some form of vocal communication, even quite sophisticated vocal communication. After all, such communication is common among all mammals. And there can be little doubt that Neandertals spoke, in some general sense. What they almost certainly did not possess, however, is language as we are familiar with it.

Language and the Emergence of Human Cognition

IF THERE IS ONE single aspect of human mental function that is more closely tied up with symbolic processes than any other, it is surely our use of language. Language is, indeed, the ultimate symbolic mental function, and it is virtually impossible to conceive of thought as we know it in its absence. For words, it is fair to say, function as the units of human thought, at least as we are aware of it. They are certainly the medium by which we explain our thoughts to one another and, as incomparably social creatures, seek to influence what is going on in one another's brains. Thus, if we are seeking a single cultural releasing factor that opened the way to symbolic cognition, the invention of language is the most obvious candidate. Indeed, it is perhaps the only plausible one that it has so far proved possible to identify. What might have happened? Here we have to return to notions of exaptation, for language is a unique aptitude that doesn't seem to have emerged from apelike "protolanguage" and certainly did not do so directly. Still, it has been argued that since the general ability to acquire language appears to be deeply and universally embedded in the human psyche, this ability must be hardwired into every healthy human brain, where it resides as a result of "normal" Darwinian processes of adaptation by natural selection.

It is certainly true that language is not reinvented in every generation but is rather re-expressed, as every child learns his native tongue(s) as an ordinary, if astonishing, part of the process of growing up. There is, in other words, no denying the existence in the human mind of a "language instinct." What we need to explain, however, is not only how that innate instinct was acquired but also how it made such a rapid and unprecedented appearance.

As we've seen, natural selection is not a creative force and can propel nothing into existence by itself. Rather it can only capitalize on what is already there. In a sense, this makes things easier for us since, as far as we can tell, in the emergence of symbolic thought there is no evidence of the kind of slow trend that would be expected under Darwinian selection.

CARVED FROM MAMMOTH IVORY more than 32,000 years ago, this tiny (less than five centimeters) sculpture is perhaps the earliest work of art known. Its elegant lines express the essence of the horse rather than rendering exactly the stocky proportions of horses of this period. The sculpture was found at Vogelherd, Germany.

ALEXANDER MARSHACK, © 2006 PRESIDENT AND FELLOWS OF HARVARD COLLEGE, PEABODY MUSEUM

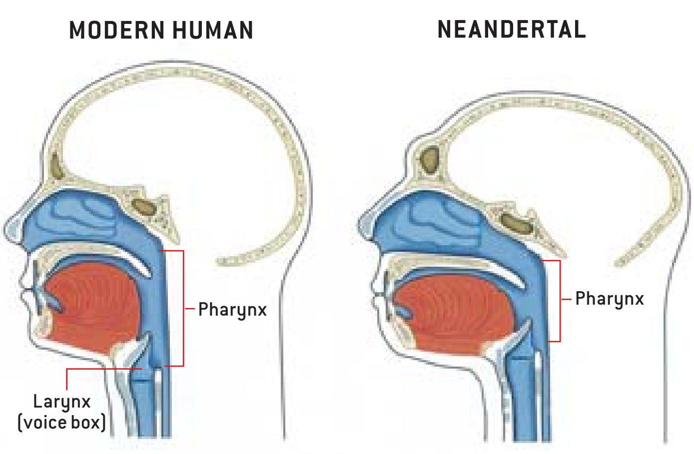
What must have happened, instead, is that after a long—and poorly understood—period of erratic brain expansion and reorganization in the human lineage, something occurred that set the stage for language acquisition. This innovation would have depended on the phenomenon of emergence, whereby a chance combination of preexisting elements results in something totally unexpected. The classic example of an emergent quality is water, most of whose remarkable characteristics are entirely unpredicted by those of its constituents, hydrogen and oxygen. Nonetheless, the combination of these ingredients gives rise to something entirely new, and expected only in hindsight. Together with exaptation, emergence provides a powerful mechanism in the evolutionary process, and it truly is a driving force, propelling innovation in new directions.

In the case of linguistic potential, with its innate presence among all humans today, we have to suppose that initially a neural change occurred in some population of the human lineage. This change was presumably rather minor in genetic terms and probably had nothing whatever to do with adaptation in the classical sense. Since during early childhood development the brain rewires itself through the creation of specific pathways from undifferentiated masses of neuronal connections, it is even possible that this event was an epigenetic rather than a genetic one, dependent on developmental stimuli. Whatever the case, it certainly seems to have made no mark on the fossil record, although ultimately its impact on the archaeological traces of the Cro-Magnons and their successors was enormous. Just as the keystone of an arch is a trivial part of the structure, yet is essential to the integrity of the whole, this innovation (whatever it may have been, and we are very far from understanding that) was the final physical element that needed to be in place to make possible language and symbolic thought—and all that has flowed from them, with such fateful consequences for the world. Once it was there, of course, the potential it embodied could lie fallow, simply doing no harm, until released by a cultural stimulus in one particular population. Almost certainly, though it's hard to prove, this stimulus was the invention of language. Everyone today has language, which by itself suggests that it was a highly advantageous acquisition. And if it is as advantageous as we would wish to believe, it is hardly surprising that language and its associated symbolic behavioral patterns were subsequently able to spread rapidly among human populations worldwide.

Among the numerous possibilities for how LANGUAGE MAY HAVE BEEN INVENTED is that an initial form was created not by adults but BY CHILDREN.

So much for the spread of language from its center of origin. Exactly how this fateful novelty may have been invented is a separate question, upon which it is beyond my expertise to speculate. But with the substrate for language in place, the possibilities are numerous. My favorite among them is that an initial form of language may have been invented not by adults but by children. Given the fact that the brain is not a static structure like a rubber ball but is rather a dynamic entity that reorganizes itself during development (and indeed, given the right stimuli, throughout life), it is not implausible that a rudimentary precursor of language as it is familiar today initially arose in a group of children, in the context of play. Such prelanguage might have involved words—sounds—strung together with additive meaning. It is hard to imagine that once this invention had been made, society as a whole would not have eventually adopted it. On a Japanese island, macaque monkeys living along the beach were fed by researchers with sweet potatoes. These delicacies became covered with beach grit, and pretty soon, young macaques started washing them in the sea to remove the sand. It took a while for the adults to catch on: first the females, and only last the dominant males. Doubtless, some of the older and most dominant males never deigned to indulge in this behavior, preferring a familiar life of grit. But a good idea is a good idea—and it is difficult to believe that, in the case of language, once the notion of associating words with objects and ideas had developed, it would not have spread quite rapidly throughout society.

Still, the transition from a nonlinguistic lifestyle to a linguistic one as we are familiar with it involved a huge cognitive and practical leap. It seems probable that the addition of syntax may have been a separate, and later, event, though perhaps

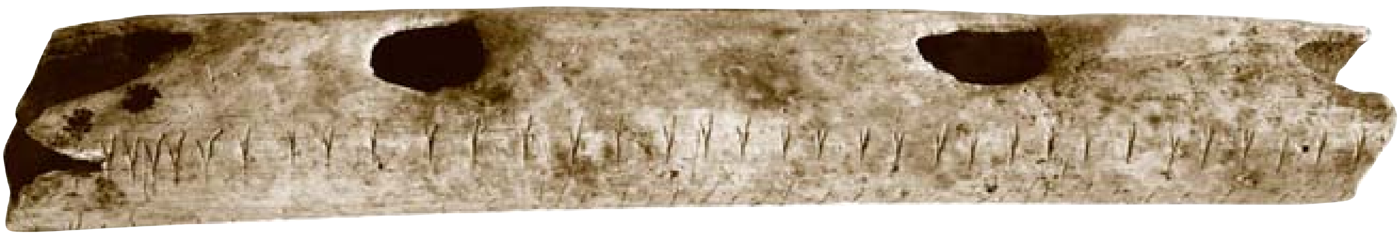


COMPARISON of the head and neck of a modern human and a (reconstructed) Neandertal shows the differences in the structure of the vocal tract. The much longer pharynx in the modern human is what makes possible the full range of sounds demanded by articulate speech.

ILLUSTRATION BY DIANA SALLES, AFTER SKETCHES BY JEFFREY LAITMAN; © IAN TATTERSALL one made inevitable by the arrival of word-object associations. A single-stage progression from inarticulacy to articulate language as we know it seems more than a little implausible, and a multiple-stage process would certainly better mirror the way in which infants acquire language, with the vocabulary beginning to develop (very rapidly) first, and syntax and (later) sentence structuring following after the age of about two years. The history of the emergence of language is undoubtedly complex—indeed, this emergence only seems even possible from our perspective because we *know* it must have occurred. Subsequent to its origin, of course, language quite obviously changed, complexified and diversified hugely, as it became ever more widely adopted among human populations. But its common structure everywhere today, independent of culture, is surely due to the fact that the underlying basis was already there in everyone, long before language itself came along.

But there still remains one other factor to be explained. To speak, you need a brain that will tell your vocal tract what to do, but you also need a vocal tract that will respond appropriately to the brain's instructions. And the primitive primate vocal tract cannot respond in this way. In fact, adult human beings are the only creatures, apes included (though some birds can mimic speech), that can physically make the sounds that are essential to articulate speech. And this ability comes at a price. The principal structures that make up the vocal tract are the larynx, the structure in the neck that houses the vocal cords; the pharynx, a tube that rises above it and opens into the oral and nasal cavities; and the tongue and its associated apparatus. Basic sounds are generated at the vocal cords, and then there is further modulation of those sounds in the pharynx and allied airways above. Among typical mammals, including the apes—and newborn humans—the larynx is positioned high in the neck, and the pharynx is consequently short, limiting what can be done to modulate vocal sounds. In adult humans, in contrast, the larynx lies low in the neck, lengthening the pharynx and increasing the potential for sound modulation. The price I've mentioned is that while the human arrangement makes a vast array of sounds possible, it also prevents simultaneous breathing and swallowing—thereby introducing the unpleasant possibility of choking to death.

