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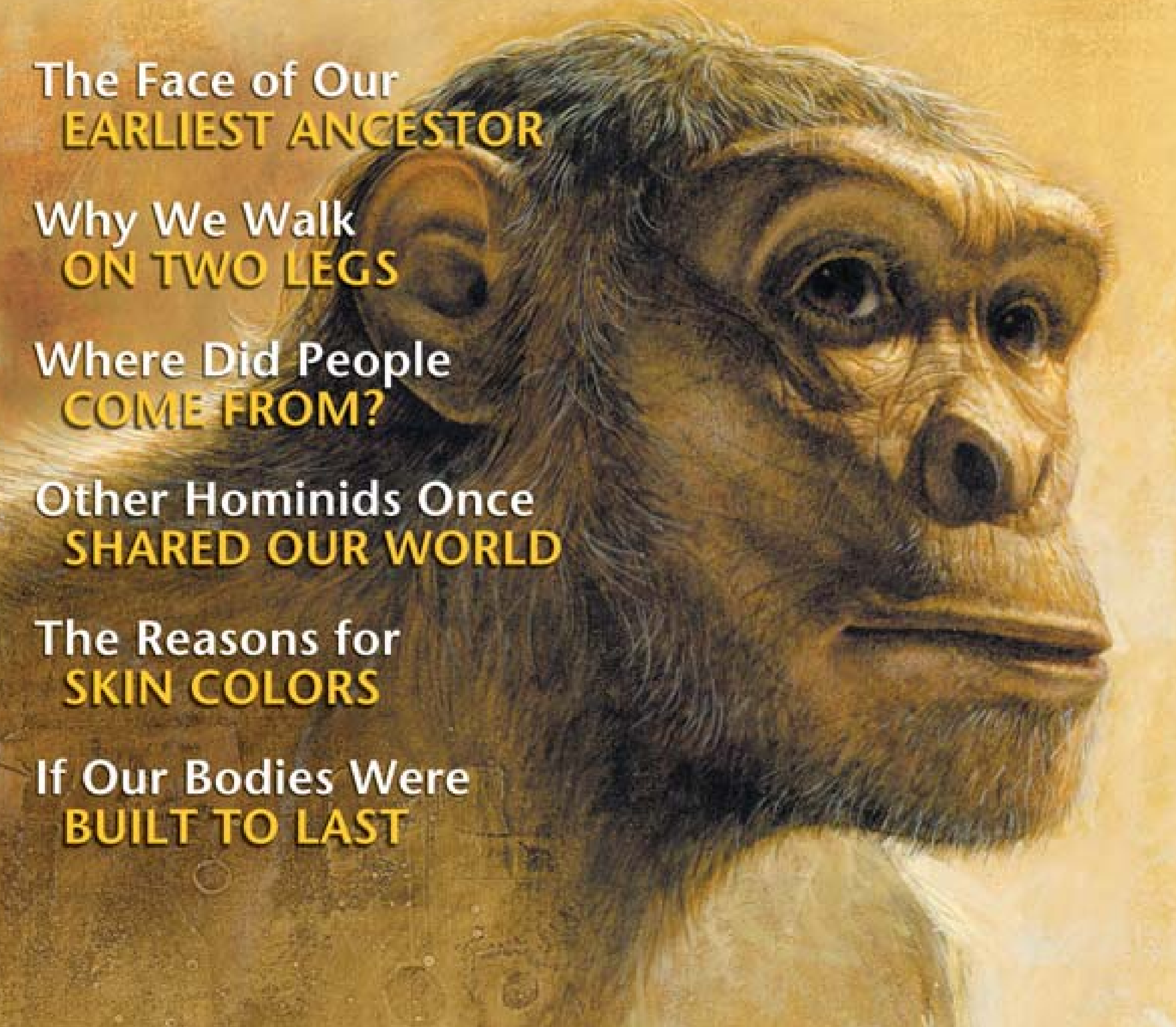
New Look at Human Evolution



The Face of Our EARLIEST ANCESTOR

Why We Walk ON TWO LEGS

Where Did People COME FROM?

Other Hominids Once SHARED OUR WORLD

The Reasons for SKIN COLORS

If Our Bodies Were BUILT TO LAST

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The Original Human Interest Story

It's quite a tale. Perhaps five million to 10 million years ago, a primate species diverged from the chimpanzee line. This was the forerunner of humanity—and a host of other beings who were almost but not quite human. For a time, a throng of hominid species shared the planet; at least four even coexisted in the same region. By around four million years ago, our progenitors and others had mastered the art of walking upright. Some two million years later they strode out of Africa and colonized entirely new lands. Certain groups learned to make sophisticated tools and, later, artwork and musical instruments. The various species clashed, inevitably. Modern humans, who entered Europe 40,000 years ago, may have slaughtered Neandertals (when they weren't interbreeding with them). Eventually only one species, *Homo sapiens,* was left. We thus find ourselves alone and yet the most numerous and successful primates in history.

MOSAIC of primitive and advanced features marks *Sahelanthropus tchadensis,* known from a seven-million-year-old skull.

KAZUHIKO SANO

Reading the cracked brown fragments of fossils and sequences of DNA, however, scientists have found clues that the story of human origins has more convolutions. The account of our shared human heritage now includes more controversial plot twists and mysteries. Was the remarkable seven-million-year-old skull found in July 2002 in Chad really one of our first forebears, or a distant dead-end cousin with precociously evolved features? Did modern humans really originate in Africa alone, as is widely held, or in multiple locales? When (and how often) did we emigrate? Were Neandertals the crude, brutish cavemen of comic strips or—as fresh evidence suggests—did they have a refined, artistic culture? Did they copy and steal toolmaking technologies from the modern humans, or did they invent them independently? Might they even have conceived children with the moderns? And of course, why didn't our kind perish with the rest of the hominids? Were we luckier, more lingual or just more lethal than the rest?

In this special edition from *Scientific American,* we have collected articles about the latest developments in the field of human evolution—written by the experts who are leading the investigations. We invite you to explore the pages that follow, to learn more about that fascinating first chapter in everybody's family history.

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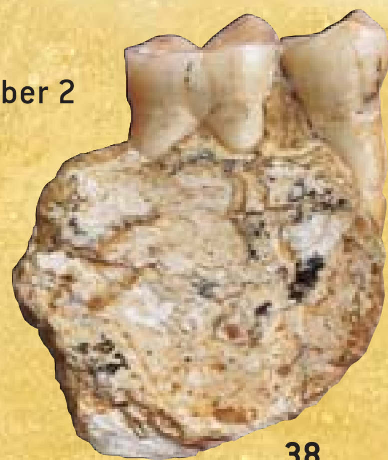

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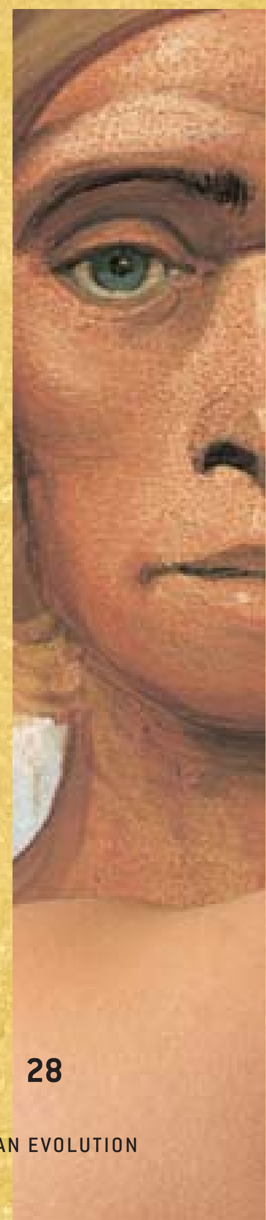

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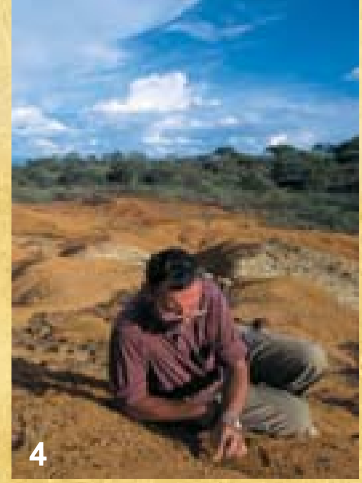
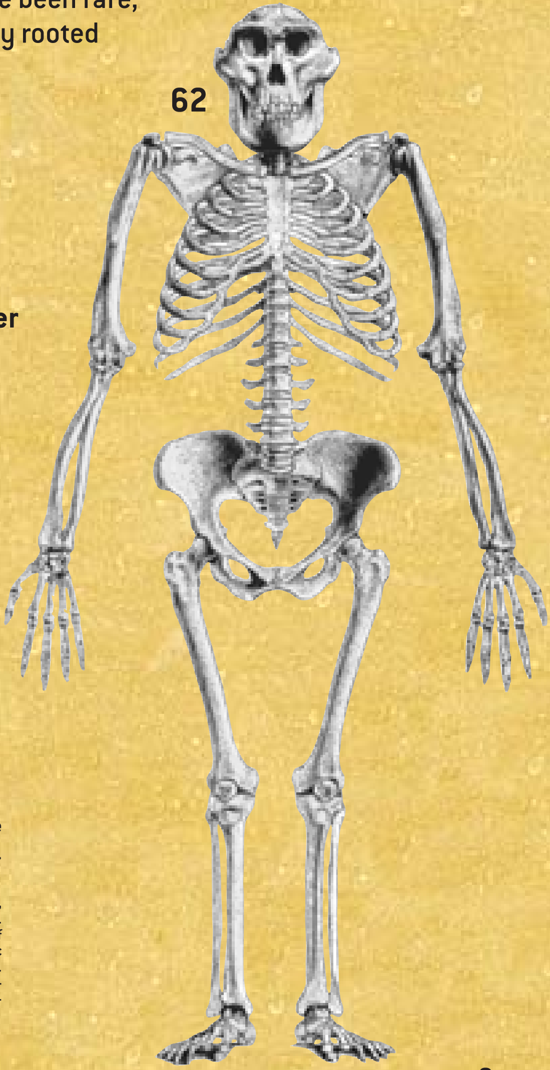


ADAPTATION



FAST-FORWARD

Cover painting by Kazuhiko Sano. This depiction of *Sahelanthropus tchadensis*—potentially the oldest hominid yet found—is based on cranial and dental remains.

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An Ancestor to Call Our Own

By Kate Wong

Controversial new fossils could bring scientists closer than ever to the origin of humanity

POITIERS, FRANCE—Michel Brunet removes the cracked, brown skull from its padlocked, foam-lined metal carrying case and carefully places it on the desk in front of me. It is about the size of a coconut, with a slight snout and a thick brow visoring its stony sockets. To my inexpert eye, the face is at once foreign and inscrutably familiar. To Brunet, a paleontologist at the University of Poitiers, it is the visage of the lost relative he has sought for 26 years. "He is the oldest one," the veteran fossil hunter murmurs, "the oldest hominid."