This alone suggests that there must be some powerful countervailing advantage in the human conformation of the vocal tract, but the ability to speak, unfortunately, is not it. We know this because the roof of the vocal tract is also the base of the skull. Thus, where this region is preserved in fossils, we can reconstruct in general terms what the vocal tract had looked like in life. The low larynx–high pharynx combination betrays itself in a flexion of the bones of the skull base. We begin to see some evidence of such flexion in *Homo ergaster,* almost 2 myr ago, and a skull of *Homo heidelbergensis* from Ethiopia shows that it had reached virtually its modern degree by about 600 kyr ago. A vocal tract capable of producing the sounds of articulate speech had thus been achieved among humans well over half a million years before we have any independent evidence that our forebears were using language or speaking.



MUSICAL INSTRUMENTS, such as this bone flute from a French site, date back at least 32,000 years. They are some of the most striking indicators of a new sensibility in early humans.

Clearly, then, the adult human vocal tract cannot in origin have been an adaptation "for" modern speech—though it might have conferred some advantage in the context of a "prelinguistic" form of vocal communication. So what, then, *is* it "for"? Inevitably we have to come back to exaptation. Despite its disadvantages, basicranial flexion appeared, and it then persisted for a very long time before being capitalized upon for its linguistic qualities. Maybe over that long period it did indeed bestow certain advantages in the production of more archaic forms of speech—forms that we are hardly in a position to characterize. Or maybe it conferred some kind of benefit in terms of respiration, which is an issue that is still very poorly understood among extinct hominids. Still, whatever the case, we have to conclude that the appearance of language and its anatomical correlates was not driven by natural selection, however beneficial these innovations may appear in hindsight to have been.

At present, then, there is no way we can come up with any even modestly convincing scenario of what happened in the origination of the extraordinary creature we are, without invoking the humble process of exaptation. Clearly, we are not the result of a constant and careful fine-tuning process over the millennia, and much of our history has been a matter of chance and hazard. Nature never "intended" us to occupy the position of dominance in the living world that, for whatever reasons, we find ourselves in. To a remarkable extent, we are accidental tourists as we cruise through Nature in our bizarre ways. But, of course, we are nonetheless remarkable for that. And still less are we free of responsibility. SA

PERSONAL ADORNMENT with jewelry and body paint may have started far earlier than previously thought. Early indications of such symbol use—believed by many archaeologists to be a key component of modern human behavior—include 75,000-year-old shell beads (*left*) from Blombos Cave in South Africa.

The Morning of the Modern Mind

Controversial discoveries suggest that the roots of our vaunted intellect run far deeper than is commonly believed

BY KATE WONG

CAPE TOWN, SOUTH AFRICA—Christopher Henshilwood empties a tiny plastic bag and hands me a square of worn blue cardstock to which 19 snail shells no larger than kernels of corn have been affixed in three horizontal rows. To the casual onlooker, they might well appear unremarkable, a handful of discarded mollusk armor, dull and gray with age. In fact, they may be more precious than the glittering contents of any velvet-lined Cartier case.

The shells, discovered in a cave called Blombos located 200 miles east of here, are perfectly matched in size, and each bears a hole in the same spot opposite the mouth, notes Henshilwood, an archaeologist at the University of Bergen in Norway. He believes they were collected and perforated by humans nearly 75,000 years ago to create a strand of lustrous, pearllike beads. If he is correct, these modest shells are humanity's crown jewels—the oldest unequivocal evidence of personal adornment to date and proof that our ancestors were thinking like us far earlier than is widely accepted.

Snail shells were collected from an estuary 12 miles away from Blombos Cave and then pierced with a bone awl. Wear marks around the holes indicate that they were strung together to create perhaps a necklace or bracelet.

A Behavioral Big Bang

BY MOST ACCOUNTS, the origin of anatomically modern *Homo sapiens* was a singularly African affair. In 2003 the unveiling of fossils found in Herto, Ethiopia, revealed that this emergence had occurred by 160,000 years ago. And in February 2005 researchers announced that they had redated *H. sapiens* remains from another Ethiopian site, Omo Kibish, potentially pushing the origin of our species back to 195,000 years ago.

Far less clear is when our kind became modern of mind. For the past two decades, the prevailing view has been that humanity underwent a behavioral revolution around 40,000 years ago. Scholars based this assessment primarily on the well-known cultural remains of Ice Age Europeans. In Europe, the relevant archaeological record is divided into the Middle Paleolithic (prior to around 40,000 years ago) and the Upper Paleolithic (from roughly 40,000 years ago onward), and the difference between the two could not be more striking. Middle Paleolithic people seem to have made mostly the same relatively simple stone tools humans had been producing for tens of thousands of years and not much else. The Upper Paleolithic, in contrast, ushered in a suite of sophisticated practices. Within a geologic blink of an eye, humans from the Rhône Valley to the Russian plain were producing advanced weaponry, forming long-distance trade networks, expressing themselves through art and music, and generally engaging in all manner of activities that archaeologists typically associate with modernity. It was, by all appearances, the ultimate Great Leap Forward.

Perhaps not coincidentally, it is during this Middle to Upper Paleolithic transition that humans of modern appearance had begun staking their claim on Europe, which until this point was strictly Neandertal territory. Although the identity of the makers of the earliest Upper Paleolithic artifacts is not known with certainty, because of a lack of human remains at the sites, they are traditionally assumed to have been anatomically modern *H. sapiens* rather than Neandertals. Some researchers have thus surmised that confrontation between the two populations awakened in the invaders a creative ability that had heretofore lain dormant.

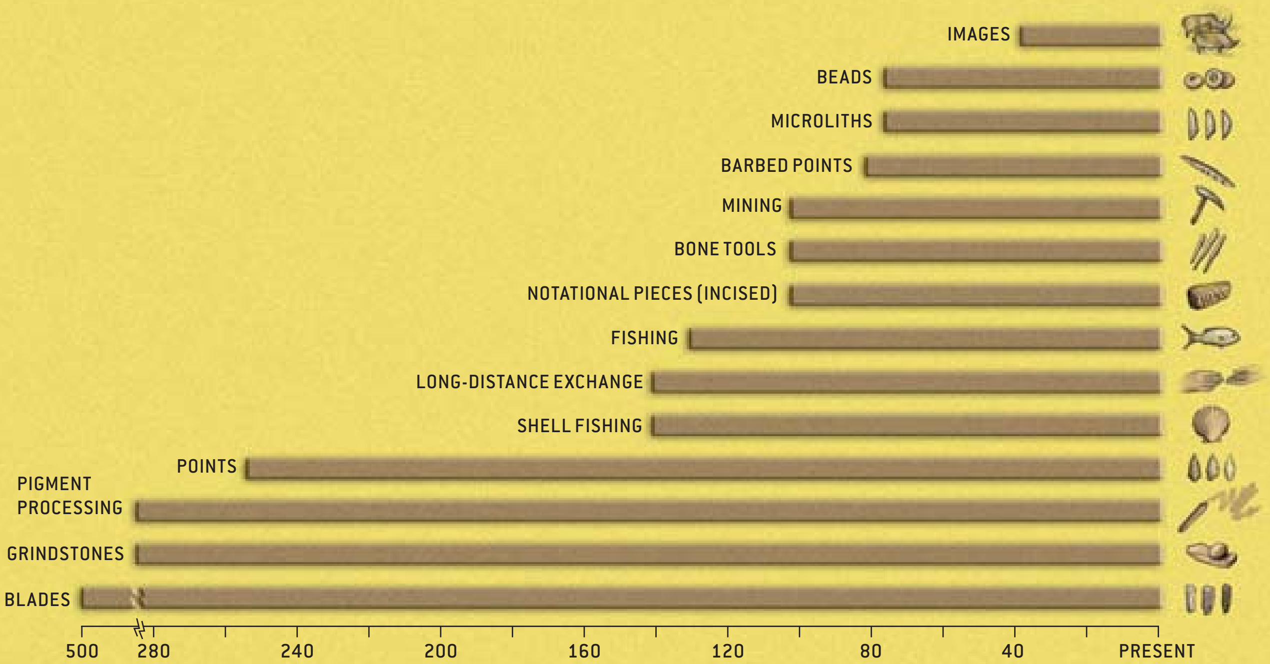
Other specialists argue that the cultural explosion evident in Europe grew out of a shift that occurred somewhat earlier in Africa. Richard G. Klein of Stanford University, for one, contends that the abrupt change from the Middle to the Upper Paleolithic mirrors a transition that took place 5,000 to 10,000 years beforehand in Africa, where the comparative culture periods are termed the Middle and Later Stone Age. The impetus for this change, he theorizes, was not an encounter with another hominid type (for by this time in Africa, *H. sapiens* was free of competition with other human species) but rather a genetic mutation some 50,000 years ago that altered neural processes and thereby unleashed our forebears' powers of innovation.