Brunet and his team set the field of paleoanthropology abuzz when they unveiled their find in July 2002. Unearthed from sandstorm-scoured deposits in northern Chad's Djurab Desert, the astonishingly complete cranium—dubbed *Sahelanthropus tchadensis* (and nicknamed Toumaï, which means "hope of life" in the local Goran language)—dates to nearly seven million years ago. It may thus represent the earliest human forebear on record, one who Brunet says "could touch with his finger" the point at which our lineage and the one leading to our closest living relative, the chimpanzee, diverged.

KAZUHIKO SANO

APE OR ANCESTOR? *Sahelanthropus tchadensis,* potentially the oldest hominid on record, forages in a woodland bordering Lake Chad some seven million years ago. Thus far the creature is known only from cranial and dental remains, so its body in this artist's depiction is entirely conjectural.

Updated from the January 2003 issue

Less than a century ago simian human precursors from Africa existed only in the minds of an enlightened few. Charles Darwin predicted in 1871 that the earliest ancestors of humans would be found in Africa, where our chimpanzee and gorilla cousins live today. But evidence to support that idea didn't come until more than 50 years later, when anatomist Raymond Dart of the University of the Witwatersrand described a fossil skull from Taung, South Africa, as belonging to an extinct human he called *Australopithecus africanus,* the "southern ape from Africa." His claim met variously with frosty skepticism and outright rejection—the remains were those of a juvenile gorilla, critics countered. The discovery of another South African specimen, now recognized as *A. robustus,* eventually vindicated Dart, but it wasn't until the 1950s that the notion of ancient, apelike human ancestors from Africa gained widespread acceptance.

In the decades that followed, pioneering efforts in East Africa headed by members of the Leakey family, among others, turned up additional fossils. By the late 1970s the australopithecine cast of characters had grown to include *A. boisei, A. aethiopicus* and *A. afarensis* (Lucy and her kind, who lived between 2.9 million and 3.6 million years ago during the Pliocene epoch and gave rise to our own genus, *Homo*). Each was adapted to its own environmental niche, but all were bipedal creatures with thick jaws, large molars and small canines—radically different from the generalized, quadrupedal Miocene apes known from farther back on the family tree. To probe human origins beyond *A. afarensis,* however, was to fall into a gaping hole in the fossil record between 3.6 million and 12 million years ago. Who, researchers wondered, were Lucy's forebears?

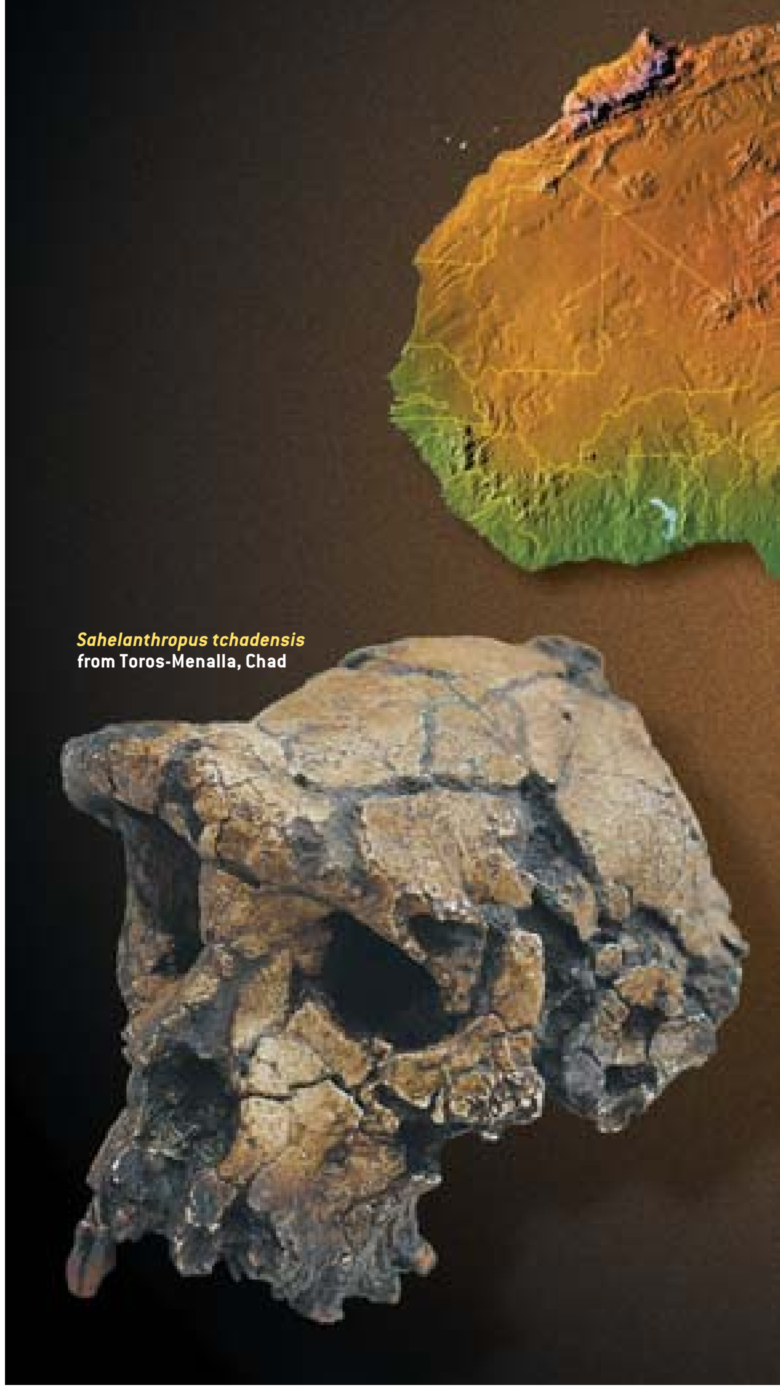
Despite widespread searching, diagnostic fossils of the right age to answer that question eluded workers for nearly two decades. Their luck finally began to change around the mid-1990s, when a team led by Meave Leakey of the National Museums of Kenya announced its discovery of *A. anamensis,* a four-million-year-old species that, with its slightly more archaic characteristics, made a reasonable ancestor for Lucy [see "Early Hominid Fossils from Africa," on page 14]. At around the

Overview/*The Oldest Hominids*

- The typical textbook account of human evolution holds that humans arose from a chimpanzeelike ancestor between roughly five million and six million years ago in East Africa and became bipedal on the savanna. But until recently, hominid fossils more than 4.4 million years old were virtually unknown.
- Newly discovered fossils from Chad, Kenya and Ethiopia may extend the human record back to seven million years ago, revealing the earliest hominids yet.
- These finds cast doubt on conventional paleoanthropological wisdom. But experts disagree over how these creatures are related to humans—if they are related at all.

AFRICAN ROOTS

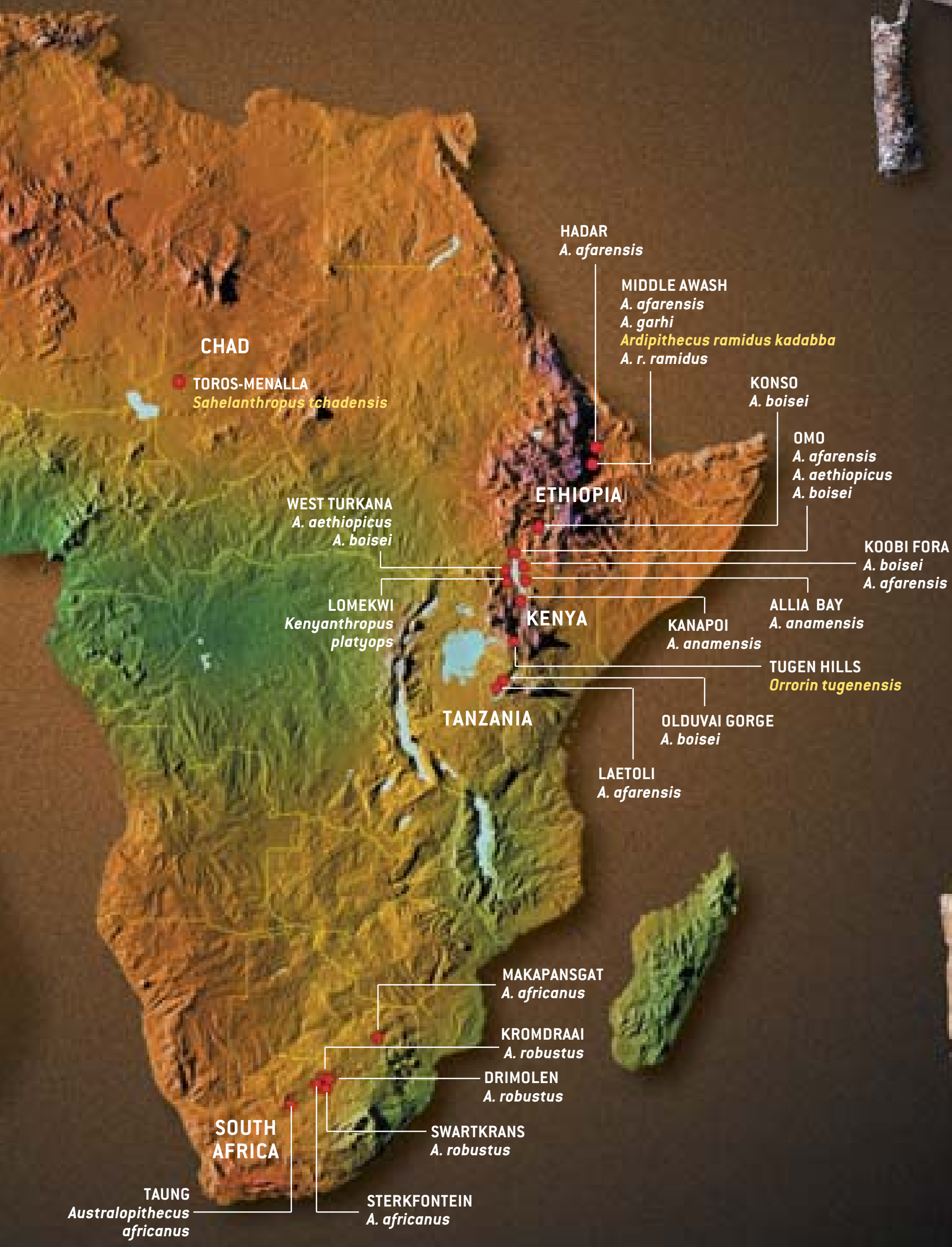
RECENT FINDS from Africa could extend in time and space the fossil record of early human ancestors. Just a few years ago remains more than 4.4 million years old were essentially unknown, and the oldest specimens all came from East Africa. In 2001 paleontologists working in Kenya's Tugen Hills and Ethiopia's Middle Awash region announced that they had discovered hominids dating back to nearly six million years ago (*Orrorin tugenensis* and *Ardipithecus ramidus kadabba,* respectively). Then, in July 2002, University of Poitiers



Sahelanthropus tchadensis
from Toros-Menalla, Chad

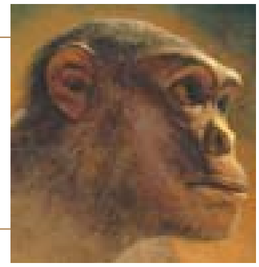
paleontologist Michel Brunet and his Franco-Chadian Paleoanthropological Mission reported having unearthed a nearly seven-million-year-old hominid, called *Sahelanthropus tchadensis,* at a site known as Toros-Menalla in northern Chad. The site lies some 2,500 kilometers west of the East African fossil localities. "I think the most important thing we have done in terms of trying to understand our story is to open this new window," Brunet remarks. "We are proud to be the pioneers of the West."