Overview/*Evolved Thinking*

- Archaeologists have traditionally envisioned *Homo sapiens* becoming modern of mind quickly and recently—sometime in the past 50,000 years, more than 100,000 years after attaining anatomical modernity.
- New discoveries in Africa indicate that many of the elements of modern human behavior can be traced much farther back in time.
- The finds suggest that our species had a keen intellect at its inception and exploited that creativity in archaeologically visible ways only when it was advantageous to do so—when population size increased, for instance.
- *H. sapiens* may not have been the only hominid to possess such advanced cognition: some artifacts hint that Neandertals were comparably gifted.

RANDY HARRIS (*preceding page*); FRANCESCO D'ERRICO *University of Bordeaux*; AFRICAN HERITAGE RESEARCH INSTITUTE AND UNIVERSITY OF BERGEN (*snail shell beads, page 74 and this page*)

STONE AGE SOPHISTICATION



Archaeological discoveries in Africa have revealed that elements of modern human behavior can be traced back far beyond the 40,000-year mark (*above*), contrary to earlier claims based on the European record. But experts agree that many more people routinely engaged in these practices after that date than before it. A number of hypotheses for what set the stage for this tipping point—not all of which are mutually exclusive—have been put forth (*below*).

Symbolism. The invention of external storage of information—whether in jewelry, art, language or tools—was the watershed event in modern human behavioral evolution, according to Christopher Henshilwood of the University of Bergen in Norway. *Homo sapiens* probably had the hardware required for symbolic thought by the time the species arose, at least 195,000 years ago, hence the occasional early glimpses of it in the archaeological record. But only once symbolism became the basis for human behavioral organization—resulting in the formation of trade and alliance networks, for example—was its full potential realized.

Ecological disaster. Genetic data suggest that *H. sapiens* experienced a bottleneck some 70,000 years ago. Stanley H. Ambrose of the University of Illinois posits that it was the fallout from an eruption of Sumatra's Mount Toba at around that time that may have brought on a devastating six-year-long volcanic winter and subsequent 1,000-year ice age. Those individuals who cooperated and shared resources with one another—beyond their local group boundaries—were the best equipped to survive in the harsh environs and pass their genes along to the next generation. The extreme conditions favored a transition from the troop level of social organization to that of the tribe.

Projectile technology. The innovation of projectile weapons between 45,000 and 35,000 years ago allowed humans to kill large game—and other humans—from a safe distance. This, says John Shea of Stony Brook University, provided people with a strong incentive to cooperate, which would in turn have fostered the development of social networks through which information could be readily shared.

Population growth. Modern ways bubbled up and disappeared at different times and in different places until the population size reached critical mass. At that point, confrontation between groups and competition for resources sparked symbolic behavior and spurred technological innovation, contend researchers, including Alison Brooks of George Washington University and Sally McBrearty of the University of Connecticut. And with more people to pass on these traditions, they began to stick, rather than dying out with the last member of a group.

Brain mutation. A genetic mutation roughly 50,000 years ago had the lucky effect of rewiring the human brain such that it was capable of symbolic thought—including language—argues Richard G. Klein of Stanford University. Humans carrying this mutation had a considerable advantage over those who did not and quickly outcompeted and replaced them.

ALISON KENDALL; SOURCE: UPDATED FROM S. MCBREARTY AND A. S. BROOKS IN *JOURNAL OF HUMAN EVOLUTION*, VOL. 39, NO. 5, PAGES 453–563; NOVEMBER 2000

Mapping Modernity

Humans who looked like us had evolved by 195,000 years ago, as evidenced by *Homo sapiens* fossils from the site of Omo Kibish in Ethiopia. But received archaeological wisdom holds that humans did not begin behaving like us until nearly 150,000 years later. That notion stems largely from cultural remains uncovered in Europe, where art, ritual, technological advances and other indications of modern thinking flowered spectacularly and suddenly after about 40,000 years ago, around the time that anatomically modern humans started colonizing Europe.

Recent finds, including those from Blombos Cave in South Africa, are revealing that many sophisticated practices emerged long before 40,000 years ago at sites outside of Europe, suggesting that humans were our cognitive equals by the time they attained anatomical modernity, if not earlier. Indeed, the fact that at least some Neandertals appear to have thought symbolically raises the possibility that such capacities were present in the last common ancestor of Neandertals and *H. sapiens*. The map below shows the locations of the sites mentioned in the article.

Neandertal-made pierced tooth from Arcy-sur-Cure in France: 33,000 years old

Oldest evidence of painting in Africa from Apollo 11 Rock Shelter in Namibia: 28,000 years old

Ivory water bird, among the earliest pieces of figurative art known, from Hohle Fels Cave in Germany: 30,000–35,000 years old

Scraped, heat-treated red ochre, possibly used in ritual burial act, from Qafzeh Cave in Israel: 92,000 years old

Bone harpoon from Katanda in the Democratic Republic of the Congo: 80,000 years old

Ostrich eggshell bead from Loiyangalani in Tanzania: perhaps 70,000 years old

LUCY READING-IKKANDA (*map*); RANDALL WHITE *New York University* (*pierced tooth*); GERALD NEWLANDS (*Apollo 11 painting*); HILDE JENSEN *University of Tübingen* (*ivory water bird*); GAVRIEL LARON AND ERELLA HOVERS *Institute of Archaeology, Hebrew University of Jerusalem* (*red ochre*); CHIP CLARK *National Museum of Natural History* (*bone harpoon*); ARIZONA STATE UNIVERSITY (*ostrich eggshell bead*)

Key evidence for this model, Klein says, comes from a site in central Kenya called Enkapune Ya Muto, the "twilight cave," that places the origin of the Later Stone Age at 45,000 to 50,000 years ago. There Stanley H. Ambrose of the University of Illinois and his team have uncovered obsidian knives, thumbnail-size scrapers and—most notably—tiny disk-shaped beads fashioned from ostrich eggshell in Later Stone Age levels dating back some 43,000 years. Strands of similar beads are still exchanged as gifts today among the !Kung San hunter-gatherers of Botswana. Ambrose posits that the ancient bead makers at Enkapune Ya Muto created them for the same reason: to foster good relationships with other groups as a hedge against hard times. If so, according to Klein, a genetically conferred ability to communicate through symbols—in concert with the cognitive prowess to conceive of better hunting technology and resource use—may have been what enabled our species finally, nearly 150,000 years after it originated, to set forth from its mother continent and conquer the world.

Seeds of Change

IN RECENT YEARS, however, a small but growing number of archaeologists have eschewed the big bang theories of the origin of culture in favor of a fundamentally different model. Proponents believe that there was no lag between body and brain. Rather, they contend, modern human behavior emerged over a long period in a process more aptly described as evolution than revolution. And some workers believe that cognitive modernity may have evolved in other species, such as the Neandertals, as well.

The notion that our species' peerless creativity might have primeval roots is not new. For years, scientists have known of a handful of objects that, taken at face value, suggest that humans were engaging in modern practices long before *H. sapiens* first painted a cave wall in France. They include three 400,000-year-old wooden throwing spears from Schöningen in Germany; a 233,000-year-old putative figurine from the site of Berekhat Ram in Israel; a 60,000-year-old piece of flint incised with concentric arcs from Quneitra in Israel; two 100,000-year-old fragments of notched bone from South Africa's Klasies River Mouth Cave; and a polished plate of mammoth tooth from Tata in Hungary, dated to between 50,000 and 100,000 years ago. Many archaeologists looked askance at these remains, however, noting that their age was uncertain or that their significance was unclear. Any sign of advanced intellect that did seem legitimately ancient was explained away as a one-off accomplishment, the work of a genius among average Joes.

That position has become harder to defend in the face of the growing body of evidence in Africa that our forebears' mental metamorphosis began well before the start of the Later Stone Age. In a paper entitled "The Revolution That Wasn't: A New Interpretation of the Origin of Modern Human Behavior," published in the *Journal of Human Evolution* in 2000, Sally McBrearty of the University of Connecticut and Alison

S. Brooks of George Washington University laid out their case. Many of the components of modern human behavior said to emerge in lockstep between 40,000 and 50,000 years ago, they argued, are visible tens of thousands of years earlier at Middle Stone Age locales. Moreover, they appear not as a package but piecemeal, at sites far-flung in time and space.

At three sites in Katanda in the Democratic Republic of the Congo, Brooks and John Yellen of the Smithsonian Institution have found elaborate barbed harpoons carved from bone that they say date to at least 80,000 years ago, which would place them firmly within the Middle Stone Age. These artifacts exhibit a level of sophistication comparable to that seen in 25,000-year-old harpoons from Europe, not only in terms of the complexity of the weapon design but the choice of raw material: the use of bone and ivory in tool manufacture was not thought to have occurred until the Later Stone Age and Upper Paleolithic. In addition, remains of giant Nile catfish have turned up with some of the Katanda harpoons, suggesting to the excavators that people were going there when the fish were spawning—the kind of seasonal mapping of resources previously thought to characterize only later humans.

Other Middle Stone Age sites, such as ≠Gi (the "≠" denotes a click sound) in Botswana's Kalahari Desert, which is dated to 77,000 years ago, have yielded butchered animal remains that have put paid to another oft-made claim, namely, that these ancient people were not as competent at hunting as Later Stone Age folks. The residents at ≠Gi appear to have regularly pursued such large and dangerous prey as zebra and Cape warthog. And Hilary J. Deacon of Stellenbosch University has suggested that at sites such as South Africa's Klasies River Mouth Cave humans more than 60,000 years ago were deliberately burning grassland to encourage the growth of nutritious tubers, which are known to germinate after exposure to fire.

Some discoveries hint that certain alleged aspects of behavioral modernity arose even before the genesis of *H. sapiens*. Excavations in mid-2004 by McBrearty's team at a site near Lake Baringo in Kenya turned up stone blades—once a hallmark of the Upper Paleolithic material cultures—more than 510,000 years old. At a nearby locality, in levels dated to at least 285,000 years ago, her team has uncovered vast quantities of red ochre (a form of iron ore) and grindstones for processing it, signaling to McBrearty that the Middle Stone Age people at Baringo were using the pigment for symbolic purposes—to decorate their bodies, for instance—just as many humans do today. (Baringo is not the only site to furnish startlingly ancient evidence of ochre processing—Twin Rivers Cave in Zambia has yielded similar material dating back to more than 200,000 years ago.) And 130,000-year-old tool assemblages from Mumba Rock Shelter in Tanzania include flakes crafted from obsidian that came from a volcanic flow about 200 miles away—compelling evidence that the hominids who made the implements traded with other groups for the exotic raw material.

Critics, however, have dismissed these finds on the basis of uncertainties surrounding, in some cases, the dating and, in others, the intent of the makers. Ochre, for one, may have been used as mastic for attaching blades to wooden handles or as an antimicrobial agent for treating animal hides, skeptics note.

Blombos ochre, engraved with a stone point, may reflect record keeping or a design aesthetic. The effort required to prepare the substrate and produce the markings suggests a premeditated act, rather than doodling.

CHAD HENNING; AFRICAN HERITAGE RESEARCH INSTITUTE AND UNIVERSITY OF BERGEN

Smart for Their Age

IT IS AGAINST this backdrop of longstanding controversy that the discoveries at Blombos Cave have come to light. Henshilwood discovered the archaeological deposits at Blombos in 1991 while looking for much younger coastal hunter-gatherer sites to excavate for his Ph.D. Located near the town of Still Bay in South Africa's southern Cape, on a bluff overlooking the Indian Ocean, the cave contained few of the Holocene artifacts he was looking for but appeared rich in Middle Stone Age material. As such, it was beyond the scope of his research at the time. In 1997, however, he raised the money to return to Blombos to begin excavating in earnest. Since then, Henshilwood and his team have unearthed an astonishing assemblage of sophisticated tools and symbolic objects and in so doing have sketched a portrait of a long-ago people who thought like us.

From levels dated by several methods to 75,000 years ago have come an array of advanced implements, including 40 bone tools, several of which are finely worked awls, and hundreds of bifacial points made of silcrete and other difficult-to-shape stones, which the Blombos people could have used to hunt the antelopes and other game that roamed the area. Some of the points are just an inch long, suggesting that they may have been employed as projectiles. And the bones of various species of deep-sea fish—the oldest of which may be more than 130,000 years old—reveal that the Blombos people had the equipment required to harvest creatures in excess of 80 pounds from the ocean.

Hearths for cooking indicate that the cave was a living site, and teeth representing both adults and children reveal that a family group dwelled there. But there are so many of the stone points, and such a range in their quality, that Henshilwood wonders whether the occupants may have also had a workshop in the tiny cave, wherein masters taught youngsters how to make the tools.

They may have passed along other traditions as well. The most spectacular material to emerge from Blombos is that which demonstrates that its occupants thought symbolically. By 2005 the team had recovered one piece of incised bone, nine slabs of potentially engraved red ochre and dozens of the tiny beads—all from the same 75,000-year-old layers that yielded the tools. In addition, sediments that may date back to more than 130,000 years ago contain vast quantities of processed ochre, some in crayon form.

Scientists may never know exactly what meaning the enigmatic etchings held for their makers. But it is clear that they were important to them. Painstaking analyses of two of the engraved ochres, led by Francesco d'Errico of the University of Bordeaux in France, have revealed that the rust-colored rocks were hand-ground on one side to produce a facet that was then etched repeatedly with a stone point. On the largest ochre, bold lines frame and divide the cross-hatched design.

Bead manufacture was likewise labor-intensive. Henshilwood believes the marine tick shells, which belong to the *Nassarius kraussianus* snail, were collected from either of two estuaries, located 12 miles from the cave, that still exist today. Writing in the January 2005 issue of the *Journal of Human Evolution,* Henshilwood, d'Errico and their colleagues report that experimental reconstruction of the process by which the shells were perforated indicates that the precocious jewelers used bone points to punch through the lip of the shell from the inside out—a technique that commonly broke the shells when attempted by team members. Once pierced, the beads appear to have been strung, as evidenced by the wear facets ringing the perforations, and traces of red ochre on the shells hint that they may have lain against skin painted with the pigment.

In the case for cognitive sophistication in the Middle Stone Age, "Blombos is the smoking gun," McBrearty declares. But Henshilwood has not convinced everyone of his interpretation. Doubts have come from Randall White of New York University, an expert on Upper Paleolithic body ornaments. He suspects that the perforations and apparent wear facets on the *Nassarius* shells are the result of natural processes, not human handiwork.

Here Today, Gone Tomorrow

IF READ CORRECTLY, however, the remarkable discoveries at Blombos offer weighty evidence that at least one group of humans possessed a modern mind-set long before 50,000 years ago, which may in some ways make previous claims for early behavioral modernity easier to swallow. So, too, may recent finds from sites such as Diepkloof in South Africa's Western Cape, which has produced pieces of incised ostrich eggshell dated to around 60,000 years ago, and Loiyangalani in Tanzania, where workers have found ostrich eggshell beads estimated to be on the order of 70,000 years old.

BLOMBOS CAVE was a veritable garden of Eden when humans lived there 75,000 years ago, observes discoverer Christopher Henshilwood. Freshwater springs burbled at the base of the cliff, and the bounty of the sea lay in the backyard. Tasty eland and other antelope roamed the area, and the climate was about as mild as it is today. Henshilwood and his team have been digging in the cave's Middle Stone Age deposits since 1997, carefully recording the location of each artifact unearthed.

CHRISTOPHER S. HENSHILWOOD *African Heritage Research Institute and University of Bergen*

Yet it remains the case that most Middle Stone Age sites show few or none of the traits researchers use to identify fully developed cognition in the archaeological record. Several other locales in South Africa, for example, have yielded the sophisticated bifacial points but no evidence of symbolic behavior. Of course, absence of evidence is not evidence of absence, as prehistorians are fond of saying. It is possible the people who lived at these sites did make art and decorate their bodies, but only their stone implements have survived.

Perhaps the pattern evident thus far in the African record—that of ephemeral glimpses of cognitive modernity before the start of the Later Stone Age and ubiquitous indications of it after that—is just an artifact of preservational bias or the relatively small number of African sites excavated so far. Then again, maybe these fits and starts are exactly what archaeologists should expect to see if anatomically modern *H. sapiens* possessed the capacity for modern human behavior from the get-go but tapped that potential only when it provided an advantage, as many gradualists believe.

The circumstances most likely to elicit advanced cultural behaviors, McBrearty and others hypothesize, were those related to increased population size. The presence of more people put more pressure on resources, forcing our ancestors to devise cleverer ways to obtain food and materials for toolmaking, she submits. More people also raised the chances of encounters among groups. Beads, body paint and even stylized tool manufacture may have functioned as indicators of an individual's membership and status in a clan, which would have been especially important when laying claim to resources in short supply. Symbolic objects may have also served as a social lubricant during stressful times, as has been argued for the beads from Enkapune Ya Muto.

"You have to make good with groups around you because that's how you're going to get partners," Henshilwood observes. "If a gift exchange system is going on, that's how you're maintaining good relations." Indeed, gift giving may explain why some of the tools at Blombos are so aesthetically refined. A beautiful tool is not going to be a better weapon, he remarks, it is going to function as a symbolic artifact, a keeper of the peace.

Conversely, when the population dwindled, these advanced practices subsided—perhaps because the people who engaged in them died out or because in the absence of competition they simply did not pay off and were therefore forgotten. The Tasmanians provide a recent example of this relationship: when Europeans arrived in the region in the 17th century, they encountered a people whose material culture was simpler than even those of the Middle Paleolithic, consisting of little more than basic stone flake tools. Indeed, from an archaeological standpoint, these remains would have failed nearly all tests of modernity that are commonly applied to prehistoric sites. Yet the record shows that several thousand years ago, the Tasmanians possessed a much more complex tool kit, one that included bone tools, fishing nets, and bows and arrows. It seems that early Tasmanians had all the latest gadgetry before rising sea levels cut the island off from the mainland 10,000 years ago but lost the technology over the course of their small group's separation from the much larger Aboriginal Australian population.

This might be why South African sites between 60,000 and 30,000 years old so rarely seem to bear the modern signature: demographic reconstructions suggest that the human population in Africa crashed around 60,000 years ago because of a precipitous drop in temperature. Inferring capacity from what people produced is inherently problematic, White observes. Medieval folks doubtless had the brainpower to go to the moon, he notes. Just because they did not does not mean they were not our cognitive equals. "At any given moment," White reflects, "people don't fulfill their entire potential."

Tools from Blombos are more sophisticated than those typically found at Middle Stone Age sites. The bone implements include awls worked to a fine point and polished with ochre to achieve a smooth patina.