Ardipithecus ramidus kadabba
from Middle Awash, Ethiopia



Orrorin tugenensis
from Tugen Hills, Kenya

PATRICK ROBERT *Corbis Sygma* (*Sahelanthropus tchadensis skull*); © 1999 TIM D. WHITE *Brill Atlanta\National Museum of Ethiopia* (*A. r. kadabba fossils*); GAMMA (*O. tugenensis fossils*); EDWARD BELL (*map illustration*)



It is the visage of the lost relative he has sought for 26 years. **"He is the oldest one,"** *the veteran fossil hunter murmurs,* **"the oldest hominid."**

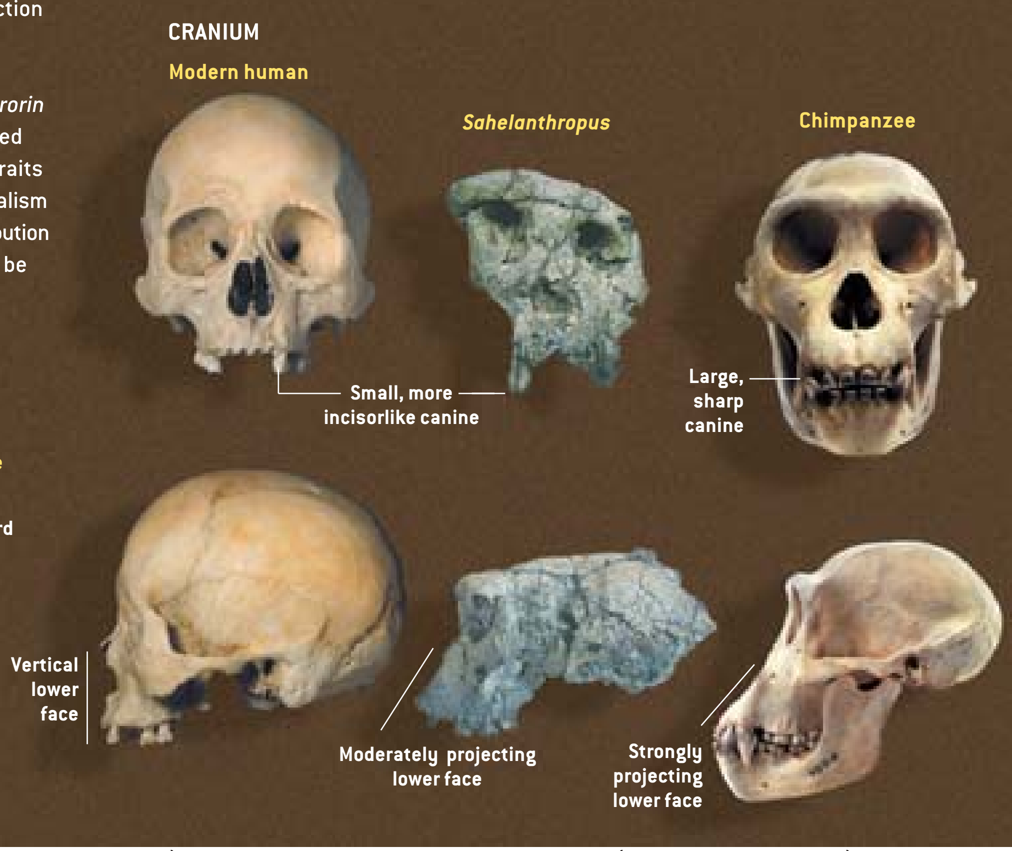
same time, Tim D. White of the University of California at Berkeley and his colleagues described a collection of 4.4-million-year-old fossils recovered in Ethiopia that represent an even more primitive hominid, now known as *Ardipithecus ramidus ramidus*. Those findings gave scholars a tantalizing glimpse into Lucy's past. But estimates from some molecular biologists of when the split between chimps and humans occurred suggested that even older hominids lay waiting somewhere to be discovered.

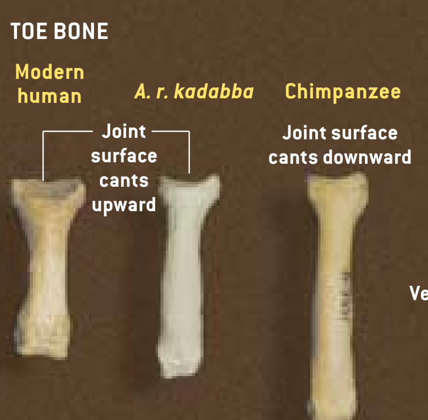
Those intriguing predictions have recently been borne out. Over the past few years, researchers have made a string of stunning discoveries—Brunet's among them—that may go a long way toward bridging the remaining gap between humans and their African ape ancestors. These fossils, which range from roughly five million to seven million years old, are upending long-held ideas about when and where our lineage arose and what the last common ancestor of humans and chimpanzees looked like.

Not surprisingly, they have also sparked vigorous debate. Indeed, experts are deeply divided over where on the family tree the new species belong and even what constitutes a hominid in the first place.

ANATOMY OF AN ANCESTOR

KEY TRAITS link putative hominids *Ardipithecus ramidus kadabba, Orrorin* and *Sahelanthropus* to humans and distinguish them from apes such as chimpanzees. The fossils exhibit primitive apelike characteristics, too, as would be expected of creatures this ancient. For instance, the *A. r. kadabba* toe bone has a humanlike upward tilt to its joint surface, but the bone is long and curves downward like a chimp's does (which somewhat obscures the joint's cant). Likewise, *Sahelanthropus* has a number of apelike traits—its small braincase among them—but is more humanlike in the form of the canines and the projection of the lower face. (Reconstruction of the *Sahelanthropus* cranium, which is distorted, will give researchers a better understanding of its morphology.) The *Orrorin* femur has a long neck and a groove carved out by the obturator externus muscle—traits typically associated with habitual bipedalism and therefore with humans—but the distribution of cortical bone in the femoral neck may be more like that of a quadrupedal ape.

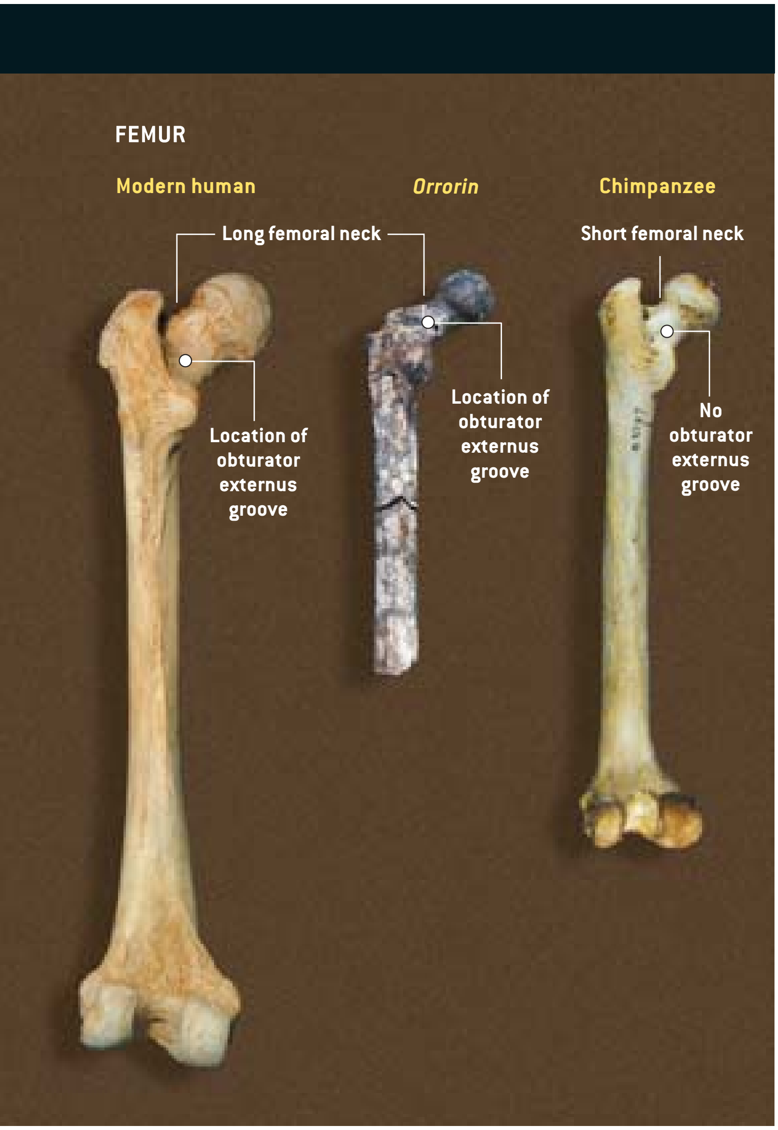




© C. OWEN LOVEJOY*Brill Atlanta* (*human*, A. r. kadabba *and chimpanzee toe bones*); CHRISTIAN SIDOR *New York College of Osteopathic Medicine* (*human skull and human femur*); MISSION PALÉOANTHROPOLOGIQUE FRANCO-TCHADIENNE (Sahelanthropus *skull*); © 1996 DAVID L. BRILL\DIVISION OF MAMMALS, NATIONAL MUSEUM OF NATURAL HISTORY, SMITHSONIAN INSTITUTION (*chimpanzee skull*); GAMMA (Orrorin *femur*); C. OWEN LOVEJOY *Kent State University* (*chimpanzee femur*)

Standing Tall

THE FIRST HOMINID CLUE to come from beyond the 4.4-million-year mark was announced in the spring of 2001. Paleontologists Martin Pickford and Brigitte Senut of the National Museum of Natural History in Paris found in Kenya's Tugen Hills the six-million-year-old remains of a creature they called *Orrorin tugenensis*. To date, the researchers have amassed 21 specimens, including bits of jaw, isolated teeth, finger and arm bones, and some partial upper leg bones, or femurs. According to Pickford and Senut, *Orrorin* exhibits several characteristics that clearly align it with the hominid family—notably those suggesting that, like all later members of our group, it walked on two legs. "The femur is remarkably humanlike," Pickford observes. It has a long femoral neck, which would have placed the shaft at an angle relative to the lower leg (thereby stabilizing the hip), and a groove on the back of that femoral neck, where a muscle known as the obturator externus pressed against the bone during upright walking. In other respects, *Orrorin* was a primitive animal: its canine teeth are large and pointed relative to human canines, and its arm and finger bones retain adaptations for climbing. But the femur characteristics signify to Pickford and Senut that when it was on the ground, *Orrorin* walked like a man.



In fact, they argue, *Orrorin* appears to have had a more humanlike gait than the much younger Lucy did. Breaking with paleoanthropological dogma, the team posits that *Orrorin* gave rise to *Homo* via the proposed genus *Praeanthropus* (which comprises a subset of the fossils currently assigned to *A. afarensis* and *A. anamensis*), leaving Lucy and her kin on an evolutionary sideline. *Ardipithecus,* they believe, was a chimpanzee ancestor.

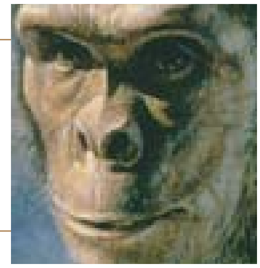
Not everyone is persuaded by the femur argument. C. Owen Lovejoy of Kent State University counters that published computed tomography scans through *Orrorin*'s femoral neck—which Pickford and Senut say reveal humanlike bone structure—actually show a chimplike distribution of cortical bone, an important indicator of the strain placed on that part of the femur during locomotion. Cross sections of *A. afarensis*'s femoral neck, in contrast, look entirely human, he states. Lovejoy suspects that *Orrorin* was frequently—but not habitually—bipedal and spent a significant amount of time in the trees. That wouldn't exclude it from hominid status, because full-blown bipedalism almost certainly didn't emerge in one fell swoop. Rather *Orrorin* may have simply not yet evolved the full complement of traits required for habitual bipedalism. Viewed that way, *Orrorin* could still be on the ancestral line, albeit further removed from *Homo* than Pickford and Senut would have it.

Better evidence of early routine bipedalism, in Lovejoy's view, surfaced a few months after the *Orrorin* report, when Berkeley graduate student Yohannes Haile-Selassie announced the discovery of slightly younger fossils from Ethiopia's Middle Awash region. Those 5.2-million- to 5.8-million-year-old remains, which have been classified as a subspecies of *Ardipithecus ramidus, A. r. kadabba,* include a complete foot phalanx, or toe bone, bearing a telltale trait. The bone's joint is angled in precisely the way one would expect if *A. r. kadabba* "toed off" as humans do when walking, reports Lovejoy, who has studied the fossil.

Other workers are less impressed by the toe morphology. "To me, it looks for all the world like a chimpanzee foot phalanx," comments David Begun of the University of Toronto, noting from photographs that it is longer, slimmer and more curved than a biped's toe bone should be. Clarification may come when White and his collaborators publish findings on an as yet undescribed partial skeleton of *Ardipithecus,* which White says they hope to do within the next year or two.

Differing anatomical interpretations notwithstanding, if either *Orrorin* or *A. r. kadabba* were a biped, that would not only push the origin of our strange mode of locomotion back by nearly 1.5 million years, it would also lay to rest a popular idea about the conditions under which our striding gait evolved. Received wisdom holds that our ancestors became bipedal on the African savanna, where upright walking may have kept the blistering sun off their backs, given them access

Humanity may have arisen more than a million years earlier than a number of molecular studies had estimated. More important, it may have originated in a different locale.



to previously out-of-reach foods, or afforded them a better view above the tall grass. But paleoecological analyses indicate that *Orrorin* and *Ardipithecus* dwelled in forested habitats, alongside monkeys and other typically woodland creatures. In fact, Giday WoldeGabriel of Los Alamos National Laboratory and his colleagues, who studied the soil chemistry and animal remains at the *A. r. kadabba* site, have noted that early hominids may not have ventured beyond these relatively wet and wooded settings until after 4.4 million years ago.

If so, climate change may not have played as important a role in driving our ancestors from four legs to two as has been thought. For his part, Lovejoy observes that a number of the savanna-based hypotheses focusing on posture were not especially well conceived to begin with. "If your eyes were in your toes, you could stand on your hands all day and look over tall grass, but you'd never evolve into a hand-walker," he jokes. In other words, selection for upright posture alone would not, in his view, have led to bipedal locomotion. The most plausible explanation for the emergence of bipedalism, Lovejoy says, is that it freed the hands and allowed males to collect extra food with which to woo mates. In this model, which he developed in the 1980s, females who chose good providers could devote more energy to child rearing, thereby maximizing their reproductive success.

The Oldest Ancestor?

THE PALEOANTHROPOLOGICAL community was still digesting the implications of the *Orrorin* and *A. r. kadabba* discoveries when Brunet's fossil find from Chad came to light. With *Sahelanthropus* have come new answers—and new questions. Unlike *Orrorin* and *A. r. kadabba,* the *Sahelanthropus* material does not include any postcranial bones, making it impossible at this point to know whether the animal was bipedal, the traditional hallmark of humanness. But Brunet argues that a suite of features in the teeth and skull, which he believes belongs to a male, judging from the massive brow ridge, clearly links this creature to all later hominids. Characteristics of *Sahelanthropus*'s canines are especially important in his assessment. In all modern and fossil apes, and therefore presumably in the last common ancestor of chimps and humans, the large upper canines are honed against the first lower premolars, producing a sharp edge along the back of the canines. This so-called honing canine-premolar complex is pronounced in males, who use their canines to compete with one another for females. Humans lost these fighting teeth, evolving smaller, more incisorlike canines that occlude tip to tip, an arrangement that creates a distinctive wear pattern over time. In their size, shape and wear, the *Sahelanthropus* canines are modified in the human direction, Brunet asserts.

At the same time, *Sahelanthropus* exhibits a number of apelike traits, such as its small braincase and widely spaced eye sockets. This mosaic of primitive and advanced features, Brunet says, suggests a close relationship to the last common ancestor. Thus, he proposes that *Sahelanthropus* is the earliest member of the human lineage and the ancestor of all later hominids, including *Orrorin* and *Ardipithecus*. If Brunet is correct,

WITNESS/GAMMA

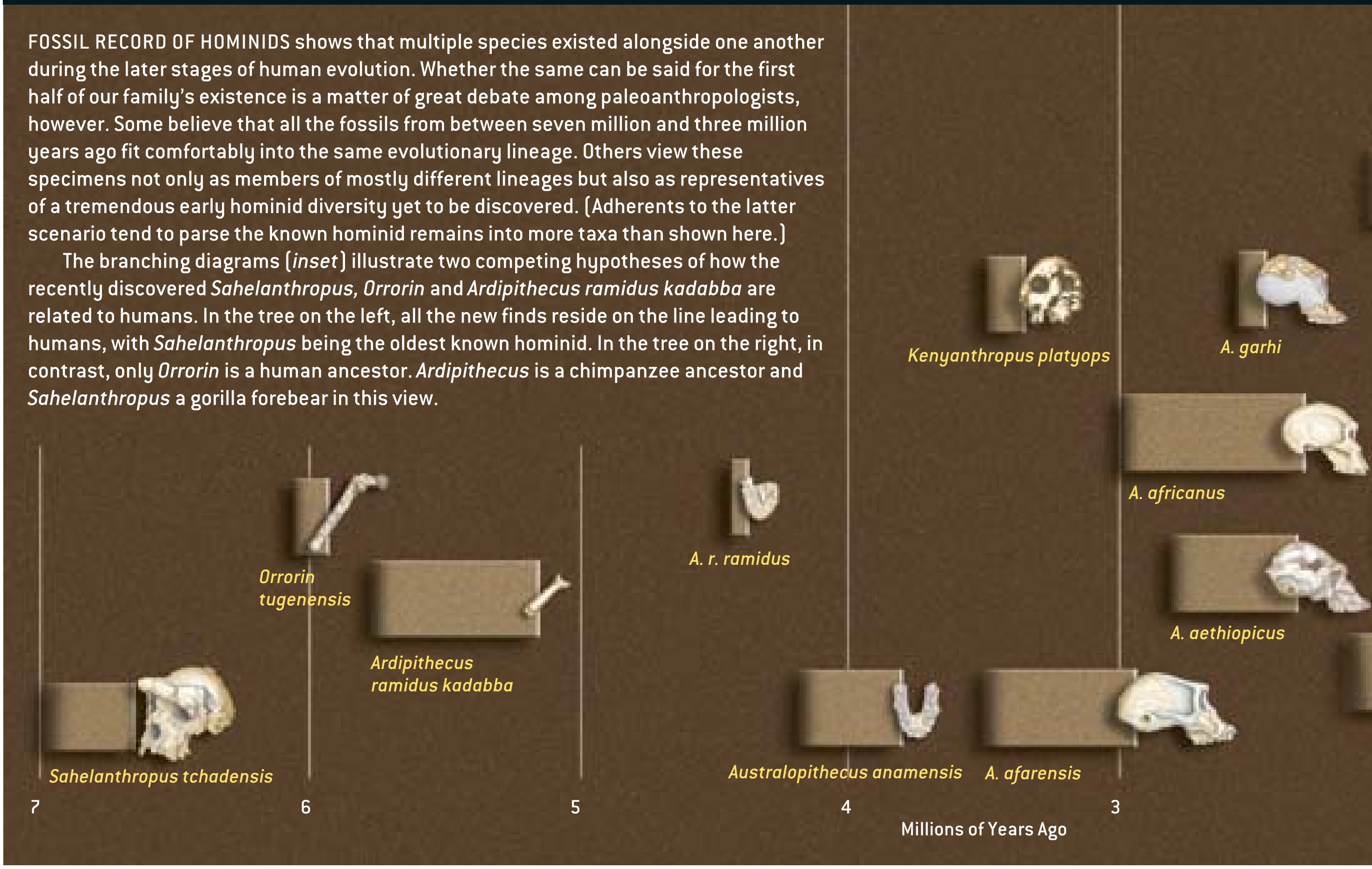
HUNTING FOR HOMINIDS: Michel Brunet (*left*), whose team uncovered *Sahelanthropus,* has combed the sands of the Djurab Desert in Chad for nearly a decade. Martin Pickford and Brigitte Senut (*center*) discovered *Orrorin* in Kenya's Tugen Hills. Tim White (*top right*) and Yohannes Haile-Selassie (*bottom right*) found *Ardipithecus* in the Middle Awash region of Ethiopia.

humanity may have arisen more than a million years earlier than a number of molecular studies had estimated. More important, it may have originated in a different locale than has been posited. According to one model of human origins, put forth in the 1980s by Yves Coppens of the College of France, East Africa was the birthplace of humankind. Coppens, noting that the oldest human fossils came from East Africa, proposed that the continent's Rift Valley—a gash that runs from north to south—split a single ancestral ape species into two populations. The one in the east gave rise to humans; the one in the west spawned today's apes [see "East Side Story: The Origin of Humankind," by Yves Coppens; SCIENTIFIC AMERICAN, May 1994]. Scholars have recognized for some time that the apparent geographic separation might instead be an artifact of the scant fossil record. The discovery of a seven-million-year-old hominid in Chad, some 2,500 kilometers west of the Rift Valley, would deal the theory a fatal blow.