HARRY TYLER; AFRICAN HERITAGE RESEARCH INSTITUTE AND UNIVERSITY OF BERGEN

Symbol-Minded

THE DEBATE OVER when, where and how our ancestors became cognitively modern is complicated by the fact that experts disagree over what constitutes modern human behavior in the first place. In the strictest sense, the term encompasses every facet of culture evident today—from agriculture to the iPod. To winnow the definition into something more useful to archaeologists, many workers employ the list of behavioral traits that distinguish the Middle and Upper Paleolithic in Europe. Others use the material cultures of modern and recent hunter-gatherers as a guide. Ultimately, whether or not a set of remains is deemed evidence of modernity can hinge on the preferred definition of the evaluator.

Taking that into consideration, some experts instead advocate focusing on the origin and evolution of arguably the most important characteristic of modern human societies: symbolically organized behavior, including language. "The ability to store symbols externally, outside of the human brain, is the key to everything we do today," Henshilwood asserts. A symbol-based system of communication might not be a perfect proxy for behavioral modernity in the archaeological record, as the Tasmanian example illustrates, but at least researchers seem to accept it as a defining aspect of the human mind as we know it, if not *the* defining aspect.

It remains to be seen just how far back in time symbolic culture arose. And discoveries outside of Africa and Europe are helping to flesh out the story. Controversial evidence from the rock shelters of Malakunanja II and Nauwalabila I in Australia's Northern Territory, for instance, suggests that people had arrived there by 60,000 years ago. To reach the island continent, emigrants traveling from southeastern Asia would have had to have built sturdy watercraft and navigated a minimum of 50 miles of open water, depending on the sea level. Scholars mostly agree that any human capable of managing this feat must have been fully modern. And in Israel's Qafzeh Cave, Erella Hovers of the Hebrew University of Jeru-

SYMBOLIC BEHAVIOR may not have originated in Europe, but its early record there is rich. Chauvet Cave, in the Ardèche region of France, contains the oldest cave paintings in the world. Its galleries showcase a menagerie of Ice Age creatures, including lions (*top left*), rendered in ochre 35,000 years ago. Ancient Europeans also had a love of music, as evidenced by this 32,000-year-old bone flute from Isturitz in France (*bottom left*). And they buried their dead with sometimes breathtaking ceremony, as seen above in this replica of a 28,000-year-old burial of two children and thousands of beads and other grave goods from Sungir in Russia.

JEAN CLOTTES; FRENCH MINISTRY OF CULTURE (*Chauvet Cave*); RÉUNION DES MUSÉES NATIONAUX/ART RESOURCE, NY (*bone flute*); KENNETH GARRETT *National Geographic Image Collection* (*Sungir burial*)

salem and her team have recovered dozens of pieces of red ochre near 92,000-year-old graves of *H. sapiens*. They believe the lumps of pigment were heated in hearths to achieve a specific hue of scarlet and then used in funerary rituals.

Other finds raise the question of whether symbolism is unique to anatomically modern humans. Neandertal sites commonly contain evidence of systematic ochre processing, and toward the end of their reign in Europe, in the early Upper Paleolithic, Neandertals apparently developed their own cultural tradition of manufacturing body ornaments, as evidenced by the discovery of pierced teeth and other objects at sites such as Quinçay and the Grotte du Renne at Arcy-sur-Cure in France. They also interred their dead. The symbolic nature of this behavior in their case is debated because the burials lack grave goods. But in April 2005, at the annual meeting of the Paleoanthropology Society, Jill Cook of the British Museum reported that digital microscopy of remains from Krapina Rock Shelter in Croatia bolsters the hypothesis that Neandertals were cleaning the bones of the deceased, possibly in a kind of mortuary ritual, as opposed to defleshing them for food.

Perhaps the ability to think symbolically evolved independently in Neandertals and anatomically modern *H. sapiens*. Or maybe it arose before the two groups set off on separate evolutionary trajectories, in a primeval common ancestor. "I can't prove it, but I bet [*Homo*] *heidelbergensis* [a hominid that lived as much as 400,000 years ago] was capable of this," White speculates.

For his part, Henshilwood is betting that the dawn of symbol-driven thinking lies in the Middle Stone Age. After nine field seasons at Blombos, he and his team had sifted through a third of the cave's 75,000-year-old deposits, leaving the rest to future archaeologists with as yet unforeseen advances in excavation and dating techniques. "We don't really need to go further in these levels at Blombos," Henshilwood says. "We need to find other sites now that date to this time period." He is confident that they will succeed in that endeavor, having already identified a number of very promising locales in the coastal De Hoop Nature Reserve, about 30 miles west of Blombos.

Sitting in the courtyard of the African Heritage Research Institute pondering the dainty snail shells in my hand, I consider what they might have represented to the Blombos people. In some ways, it is difficult to imagine our ancient ancestors setting aside basic concerns of food, water, predators and shelter to make such baubles. But later, perusing a Cape Town jeweler's offerings—from cross pendants cast in gold to diamond engagement rings—it is harder still to conceive of *Homo sapiens* behaving any other way. The trinkets may have changed somewhat since 75,000 years ago, but the all-important messages they encode are probably still the same. SA

Kate Wong is editorial director of ScientificAmerican.com

MORE TO EXPLORE

The Revolution That Wasn't: A New Interpretation of the Origin of Modern Human Behavior. Sally McBrearty and Alison S. Brooks in *Journal of Human Evolution,* Vol. 39, No. 5, pages 453–563; November 2000.

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***Nassarius kraussianus* Shell Beads from Blombos Cave: Evidence for Symbolic Behavior in the Middle Stone Age.** Francesco d'Errico, Christopher Henshilwood, Marian Vanhaeren and Karen van Niekerk in *Journal of Human Evolution,* Vol. 48, No. 1, pages 3–24; January 2005.

The Emergence of Intelligence

BY WILLIAM H. CALVIN

CHIMPANZEES have a remarkable aptitude for simple language and tool-usage skills, such as poking sticks into termite mounds to fish for snacks. Yet compared with those of humans, the abilities of these animals are fairly rudimentary. Human intelligence may have evolved through the enhancement of neural machinery that assists with the planning of quick hand and mouth movements.

JAMES BALOG *The Image Bank/Getty Images*

Language, foresight and other hallmarks of intelligence are very likely connected through an underlying facility that plans rapid, novel movements

To most observers, the essence of intelligence is cleverness, a versatility in solving novel problems. Bertrand Russell once wryly noted: "Animals studied by Americans rush about frantically, with an incredible display of hustle and pep, and at last achieve the desired result by chance. Animals observed by Germans sit still and think, and at last evolve the solution out of their inner consciousness." Besides commenting on the scientific fashions of 1927, Russell's remark illustrates the false dichotomy usually made between random trial and error (which intuitively seems unrelated to intelligent behavior) and insight. It takes an interplay between both.

Foresight is also said to be an essential aspect of intelligence—particularly after an encounter with one of those terminally clever people who are all tactics and no strategy. Psychologist Jean Piaget emphasized that intelligence was the sophisticated groping that we use when not knowing what to do. Personally, I like the way neurobiologist Horace Barlow of the University of Cambridge frames the issue. He says intelligence is all about making a guess that discovers some new underlying order. This idea neatly covers a lot of ground: finding the solution to a problem or the logic of an argument, happening on an appropriate analogy, creating a pleasing harmony or a witty reply, or guessing what is likely to happen next. Indeed, we all routinely predict what comes next, even when passively listening to a narrative or a melody. That is why a joke's punch line or a musical parody brings you up short—you were subconsciously predicting something else and are surprised by the mismatch.

Both intelligence and consciousness concern the high end of our mental life, but they are frequently confused with more elementary mental processes, such as ones we would use to recognize a friend or tie a shoelace. Of course, such simple neural mechanisms are probably the foundations from which our abilities to handle logic and metaphor evolved.

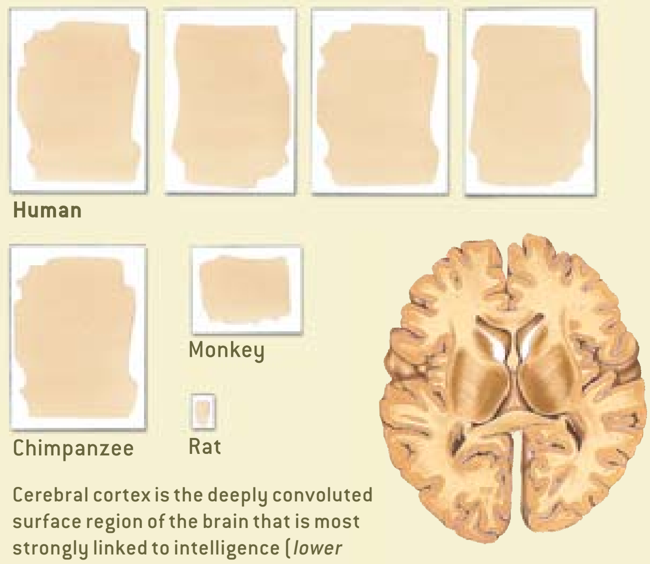
But how did that occur? That's an evolutionary question and a neurophysiological one as well. Both kinds of answers are needed if we are to understand our own intelligence. They might even help us appreciate how an artificial or an exotic intelligence could evolve.

Did our intelligence arise from having more of what other animals have? The two-millimeter-thick cerebral cortex is the part of the brain most involved with making novel associations. Ours is extensively wrinkled, but were it flattened, it would occupy four sheets of typing paper. A chimpanzee's cortex would fit on one sheet, a monkey's on a postcard, a rat's on a stamp.