Most surprising of all may be what *Sahelanthropus* reveals about the last common ancestor of humans and chimpanzees. Paleoanthropologists have typically imagined that that creature resembled a chimp in having, among other things, a strongly projecting lower face, thinly enameled molars and large canines. Yet *Sahelanthropus,* for all its generally apelike traits, has only a moderately prognathic face, relatively thick enamel, small canines and a brow ridge larger than that of any living ape. "If *Sahelanthropus* shows us anything, it shows us that the last common ancestor was not a chimpanzee," Berkeley's White remarks. "But why should we have expected otherwise?" Chimpanzees have had just as much time to evolve as humans have had, he points out, and they have become highly specialized, fruit-eating apes.

Brunet's characterization of the Chadian remains as those of a human ancestor has not gone unchallenged, however. "Why *Sahelanthropus* is necessarily a hominid is not particularly clear," comments Carol V. Ward of the University of Missouri. She and others are skeptical that the canines are as humanlike as Brunet claims. Along similar lines, in a letter published last October in the journal *Nature,* in which Brunet's team initially reported its findings, University of Michigan paleoanthropologist Milford H. Wolpoff, along with *Orrorin* discoverers Pickford and Senut, countered that *Sahelanthropus* was an ape rather than a hominid. The massive brow and certain features on the base and rear of *Sahelanthropus*'s skull, they observed, call to mind the anatomy of a quadrupedal ape with a difficult-to-chew diet, whereas the small canine suggests that it was a female of such a species, not a male human ancestor. Lacking proof that *Sahelanthropus* was bipedal, so their reasoning goes, Brunet doesn't have a leg to stand on. (Pickford and Senut further argue that the animal was specifically a gorilla ancestor.) In a barbed response, Brunet likened his detractors to those Dart encountered in 1925, retorting that

HOMINIDS IN TIME



FOSSIL RECORD OF HOMINIDS shows that multiple species existed alongside one another during the later stages of human evolution. Whether the same can be said for the first half of our family's existence is a matter of great debate among paleoanthropologists, however. Some believe that all the fossils from between seven million and three million years ago fit comfortably into the same evolutionary lineage. Others view these specimens not only as members of mostly different lineages but also as representatives of a tremendous early hominid diversity yet to be discovered. (Adherents to the latter scenario tend to parse the known hominid remains into more taxa than shown here.)

The branching diagrams (*inset*) illustrate two competing hypotheses of how the recently discovered *Sahelanthropus, Orrorin* and *Ardipithecus ramidus kadabba* are related to humans. In the tree on the left, all the new finds reside on the line leading to humans, with *Sahelanthropus* being the oldest known hominid. In the tree on the right, in contrast, only *Orrorin* is a human ancestor. *Ardipithecus* is a chimpanzee ancestor and *Sahelanthropus* a gorilla forebear in this view.

Sahelanthropus's apelike traits are simply primitive holdovers from its own ape predecessor and therefore uninformative with regard to its relationship to humans.

The conflicting views partly reflect the fact that researchers disagree over what makes the human lineage unique. "We have trouble defining hominids," acknowledges Roberto Macchiarelli, also at the University of Poitiers. Traditionally paleoanthropologists have regarded bipedalism as the characteristic that first set human ancestors apart from other apes. But subtler changes—the metamorphosis of the canine, for instance—may have preceded that shift.

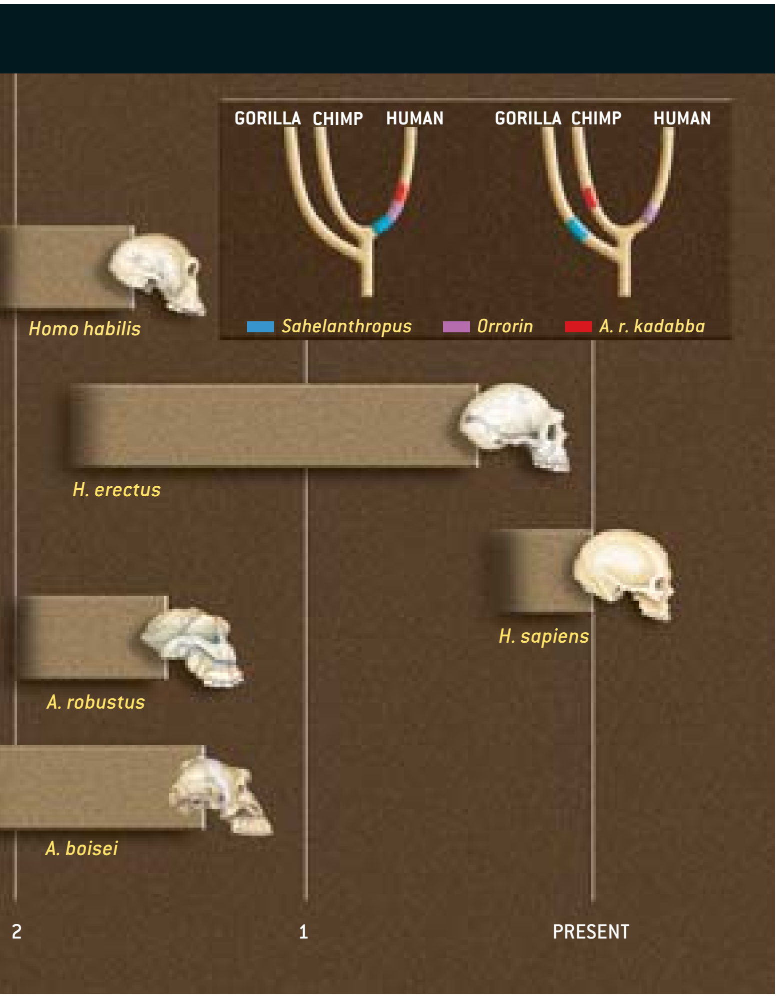
To understand how animals are related to one another, evolutionary biologists employ a method called cladistics, in which organisms are grouped according to shared, newly evolved traits. In short, creatures that have these derived characteristics in common are deemed more closely related to one another than they are to those that exhibit only primitive traits inherited from a more distant common ancestor. The first occurrence in the fossil record of a shared, newly acquired trait serves as a baseline indicator of the biological division of an ancestral species into two daughter species—in this case, the point at which chimps and humans diverged from their common ancestor—and that trait is considered the defining characteristic of the group.

Thus, cladistically "what a hominid is from the point of view of skeletal morphology is summarized by those characters preserved in the skeleton that are present in populations that directly succeeded the genetic splitting event between chimps and humans," explains William H. Kimbel of Arizona State University. With only an impoverished fossil record to work from, paleontologists can't know for certain what those traits were. But the two leading candidates for the title of seminal hominid characteristic, Kimbel says, are bipedalism and the transformation of the canine. The problem researchers now face in trying to suss out what the initial changes were and which, if any, of the new putative hominids sits at the base of the human clade is that so far *Orrorin, A. r. kadabba* and *Sahelanthropus* are represented by mostly different bony elements, making comparisons among them difficult.

How Many Hominids?

MEANWHILE THE ARRIVAL of three new taxa to the table has intensified debate over just how diverse early hominids were. Experts concur that between three million and 1.5 million years ago, multiple hominid species existed alongside one another at least occasionally. Now some scholars argue that this rash of discoveries demonstrates that human evolution was

ILLUSTRATIONS BY PATRICIA J. WYNNE AND CORNELIA BLIK



a complex affair from the outset. Toronto's Begun—who believes that the Miocene ape ancestors of modern African apes and humans spent their evolutionarily formative years in Europe and western Asia before reentering Africa—observes that *Sahelanthropus* bears exactly the kind of motley features that one would expect to see in an animal that was part of an adaptive radiation of apes moving into a new milieu. "It would not surprise me if there were 10 or 15 genera of things that are more closely related to *Homo* than to chimps," he says. Likewise, in a commentary that accompanied the report by Brunet and his team in *Nature,* Bernard Wood of George Washington University wondered whether *Sahelanthropus* might hail from the African ape equivalent of Canada's famed Burgess Shale, which has yielded myriad invertebrate fossils from the Cambrian period, when the major modern animal groups exploded into existence. Viewed that way, the human evolutionary tree would look more like an unkempt bush, with some, if not all, of the new discoveries occupying terminal twigs instead of coveted spots on the meandering line that led to humans.

Other workers caution against inferring the existence of multiple, coeval hominids on the basis of what has yet been found. "That's *X-Files* paleontology," White quips. He and Brunet both note that between seven million and four million years ago, only one hominid species is known to have existed at any given time. "Where's the bush?" Brunet demands. Even at humanity's peak diversity, two million years ago, White says, there were only three taxa sharing the landscape. "That ain't the Cambrian explosion," he remarks dryly. Rather, White suggests, there is no evidence that the base of the family tree is anything other than a trunk. He thinks that the new finds might all represent snapshots of the *Ardipithecus* lineage through time, with *Sahelanthropus* being the earliest hominid and with *Orrorin* and *A. r. kadabba* representing its lineal descendants. (In this configuration, *Sahelanthropus* and *Orrorin* would become species of *Ardipithecus*.)

Investigators agree that more fossils are needed to elucidate how *Orrorin, A. r. kadabba* and *Sahelanthropus* are related to one another and to ourselves, but obtaining a higher-resolution picture of the roots of humankind won't be easy. "We're going to have a lot of trouble diagnosing the very earliest members of our clade the closer we get to that last common ancestor," Missouri's Ward predicts. Nevertheless, "it's really important to sort out what the starting point was," she observes. "Why the human lineage began is the question we're trying to answer, and these new finds in some ways may hold the key to answering that question—or getting closer than we've ever gotten before."

It may be that future paleoanthropologists will reach a point at which identifying an even earlier hominid will be well nigh impossible. But it's unlikely that this will keep them from trying. Indeed, it would seem that the search for the first hominids is just heating up. "The *Sahelanthropus* cranium is a messenger [indicating] that in central Africa there is a desert full of fossils of the right age to answer key questions about the genesis of our clade," White reflects. For his part, Brunet, who for more than a quarter of a century has doggedly pursued his vision through political unrest, sweltering heat and the blinding sting of an unrelenting desert wind, says that ongoing work in Chad will keep his team busy for years to come. "This is the beginning of the story," he promises, "just the beginning." As I sit in Brunet's office contemplating the seven-million-year-old skull of *Sahelanthropus,* the fossil hunter's quest doesn't seem quite so unimaginable. Many of us spend the better part of a lifetime searching for ourselves. SA

Kate Wong is editorial director of ScientificAmerican.com

MORE TO EXPLORE

Late Miocene Hominids from the Middle Awash, Ethiopia. Yohannes Haile-Selassie in *Nature,* Vol. 412, pages 178–181; July 12, 2001.

Extinct Humans. Ian Tattersall and Jeffrey H. Schwartz. Westview Press, 2001.

Bipedalism in *Orrorin tugenensis* Revealed by Its Femora. Martin Pickford, Brigitte Senut, Dominique Gommercy and Jacques Treil in *Comptes Rendus: Palevol,* Vol. 1, No. 1, pages 1–13; 2002.

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The Primate Fossil Record. Edited by Walter C. Hartwig. Cambridge University Press, 2002.

early hominid fossils from AFRICA

The year was 1965.

Bryan Patterson, a paleoanthropologist from Harvard University, unearthed a fragment of a fossil arm bone at a site called Kanapoi in northern Kenya. He and his colleagues knew it would be hard to make a great deal of anatomical or evolutionary sense out of a small piece of elbow joint. Nevertheless, they did recognize some features reminiscent of a species of early hominid (a hominid is any upright-walking primate) known as *Australopithecus,* first discovered 40 years earlier in South Africa by Raymond Dart of the University of the Witwatersrand. In most details, however, Patterson and his team considered the fragment of arm bone to be more like those of modern humans than the one other *Australopithecus* humerus known at the time.

And yet the age of the Kanapoi fossil proved somewhat surprising. Although the techniques for dating the rocks where the fossil was uncovered were still fairly rudimentary, the group working in Kenya was able to show that the bone was probably older than the various *Australopithecus* specimens that had previously been found. Despite this unusual result, however, the significance of Patterson's discovery was not to be confirmed for another 30 years. In the interim, researchers identified the remains of so many important early hominids that the humerus from Kanapoi was rather forgotten.

AUSTRALOPITHECUS ANAMENSIS (*right*) lived roughly four million years ago. Only a few *anamensis* fossils have been found—the ones shown at the left include a jawbone and part of the front of the face (*left*), parts of an arm bone (*center*) and fragments of a lower leg bone (*right*)—and thus researchers cannot determine much about the species' physical appearance. But scientists have established that *anamensis* walked upright, making it the earliest bipedal creature yet to be discovered.

MATT MAHURIN (*illustration*); ROBERT CAMPBELL (*left*); ALAN WALKER; © NATIONAL MUSEUMS OF KENYA (*center* and *right*)

Yet Patterson's fossil would eventually help establish the existence of a new species of *Australopithecus*—the oldest yet to be identified—and push back the origins of upright walking to more than four million years ago. But to see how this happened, we need to trace the steps that paleoanthropologists have taken in constructing an outline for the story of hominid evolution.

An Evolving Story

SCIENTISTS CLASSIFY the immediate ancestors of the genus *Homo* (which includes our own species, *Homo sapiens*) in the genus *Australopithecus.* For several decades it was believed that these ancient hominids first inhabited the earth at least three and a half million years ago. The specimens found in South Africa by Dart and others indicated that there were at least two types of *Australopithecus*—*A. africanus* and *A. robustus.* The leg bones of both species suggested that they had the striding, bipedal locomotion that is a hallmark of humans among living mammals. (The upright posture of these creatures was vividly confirmed in 1978 at the Laetoli site in Tanzania, where a team led by archaeologist Mary Leakey discovered a spectacular series of footprints made 3.6 million years ago by three *Australopithecus* individuals as they walked across wet volcanic ash.) Both *A. africanus* and *A. robustus* were relatively small-brained and had canine teeth that differed from

Updated from the June 1997 issue

A new species of *Australopithecus,* the ancestor of *Homo,* pushes back the origins of bipedalism to some four million years ago

By Meave Leakey and Alan Walker

those of modern apes in that they hardly projected past the rest of the tooth row. The younger of the two species, *A. robustus,* had bizarre adaptations for chewing—huge molar and premolar teeth combined with bony crests on the skull where powerful chewing muscles would have been attached.

Paleoanthropologists identified more species of *Australopithecus* over the next several decades. In 1959 Mary Leakey unearthed a skull from yet another East African species closely related to *robustus*. Skulls of these species uncovered during the past 45 years in the northeastern part of Africa, in Ethiopia and Kenya, differed considerably from those found in South Africa; as a result, researchers think that two separate *robustus*-like species—a northern one and a southern one—existed.

In 1978 Donald C. Johanson, now at the Institute of Human Origins at Arizona State University, along with his colleagues, identified still another species of *Australopithecus*. Johanson and his team had been studying a small number of hominid bones and teeth discovered at Laetoli, as well as a large and very important collection of specimens from the Hadar region of Ethiopia (including the famous "Lucy" skeleton). The group named the new species *afarensis*. Radiometric dating revealed that the species had lived between 3.6 and 2.9 million years ago, making it the oldest *Australopithecus* known at the time.

This early species is probably the best studied of all the *Australopithecus* recognized so far, and it is certainly the one that has generated the most controversy over the past 30 years. The debates have ranged over many issues: whether the *afarensis* fossils were truly distinct from the *africanus* fossils from South Africa; whether there was one or several species at Hadar; whether the Tanzanian and Ethiopian fossils were of the same species; and whether the fossils had been dated correctly.

But the most divisive debate concerns the issue of how extensively the bipedal *afarensis* climbed in trees. Fossils of *afarensis* include various bone and joint structures typical of tree climbers. Some scientists argue that such characteristics indicate that these hominids must have spent at least some time in the trees. But others view these features as simply evolutionary baggage, left over from arboreal ancestors. Underlying this discussion is the question of where *Australopithecus* lived—in forests or on the open savanna.

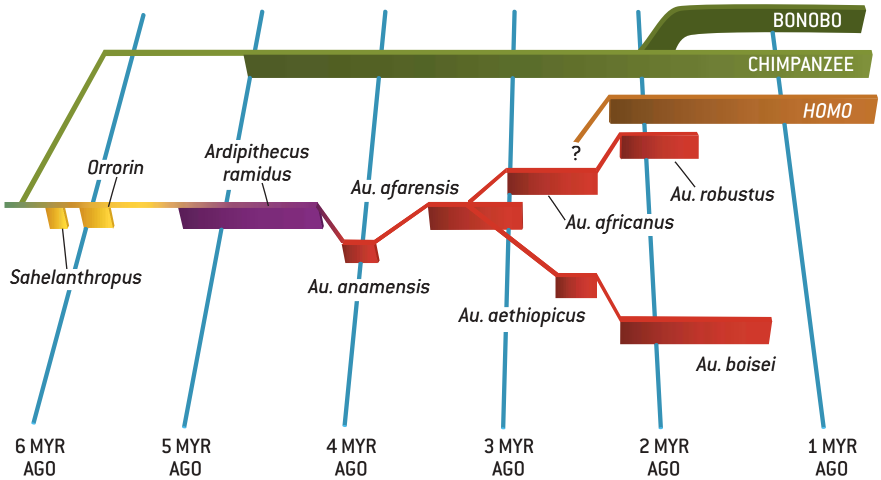
By the beginning of the 1990s, researchers knew a fair amount about the various species of *Australopithecus* and how each had adapted to its environmental niche. A description of any one of the species would mention that the creatures were bipedal and that they had ape-size brains and large, thickly enameled teeth in strong jaws, with nonprojecting canines. Males were typically larger than females, and individuals grew and matured rapidly. But the origins of *Australopithecus* were only hinted at, because the gap between the earliest well-known species in the group (*afarensis*, from about 3.6 million years ago) and the postulated time of the last common ancestor of chimpanzees and humans (about six million years ago, according to molecular evidence) was still very great. Fossil hunters had unearthed only a few older fragments of bone, tooth and jaw from the intervening 1.5 million years to indicate the anatomy and course of evolution of the earliest hominids.

Filling the Gap

DISCOVERIES IN KENYA over the past several years have filled in some of the missing interval between 3.5 million and 5 million years ago. Beginning in 1982, expeditions run by the National Museums of Kenya to the Lake Turkana basin in northern Kenya began finding hominid fossils nearly four million years old. But because these fossils were mainly isolated teeth—no jawbones or skulls were preserved—very little could be said about them except that they resembled the remains of *afarensis* from Laetoli. But our excavations at an unusual site, just inland from Allia Bay on the east side of Lake Turkana [*see maps on page 18*], yielded more complete fossils.

THE AUTHORS

MEAVE LEAKEY and *ALAN WALKER*, together with Leakey's husband, Richard, have collaborated for many years on the discovery and analysis of early hominid fossils from Kenya. Meave Leakey is a researcher and former head of the division of paleontology at the National Museums of Kenya in Nairobi. Walker is Evan Pugh Professor of Anthropology and Biology at Pennsylvania State University. He is a MacArthur Fellow and a member of the American Academy of Arts and Sciences.