Yet a purely quantitative explanation seems incomplete. I will argue that our intelligence arose primarily through the refinement of some brain specialization, such as that for language. The specialization would allow a quantum leap in cleverness and foresight during the evolution of humans from apes—perhaps the creative explosion seen about 50,000 years ago, when people who had looked like us since 200,000 years ago finally began acting like us. If, as I suspect, that specialization involves a core facility common to language, the planning of hand movements, music and dance, it has even greater explanatory power.

A particularly intelligent person often seems "quick" and capable of juggling many ideas at once. Indeed, the two strongest influences on your IQ score are how many novel questions you can answer in a fixed length of time and how good you

SMARTER ON PAPER



Cerebral cortex is the deeply convoluted surface region of the brain that is most strongly linked to intelligence (*lower right*). A human's cerebral cortex, if flattened, would cover four pages of typing paper; a chimpanzee's would cover only one; a monkey's would cover a postcard; and a rat's would cover a postage stamp.

are at manipulating half a dozen mental images—as in those analogy questions: A is to B as C is to (D, E or F).

Mental Matching

VERSATILITY is another characteristic of intelligence. Most animals are narrow specialists, especially in matters of diet: the mountain gorilla consumes 50 pounds of green leaves each and every day. In comparison, a chimpanzee switches around a lot—it will eat fruit, termites, leaves, and even a small monkey or piglet if it is lucky enough to catch one. Omnivores have more basic moves in their general behavior because their ancestors had to switch between many different food sources. They need more sensory templates, too—mental images of things such as foods and predators for which they are "on the lookout." Their behavior emerges through the matching of these sensory templates to responsive movements.

Sometimes animals try out a novel combination of search image and movement during play and find a use for it later. Many animals are playful only as juveniles; being an adult is a serious business (they have all those young mouths to feed). Having a long juvenile period, as apes and humans do, surely aids intelligence. A long life further promotes versatility by affording more opportunities to discover new behaviors.

A social life also gives individuals the chance to mimic the useful discoveries of others. Researchers have seen a troop of monkeys in Japan copy one inventive female's techniques for washing sand off food. Moreover, a social life is full of interpersonal problems to solve, such as those created by pecking orders, that go well beyond the usual environmental challenges to survival and reproduction.

Yet versatility is not always a virtue, and more of it is not always better. As frequent airline travelers know, passengers who have only carry-on bags can get all the available taxicabs while those burdened by three suitcases await their luggage. On the other hand, if the weather is so unpredictable that everyone has to travel with clothing ranging from swimsuits to Arctic parkas, the "jack of all trades" has an advantage over the "master" of one. And so it is with behavioral versatility and brain size.

When chimpanzees in Uganda arrive at a grove of fruit trees, they often discover that the efficient local monkeys are already speedily stripping the trees of edible fruit. The chimps can turn to termite fishing or perhaps catch a monkey and eat it, but in practice their population is severely limited by that competition, despite a brain twice the size of their specialist rivals'.

Whether versatility is advantageous depends on the timescales: for both the modern traveler and the evolving ape, it is how fast the weather changes and how long the trip lasts. Paleoclimatologists have discovered that many parts of the earth suffer sudden climate changes, as abrupt in onset as a decade-long drought but lasting for centuries. A climatic flip that eliminated fruit trees would be disastrous for many monkey species. It would hurt the more omnivorous animals, too, but they could make do with other foods, and eventually they would enjoy a population boom when the food crunch ended and few of their competitors remained.

Coping with Climate Change

ALTHOUGH AFRICA was cooling and drying as upright posture was becoming established four million to six million years ago, brain size did not change much. The fourfold expansion of the hominid brain did not start until the ice ages began, 2.5 million years ago. Ice cores from Greenland show frequent abrupt cooling episodes superimposed on the more stately rhythms of ice advance and retreat. Entire forests disappeared within several decades because of drastic drops in temperature and rainfall. The warm rains returned even more abruptly a few centuries later.

The evolution of anatomic adaptations in the hominids could not have kept pace with these abrupt climate changes, which would have occurred within the lifetime of single individuals. Still, these environmental fluctuations could have promoted the incremental accumulation of mental abilities that conferred greater behavioral flexibility.

THE AUTHOR

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DANA BURNS-PIZER (*left*); JUDITH GLICK (*right*)

One of the additions during the ice ages was the capacity for human language. In most of us, the brain area critical to language is located just above our left ear. Monkeys lack this left lateral language area: their vocalizations (and simple emotional utterances in humans) employ a more primitive language area near the corpus callosum, the band of fibers connecting the cerebral hemispheres.

Language is the most defining feature of human intelligence: without syntax—the orderly arrangement of verbal ideas—we would be little more clever than a chimpanzee. For a glimpse of life without syntax, we can look to the case of Joseph, an 11-year-old deaf boy. Because he could not hear spoken language and had never been exposed to fluent sign language, Joseph did not have the chance to learn syntax during the critical years of early childhood.

As neurologist Oliver Sacks described him in *Seeing Voices:* "Joseph saw, distinguished, categorized, used; he had no problems with *perceptual* categorization or generalization, but he could not, it seemed, go much beyond this, hold abstract ideas in mind, reflect, play, plan. He seemed completely literal—unable to juggle images or hypotheses or possibilities, unable to enter an imaginative or figurative realm.... He seemed, like an animal, or an infant, to be stuck in the present, to be confined to literal and immediate perception, though made aware of this by a consciousness that no infant could have."

To understand why humans are so intelligent, we need to understand how our ancestors remodeled the apes' symbolic repertoire and enhanced it by inventing syntax. Wild chimpanzees use about three dozen different vocalizations to convey about three dozen different meanings. They may repeat a sound to intensify its meaning, but they do not string together three sounds to add a new word to their vocabulary.

Speakers of English also use about three dozen vocalizations, called phonemes. Yet only their combinations have content: we string together meaningless sounds to make meaningful words. No one has yet explained how our ancestors got over the hump of replacing "one sound/one meaning" with a sequential combinatorial system of meaningless phonemes, but it is probably one of the most important advances that took place during ape-to-human evolution.

Furthermore, human language uses strings of strings, such as the word phrases that make up this sentence. The simplest ways of generating short sentences, as in pidgins and the utterances of a two-year-old, are known as protolanguage. In a protolanguage, the association of the words carries the message. Syntax is not needed if the sentences are short.

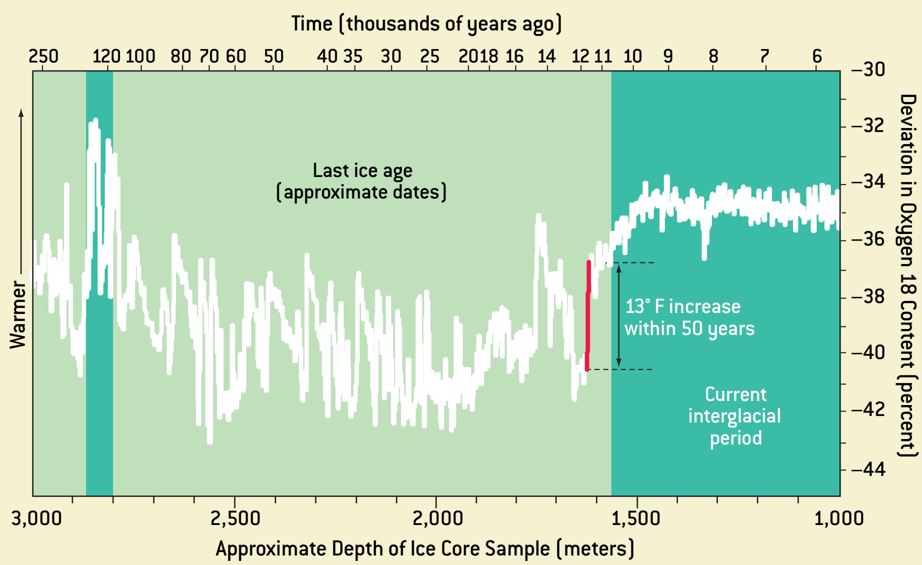
Our closest animal cousins, the common chimpanzee and the bonobo (pygmy chimpanzee), can achieve surprising levels of language comprehension when motivated by skilled teachers. Kanzi, the most accomplished bonobo, can interpret sentences he has never heard before, such as "Go to the office and bring back the red ball," about as well as a 2.5-year-old child. Neither Kanzi nor the child constructs such sentences independently, but each can demonstrate understanding.

With a year's experience in comprehension, the child starts constructing fancier sentences. The rhyme about the house that Jack built ("This is the farmer sowing the corn / That kept the cock that crowed in the morn /... That lay in the house that Jack built") is an extreme case of nesting word phrases inside one another, yet even preschoolers understand how "that" changes its meaning.

Syntax has treelike rules of reference that enable us to communicate quickly—sometimes with fewer than 100 sounds strung together—who did what to whom, where, when, why and how. Generating and speaking a long, unique sentence demonstrate whether you know the rules of syntax

CLIMATE UPS AND DOWNS

Rapid climate changes may have promoted behavioral flexibility in the ancestors of modern humans. During the last ice age, the average temperature was much lower than it is today, but it was also subject to large, abrupt fluctuations that sometimes lasted for centuries. During one climatic oscillation, for example (*red line*), the temperature rose 13 degrees Fahrenheit, rainfall increased by 50 percent, and the severity of dust storms fell, all in the space of a few decades. Cold periods began just as suddenly. Early humans may have needed considerable intellectual resources to survive these changes. This graph is based on work by W. Dansgaard of the University of Copenhagen and his colleagues using Greenland ice cores.



LUCY READING-IKKANDA

well enough to avoid ambiguities. Even children of low intelligence acquire syntax effortlessly by listening, although intelligent deaf children like Joseph may miss out.

Something close to verbal syntax also seems to contribute to another outstanding feature of human intelligence, the ability to plan. Aside from hormonally triggered preparations for winter and mating, animals exhibit surprisingly little evidence of planning more than a few minutes ahead. Some chimpanzees use long twigs to pull termites from their nests, yet as author Jacob Bronowski observed, none of the termite-fishing chimps "spends the evening going round and tearing off a nice tidy supply of a dozen probes for tomorrow."

Thinking Ahead

SHORT-TERM PLANNING does occur to an extent, and it seems to allow a crucial increment in social intelligence. Deception is seen in apes but seldom in monkeys. A chimp may give a call signaling that she has found food at one location, then quietly circle back through the dense forest to where she actually found the food. While the other chimps beat the bushes at the site of the food cry, she eats without sharing.

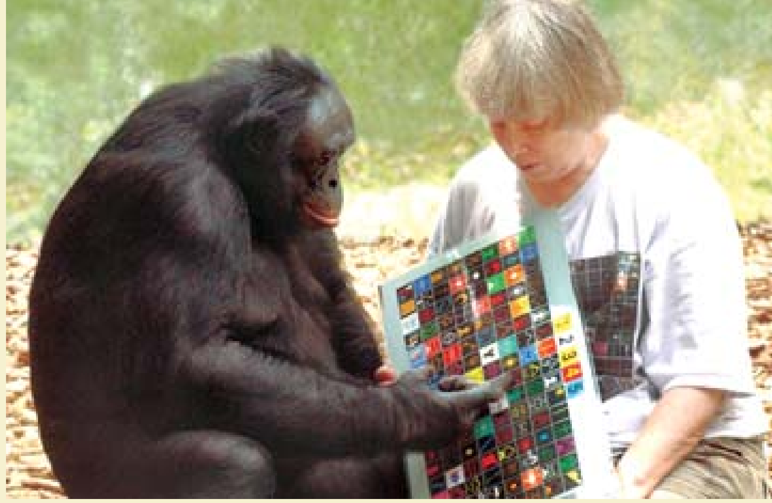
The most difficult responses to plan are those to unique situations. They require imagining multiple scenarios, as when a hunter plots various approaches to a deer or a futurist spins three scenarios bracketing what an industry will look like in another decade. Compared with apes, humans do a lot of that—we can heed the admonition sometimes attributed to British statesman Edmund Burke: "The public interest requires doing today those things that men of intelligence and goodwill would wish, five or 10 years hence, had been done."

Human planning abilities may stem from our talent for building syntactical, string-based conceptual structures larger than sentences. As writer Kathryn Morton observes about narrative:

> The first sign that a baby is going to be a human being and not a noisy pet comes when he begins naming the world and demanding the stories that connect its parts. Once he knows the first of these he will instruct his teddy bear, enforce his worldview on victims in the sandlot, tell himself stories of what he is doing as he plays and forecast stories of what he will do when he grows up. He will keep track of the actions of others and relate deviations to the person in charge. He will want a story at bedtime.

Our abilities to plan gradually develop from childhood narratives and are a major foundation for ethical choices, as we imagine a course of action, imagine its effects on others and decide whether or not to do it.

In this way, syntax raises intelligence to a new level. By borrowing the mental structures for syntax to judge other combinations of possible actions, we can extend our planning abilities and our intelligence. To some extent, we do this intelligence building by talking silently to ourselves, making narratives out of what might happen next and then applying syntaxlike rules of combination to rate a scenario as dangerous nonsense, mere nonsense, possible, likely or logical. But our thinking is not limited to languagelike constructs. Indeed, we may shout "Eureka!" when feeling a set of mental relationships click into place and yet have trouble expressing them verbally. Language and intelligence are so powerful that we might think evolution would naturally favor their increase.



KANZI, a 23-year-old bonobo, works with Sue Savage-Rumbaugh at Georgia State University in 2004. By pointing at symbols that represent various words, Kanzi can construct requests much like those of a two-year-old child. Language experiments on bonobos help researchers determine how much of syntax is uniquely human. Kanzi and Savage-Rumbaugh are now at the Great Ape Trust of Iowa.

GREAT APE TRUST OF IOWA

As evolutionary theorists are fond of demonstrating, however, the fossil record is full of plateaus. Evolution often follows indirect routes rather than "progressing" through adaptations. To account for the breadth of our abilities, we need to look at improvements in common core facilities. Environments that give the musically gifted an evolutionary advantage over the tone deaf are difficult to imagine, but there are multifunctional brain mechanisms whose improvement for one critical function might incidentally aid other functions.

We humans certainly have a passion for stringing things together: words into sentences, notes into melodies, steps into dances, narratives into games with rules of procedure. Might stringing things together be a core facility of the brain, one commonly useful to language, storytelling, planning, games and ethics? If so, natural selection for any of these talents might augment their shared neural machinery, so that an improved knack for syntactical sentences would automatically expand planning abilities, too. Such carryover is what Charles Darwin called functional change in anatomic continuity, distinguishing it from gradual adaptation. To some extent, music and dance are surely secondary uses of neural machinery shaped by sequential behaviors more exposed to natural selection, such as language.

From Hammering to *Hamlet*

AS IMPROBABLE AS the idea initially seems, the brain's planning of ballistic movements may have once promoted language, music and intelligence. Ballistic movements are extremely rapid actions of the limbs that, once initiated, cannot be modified. Striking a nail with a hammer is an example.

Although apes have elementary forms of the ballistic arm movements at which humans are expert—hammering, clubbing and throwing—they tend to be "set pieces" lacking novelty. These movements are integral to toolmaking and hunting, which in some settings were probably important additions to hominids' basic survival strategies.

Ballistic movements require a surprising amount of planning. Slow movements leave time for improvisation: when raising a cup to your lips, if the cup is lighter than you remembered, you can correct its trajectory before it hits your nose. Thus, a complete plan is not needed. You start in the right general direction and then correct your path, just as a moon rocket does.

For sudden limb movements lasting less than one eighth of a second, feedback corrections are largely ineffective because reaction times are too long. The brain has to determine every detail of the movement in advance, as though it were silently punching a roll of music for a player piano.

Hammering requires scheduling the exact sequence of activation for dozens of muscles. The problem of throwing is further compounded by the launch window—the range of times in which a projectile can be released and still hit the target. When the distance to a target doubles, the launch window becomes eight times narrower; statistical arguments indicate that programming a reliable throw would then require recruiting 64 times as many neurons to "sing" like a choir.

If mouth movements rely on the same core facility for sequencing that ballistic hand movements do, then enhancements in language skills might improve dexterity, and vice versa. Accurate throwing abilities open up the possibility of eating meat regularly, of being able to survive winter in a temperate zone. Language ability would initially be an incidental benefit—a free lunch, as it were, because of the linkage. Only later would language pay its own way.

Is there actually a sequencer common to movement and language? Much of the brain's coordination of movement occurs at a subcortical level in the basal ganglia or the cerebellum, but novel combinations of movements tend to depend on the premotor and prefrontal cortex. Two major lines of evidence point to cortical specialization for sequencing, and both suggest that the lateral language area has a lot to do with it.

Doreen Kimura of the University of Western Ontario has found that stroke patients with language problems (aphasia) resulting from damage to left lateral brain areas also have considerable difficulty executing unfamiliar sequences of hand and arm movements (apraxia). By electrically stimulating the brains of patients being operated on for epilepsy, George A. Ojemann of the University of Washington has also shown that at the center of the left lateral areas specialized for language lies a region involved in listening to sound sequences. This perisylvian region seems equally involved in producing oral-facial movement sequences—even nonlanguage ones.

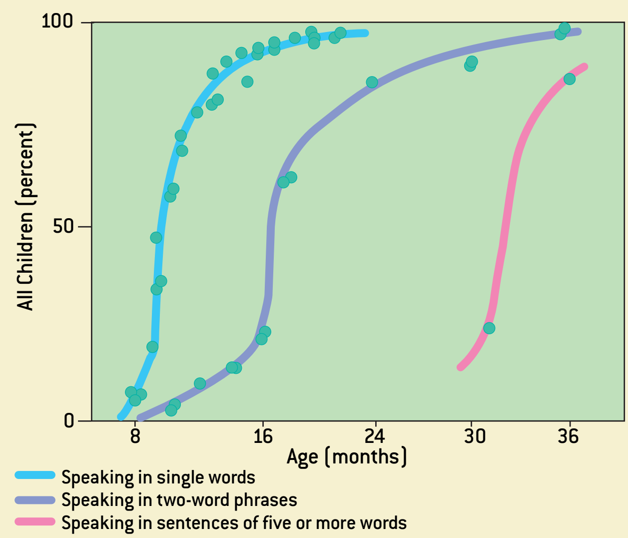
These discoveries reveal that parts of the "language cortex," as people sometimes think of it, are more multipurpose than had been suspected. The language cortex is concerned with novel sequences of various kinds: both sensations and movements, for both the hands and the mouth.

The big problem with inventing sequences and original behaviors is safety. Even simple reversals in order can be dangerous, as in "Look *after* you leap." But once we get good enough, we can simulate future courses of action and weed out the nonsense off-line; as philosopher Karl Popper said, this "permits our hypotheses to die in our stead." Creativity—indeed, the whole high end of intelligence and consciousness—involves playing mental games that shape up quality before acting. What kind of mental machinery might it take to do something like that?