FAMILY TREE of the hominid *Australopithecus* (*red*) includes a number of species that lived between roughly 4 million and 1.25 million years (Myr) ago. Just over 2 Myr ago a new genus, *Homo* (which includes our own species, *H. sapiens*), evolved from one of the species of *Australopithecus.*

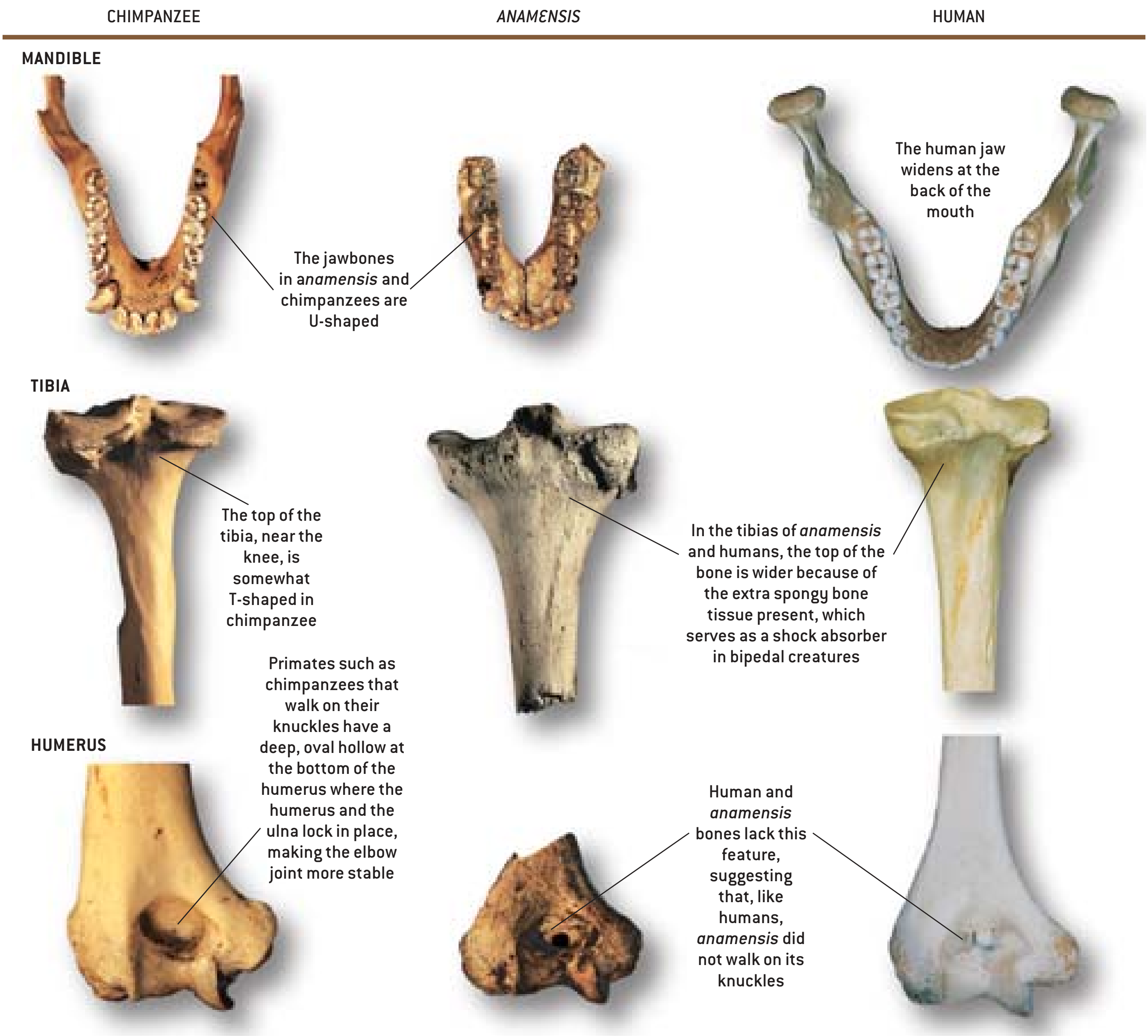
SLIM FILMS

The site at Allia Bay is a bone bed, where millions of fragments of weathered tooth and bone from a wide variety of animals, including hominids, spill out of the hillside. Exposed at the top of the hill lies a layer of hardened volcanic ash called the Moiti Tuff, which has been dated radiometrically to just over 3.9 million years old. The fossil fragments lie several meters below the tuff, indicating that the remains are older than the tuff. We do not yet understand fully why so many fossils are concentrated in this spot, but we can be certain that they were deposited by the precursor of the present-day Omo River.

Today the Omo drains the Ethiopian highlands located to the north, emptying into Lake Turkana, which has no outlet. But this has not always been so. Our colleagues Frank Brown of the University of Utah and Craig Feibel of Rutgers University have shown that the ancient Omo River dominated the Turkana area for much of the Pliocene (roughly 5.3 to 1.8 million years ago) and the early Pleistocene (1.8 to 0.7 million years ago). Only infrequently was a lake present in the area at all. Instead, for most of the past four million years, an extensive river system flowed across the broad floodplain, proceeding to the Indian Ocean without dumping its sediments into a lake.

The Allia Bay fossils are located in one of the channels of this ancient river system. Most of the fossils collected from Allia Bay are rolled and weathered bones and teeth of aquatic animals—fish, crocodiles, hippopotamuses and the like—that were damaged during transport down the river from some distance away. But some of the fossils are much better preserved; these come from the animals that lived on or near the riverbanks. Among these creatures are several different species of leaf-eating monkeys, related to modern colobus monkeys, as well as antelopes whose living relatives favor closely wooded areas. Reasonably well preserved hominid fossils can also be found here, suggesting that, at least occasionally, early hominids inhabited a riparian habitat.

Where do these *Australopithecus* fossils fit in the evolutionary history of hominids? The jaws and teeth from Allia Bay, as well as a nearly complete radius (the outside bone of the forearm) from the nearby sediments of Sibilot just



FOSSILS from *anamensis* (*center*) share a number of features in common with both humans (*right*) and modern chimpanzees (*left*). Scientists use the similarities and differences among these species to determine their interrelationships and thereby piece together the course of hominid evolution since the lineages of chimpanzees and humans split some five or six million years ago.

ALAN WALKER; © NATIONAL MUSEUMS OF KENYA (*chimpanzee* and *anamensis*); VIDEO SURGERY *Photo Researchers, Inc.* (*human*)

to the north, show an interesting mixture of characteristics. Some of the traits are primitive ones—that is, they are ancestral features thought to be present before the split occurred between the chimpanzee and human lineages. Yet these bones also share characteristics seen in later hominids and are therefore said to have more advanced features. As our team continues to unearth more bones and teeth at Allia Bay, these new fossils add to our knowledge of the wide range of traits present in early hominids.

Across Lake Turkana, some 145 kilometers (about 90 miles) south of Allia Bay, lies the site of Kanapoi, where our story began. One of us (Leakey) has mounted expeditions from the National Museums of Kenya to explore the sediments located southwest of Lake Turkana and to document the faunas present during the earliest stages of the basin's history. Kanapoi, virtually unexplored since Patterson's day, has proved to be one of the most rewarding sites in the Turkana region.

A series of deep erosion gullies, known as badlands, has exposed the sediments at Kanapoi. Fossil hunting is difficult here, though, because of a carapace of lava pebbles and gravel that makes it hard to spot small bones and teeth. Studies of the layers of sediment, also carried out by Feibel, reveal that the fossils here have been preserved by deposits from a river ancestral to the present-day Kerio River, which once flowed into the Turkana basin and emptied into an ancient lake that we call Lonyumun. This lake reached its maximum size about 4.1 million years ago and thereafter shrank as it filled with sediments.

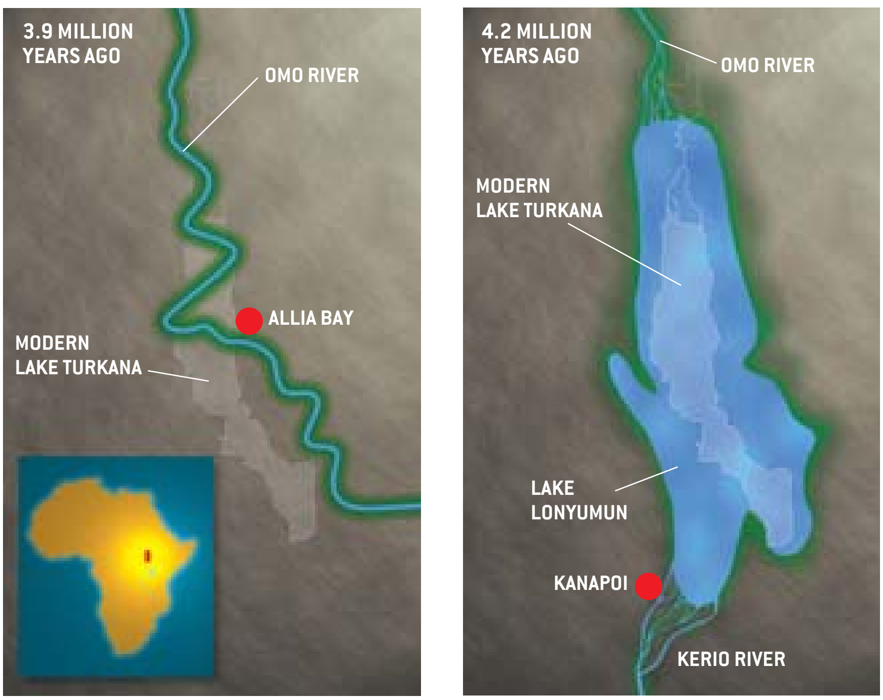
Excavations at Kanapoi have primarily yielded the remains of carnivore meals, so the fossils are rather fragmentary. But workers at the site have also recovered two nearly complete lower jaws, one complete upper jaw and lower face, the upper and lower thirds of a tibia, bits of skull and several sets of isolated teeth. After careful study of the fossils from both Allia Bay and Kanapoi—including Patterson's fragment of an arm bone—we felt that in details of anatomy, these specimens were different enough from previously known hominids to warrant designating a new species. So in 1995, in collaboration with both Feibel and Ian McDougall of the Australian National University, we named this new species *Australopithecus anamensis,* drawing on the Turkana word for "lake" (*anam*) to refer to both the present and ancient lakes.

To establish the age of these fossils, we relied on the extensive efforts of Brown, Feibel and McDougall, who have been investigating the paleogeographic history of the entire lake basin. If their study of the basin's development is correct, the *anamensis* fossils should be between 4.2 and 3.9 million years old. McDougall has determined the age of the so-called Kanapoi Tuff—the layer of volcanic ash that covers most of the fossils at this site—to be just over four million years old. Now that he has successfully ascertained the age of the tuff, we are confident in both the age of the fossils and Brown's and Feibel's understanding of the history of the lake basin.

A major question in paleoanthropology today is how the anatomical mosaic of the early hominids evolved. By comparing the nearly contemporaneous Allia Bay and Kanapoi collections of *anamensis,* we can piece together a fairly accurate picture of certain aspects of the species, even though we have not yet uncovered a complete skull.

The jaws of *anamensis* are primitive—the sides sit close together and parallel to each other (as in modern apes), rather than widening at the back of the mouth (as in later hominids, including humans). In its lower jaw, *anamensis* is also chimplike in terms of the shape of the region where the left and right sides of the jaw meet (technically known as the mandibular symphysis).

Teeth from *anamensis,* however, appear more advanced. The enamel is relatively thick, as it is in all other species of *Australopithecus;* in contrast, the tooth enamel of African great apes is much thinner. The thickened enamel suggests *anamensis* had already adapted to a changed diet—possibly much harder food—even though its jaws and some skull features were still very apelike. We also know that *anamensis* had only a tiny external ear canal. In this regard, it is more like chimpanzees and unlike all later hominids, including humans, which have large external ear canals. (The size of the external canal is unrelated to the size of the fleshy ear.)