By 1874, just 15 years after Darwin published *On the Origin of Species,* American psychologist William James was talking about mental processes operating in a Darwinian manner. In effect, he suggested, ideas might somehow "compete" with one another in the brain, leaving only the best or "fittest." Just as Darwinian evolution shaped a better brain in two million years, a similar Darwinian process operating within the brain might shape intelligent solutions to problems on the timescale of thought and action.

Researchers have demonstrated that a Darwinian process operating on an intermediate timescale of days governs the immune response following a vaccination. Through a series of cellular generations spanning several weeks, the immune system produces defensive antibody molecules that are better and better "fits" against invaders. By abstracting the essential features of a Darwinian process from what is known about species evolution and immune responses, we can see that any "Darwin machine" must have six properties.

First, it must operate on patterns of some type; in genetics, they are strings of DNA bases, but patterns of brain activity associated with a thought might qualify. Second, copies are made of these patterns. (Indeed, that which is semi-reli-



ACQUISITION OF LANGUAGE by children occurs quickly and naturally through exposure to adults.

LUCY READING-IKKANDA

ably copied defines a unit pattern.) Third, patterns must occasionally vary, whether through mutations, copying errors or a reshuffling of their parts.

Fourth, variant patterns must compete to occupy some limited space (as when bluegrass and crabgrass compete for my backyard). Fifth, the relative reproductive success of the variants is influenced by their environment (how often the grass is cut, watered, fertilized and trampled); this result is what Darwin called natural selection. And, finally, the makeup of the next generation of patterns depends on which variants survive to be copied. The patterns of the next generation will be variations spread around the currently successful ones. Many of these new variants will be less successful than their parents, but some may be better.

Sex and climatic change are not essentials, but they add spice and speed to a Darwinian process, whether it operates in milliseconds or millennia. Note that an "essential" is not Darwinian by itself: for example, selective survival can be seen when flowing water carries away sand and leaves pebbles behind.

The Darwinian Mind

LET US CONSIDER how these principles might apply to the evolution of an intelligent guess inside the brain. Thoughts are combinations of sensations and memories—in a way, they are movements that have not happened yet (and maybe never will). They exist as patterns of spatiotemporal activity in the brain, each representing an object, action or abstraction. I estimate that a single cerebral code minimally involves a few hundred cortical neurons within a millimeter of one another either firing or keeping quiet.

Evoking a memory is simply a matter of reconstituting such an activity pattern, according to psychologist Donald O. Hebb's cell-assembly hypothesis. Long-term memories are frozen patterns waiting for signals of near resonance to reawaken them, like ruts in a washboarded road waiting for a passing car to re-create a bouncing spatiotemporal pattern.

Some "cerebral ruts" are permanent, whereas others are short-lived. Short-term memories are just temporary alterations in the strengths of synaptic connections between neurons, left behind by the last spatiotemporal pattern to occupy a patch of cortex; this "long-term potentiation" may fade in a matter of minutes. The transition from short- to long-term patterning is not well understood, but structural alterations may sometimes follow potentiation, such that the synaptic connections between neurons are made strong and permanent, hardwiring the pattern of neural activity into some regions of the brain but not into others.

A Darwinian model of mind suggests that an activated memory can compete with others for "workspace" in the cortex. Perceptions of the thinker's current environment and memories of past environments may bias that competition and shape an emerging thought.

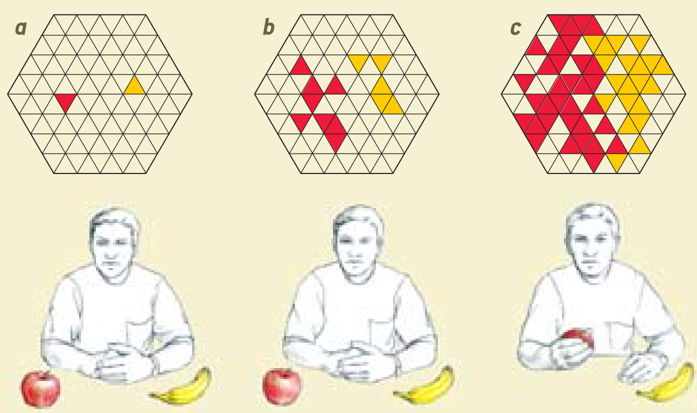
An active cerebral code could move from one part of the brain to another by making a copy of itself, much as a facsimile machine re-creates a copy of a pattern on a distant sheet of paper. The cerebral cortex also has circuitry for cloning a spatiotemporal pattern in an immediately adjacent region less than a millimeter away, although our present imaging techniques lack enough resolution to see the copying in progress. Repeated copying of the minimal pattern could colonize a region, rather the way a crystal grows or wallpaper repeats an elementary pattern.

The picture that emerges from these theoretical considerations is one of a quilt, some patches of which enlarge at the expense of their neighbors as one code copies more successfully than another. As you try to decide whether to pick an apple or a banana from the fruit bowl, so my theory goes, the cerebral code for "apple" may be having a cloning competition with the one for "banana." When one code has enough active copies to trip the action circuits, you might reach for the apple.

But the banana codes need not vanish: they could linger in the background as subconscious thoughts and undergo variations. When you try to remember someone's name, initially without success, the candidate codes might continue copying for the next half an hour until, suddenly, Jane Smith's

APPLE OR BANANA?

The Darwinian model of thinking suggests that ideas compete for "workspace" within the brain. When a person is choosing between an apple and a banana (*a*), spatiotemporal patterns of neural activity representing these possibilities (*red for apple, yellow for banana*) may appear in the cortex (*hexagon*). Copies of each pattern proliferate at different rates, depending on the individual's experiences and sensory impressions (*b*). Eventually, the number of copies of one pattern passes a threshold, and the person makes that choice—in this case, to take the apple (*c*).



DANA BURNS-PIZER

THROWING is a ballistic movement at which humans excel, despite the lack of effective feedback from the arm during most of the throw. Before the ball is thrown, the brain must plan the sequence of muscle contractions that will launch the ball toward a target. Some of the neural mechanisms that plan such movements may also facilitate other types of planning.

LISA BLUMENFELD *Getty Images*

name seems to "pop into your mind" because your variations on the spatiotemporal theme finally hit a resonance and create a critical mass of identical copies. Our conscious thought may be only the currently dominant pattern in the copying competition, with many other variants competing for dominance, one of which will win a moment later when your thoughts seem to shift focus.

It may be that Darwinian processes are only the frosting on the cognitive cake, that much of our thinking is routine or bound by rules. But we often deal with novel situations in creative ways, as when you decide what to fix for dinner tonight. You survey what is already in the refrigerator and on the kitchen shelves. You think about a few alternatives, keeping track of what else you might have to fetch from the grocery store. All this can flash through your mind within seconds—and that is probably a Darwinian process at work.

Elements of Intelligence

IN PHYLOGENY and its ontogeny, human intelligence first solves movement problems and only later graduates to ponder more abstract ones. An artificial or extraterrestrial intelligence freed of the necessity of finding food and avoiding predators might not need to move—and so might lack the what-happens-next orientation of human intelligence. There may be other ways in which high intelligence can be achieved, but up-from-movement is the known paradigm.

It is difficult to estimate how often high intelligence might emerge, given how little we know about the demands of long-term species survival and the courses evolution can follow. We can, however, compare the prospects of different species by asking how many elements of intelligence each has amassed.

Does the species have a wide repertoire of movements, concepts or other tools? Does it have tolerance for creative confusion that allows individuals to invent categories occasionally? (Primatologist Duane M. Rumbaugh of the Great Ape Trust of Iowa has noted that small monkeys and prosimians, such as lemurs, often get trapped into repeating the first set of discrimination rules they are taught, unlike the more advanced rhesus monkeys and apes.)

Does each individual have more than half a dozen mental workspaces for concurrently holding different concepts? Does it have so many that it loses our human tendency to "chunk" certain concepts, as when we create the word "ambivalence" as a stand-in for a whole sentence's worth of description? Can individuals establish new relations between the concepts in their workspaces? These relations should be fancier than "is a" and "is larger than," which many animals can grasp. Treelike relations seem particularly important for linguistic structures; our ability to compare two relations (analogy) enables operations in a metaphorical space.

Can individuals mold and refine their ideas off-line, before acting in the real world? Does that process involve all six of the essential Darwinian features, as well as some accelerating factors? Are there shortcuts that allow the process to start from something more than a primitive level? Can individuals make guesses about both long-term strategies and short-term tactics, so that they can make moves that will advantageously set the stage for future feats?

Chimps and bonobos may be missing a few of these elements, but they are doing better than the present generation of artificial-intelligence programs. Even in entities with all the elements, we would expect considerable variation in intelligence because of individual differences in processing speed, in perseverance, in implementing shortcuts and in finding the appropriate level of abstraction when using analogies.

Why are there not more species with such complex mental states? A little intelligence can be a dangerous thing. A beyond-the-apes intelligence must navigate between the twin hazards of dangerous innovation and a conservatism that ignores what the Red Queen explained to Alice in *Through the Looking Glass:* "...it takes all the running you can do, to keep in the same place." Foresight is our special form of running, essential for the intelligent stewardship that the late Stephen Jay Gould of Harvard University warned is needed for longer-term survival: "We have become, by the power of a glorious evolutionary accident called intelligence, the stewards of life's continuity on earth. We did not ask for this role, but we cannot abjure it. We may not be suited for it, but here we are." SA

MORE TO EXPLORE

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