TURKANA BASIN was home to *anamensis* roughly four million years ago. Around 3.9 million years ago a river sprawled across the basin (*left*). The fossil site Allia Bay sat within the strip of forest (*green*) that lined this river. Some 4.2 million years ago a large lake filled the basin (*right*); a second site, Kanapoi, was located on a river delta that fed into the lake.

SLIM FILMS; SOURCE: FRANK BROWN AND CRAIG FEIBEL (1991)

The most informative bone of all the ones we have uncovered from this new hominid is the nearly complete tibia—the larger of the two bones in the lower leg. The tibia is revealing because of its important role in weight bearing: the tibia of a biped is distinctly different from the tibia of an animal that walks on all four legs. In size and practically all details of the knee and ankle joints, the tibia found at Kanapoi closely resembles the one from the fully bipedal *afarensis* found at Hadar, even though the latter specimen is almost a million years younger.

Fossils of other animals collected at Kanapoi point to a somewhat different paleoecological scenario from the setting across the lake at Allia Bay. The channels of the river that laid down the sediments at Kanapoi were probably lined with narrow stretches of forest that grew close to the riverbanks in otherwise open country. Researchers have recovered the remains of the same spiral-horned antelope found at Allia Bay that very likely lived in dense thickets. But open-country antelopes and hartebeest appear to have lived at Kanapoi as well, suggesting that more open savanna prevailed away from the rivers. These results offer equivocal evidence regarding the preferred habitat of *anamensis*: we know that bushland was present at both sites that have yielded fossils of the species, but there are clear signs of more diverse habitats at Kanapoi.

An Even Older Hominid?

AT ABOUT THE SAME TIME that we were finding new hominids at Allia Bay and Kanapoi, a team led by our colleague Tim D. White of the University of California at Berkeley discovered fossil hominids in Ethiopia that are even older than *anamensis*. In 1992 and 1993 White led an expedition to the Middle Awash area of Ethiopia, where his team uncovered hominid fossils at a site known as Aramis. The group's finds include isolated teeth, a piece of a baby's mandible (the lower jaw), fragments from an adult's skull and some arm bones, all of which have been dated to around 4.4 million years ago. In 1994, together with his colleagues Berhane Asfaw of the Paleoanthropology Laboratory in Addis Ababa and Gen Suwa of the University of Tokyo, White gave these fossils a new name: *Australopithecus ramidus.* In 1995 the group renamed the fossils, moving them to a new genus, *Ardipithecus.* Earlier fossils of this genus have now been found dating back to 5.8 million years ago. Other fossils buried near the hominids, such as seeds and the bones of forest monkeys and antelopes, strongly imply that these hominids, too, lived in a closed-canopy woodland.

This new species represents the most primitive hominid known—a link between the African apes and *Australopithecus.* Many of the *Ardipithecus ramidus* fossils display similarities to the anatomy of the modern African great apes, such as thin dental enamel and strongly built arm bones. In other features, though—such as the opening at the base of the skull, technically known as the foramen magnum, through which the spinal cord connects to the brain—the fossils resemble later hominids.

Describing early hominids as either primitive or more advanced is a complex issue. Scientists now have almost decisive molecular evidence that humans and chimpanzees once had a common ancestor and that this lineage had previously split from gorillas. This is why we often use the two living species of chimpanzee (*Pan troglodytes* and *P. paniscus*) to illustrate ancestral traits. But we must remember that since their last common ancestor with humans, chimpanzees have had exactly the same amount of time to evolve as humans have. Determining which features were present in the last common ancestor of humans and chimpanzees is not easy.

But *Ardipithecus,* with its numerous chimplike features, appears to have taken the human fossil record back close to the time of the chimp-human split. More recently, White and his group have found parts of a single *Ardipithecus* skeleton in the Middle Awash region. As White and his team extract these exciting new fossils from the enclosing stone, reconstruct them and prepare them for study, the paleoanthropological community eagerly anticipates the publication of the group's analysis of these astonishing finds.

But even pending White's results, new fossil discoveries are offering other surprises. A team led by Michel Brunet of the University of Poitiers has found fragments of *Australopithecus* fossils in Chad. Surprisingly, these fossils were recovered far from either eastern or southern Africa, the only areas where *Australopithecus* had appeared. The Chad sites lie 2,500 kilometers west of the western part of the Rift Valley, thus extending the range of *Australopithecus* well into the center of Africa.

These fossils debunk a hypothesis about human evolution postulated by Dutch primatologist Adriaan Kortlandt and expounded in *Scientific American* by Yves Coppens of the College of France [see "East Side Story: The Origin of Humankind," May 1994]. This idea was that the formation of Africa's Rift Valley subdivided a single ancient species, isolating the ancestors of hominids on the east side from the ancestors of modern apes on the west side.

Brunet's latest discovery, an important cranium older than six million years, is also from Chad and shows that early hominids were probably present across much of the continent. This cranium, which the team called *Sahelanthropus tchadensis,* together with fragmentary jaws and limb bones from about six million years ago in Kenya [see "An Ancestor to Call Our Own," on page 4], are even older than the *Ardipithecus* fossils.

FOSSIL HUNTER Alan Walker (*foreground*) and two colleagues excavate the bone bed at Allia Bay, where several *anamensis* fossils have been recovered. The bone bed appears as a dark band about 18 inches thick at the top of the trench.

The significance of these exciting discoveries is now the center of an active debate.

The fossils of *anamensis* that we have identified should also provide some answers in the long-standing debate over whether early *Australopithecus* species lived in wooded areas or on the open savanna. The outcome of this discussion has important implications: for many years, paleoanthropologists have accepted that upright-walking behavior originated on the savanna, where it most likely provided benefits such as keeping the hot sun off the back or freeing hands for carrying food. Yet our evidence suggests that the earliest bipedal hominid known to date lived at least part of the time in wooded areas. The discoveries of the past several years represent a remarkable spurt in the sometimes painfully slow process of uncovering human evolutionary past. But clearly there is still much more to learn. SA

MORE TO EXPLORE

Australopithecus ramidus, a New Species of Early Hominid from Aramis, Ethiopia. Tim D. White, Gen Suwa and Berhane Asfaw in *Nature,* Vol. 371, pages 306–312; September 22, 1994.

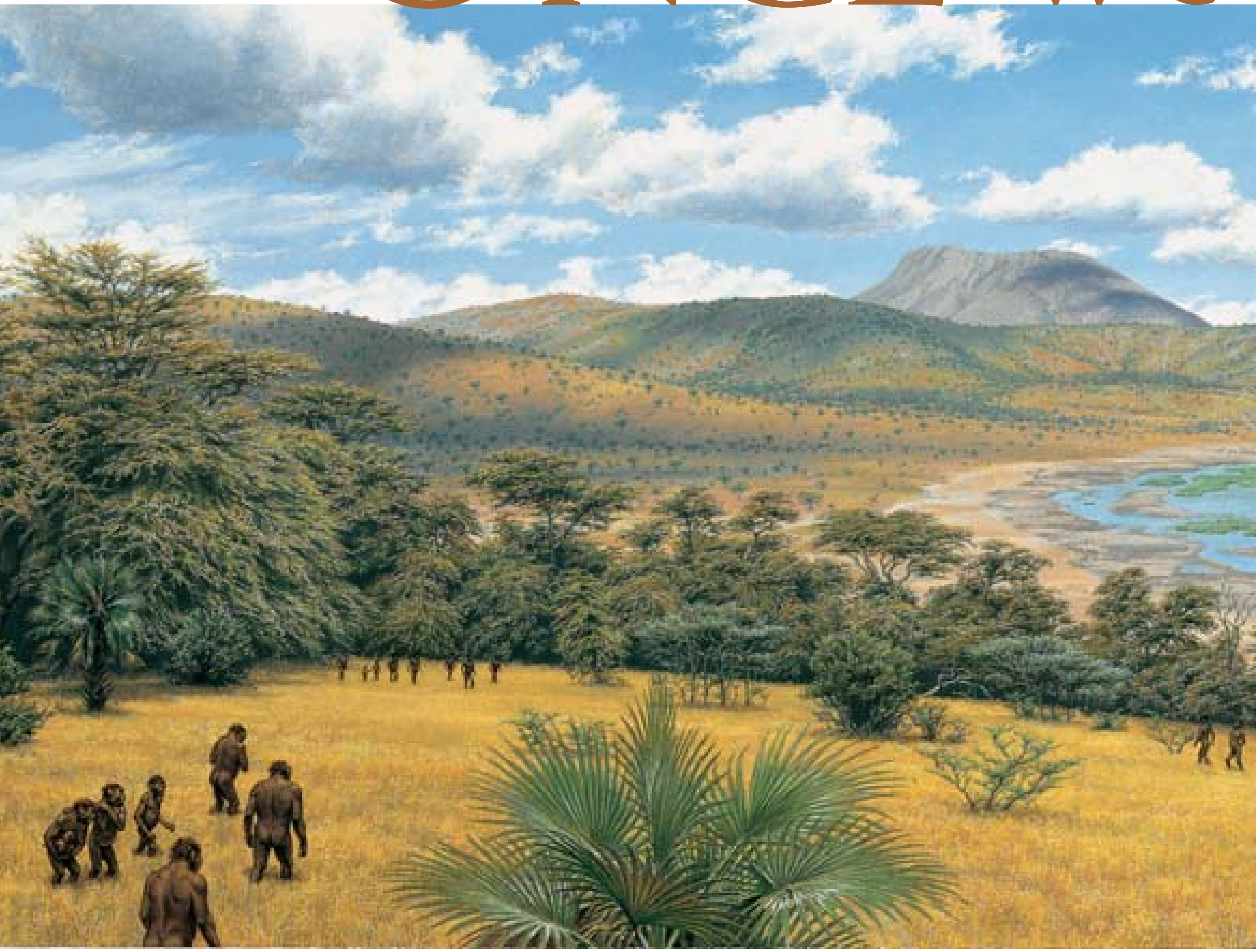
New Four-Million-Year-Old Hominid Species from Kanapoi and Allia Bay, Kenya. Meave G. Leakey, Craig S. Feibel, Ian McDougall and Alan Walker in *Nature,* Vol. 376, pages 565–571; August 17, 1995.

From Lucy to Language. Donald C. Johanson and Blake Edgar. Simon & Schuster, 1996.

The Earliest Known _Australopithecus, A. anamensis._ C. V. Ward, M. G. Leakey and A. Walker in *Journal of Human Evolution,* Vol. 41, pages 255–368; 2001.

TODAY WE TAKE FOR GRANTED THAT *HOMO SAPIENS* FOUR MILLION YEARS MANY HOMINID SPECIES

ONCE we

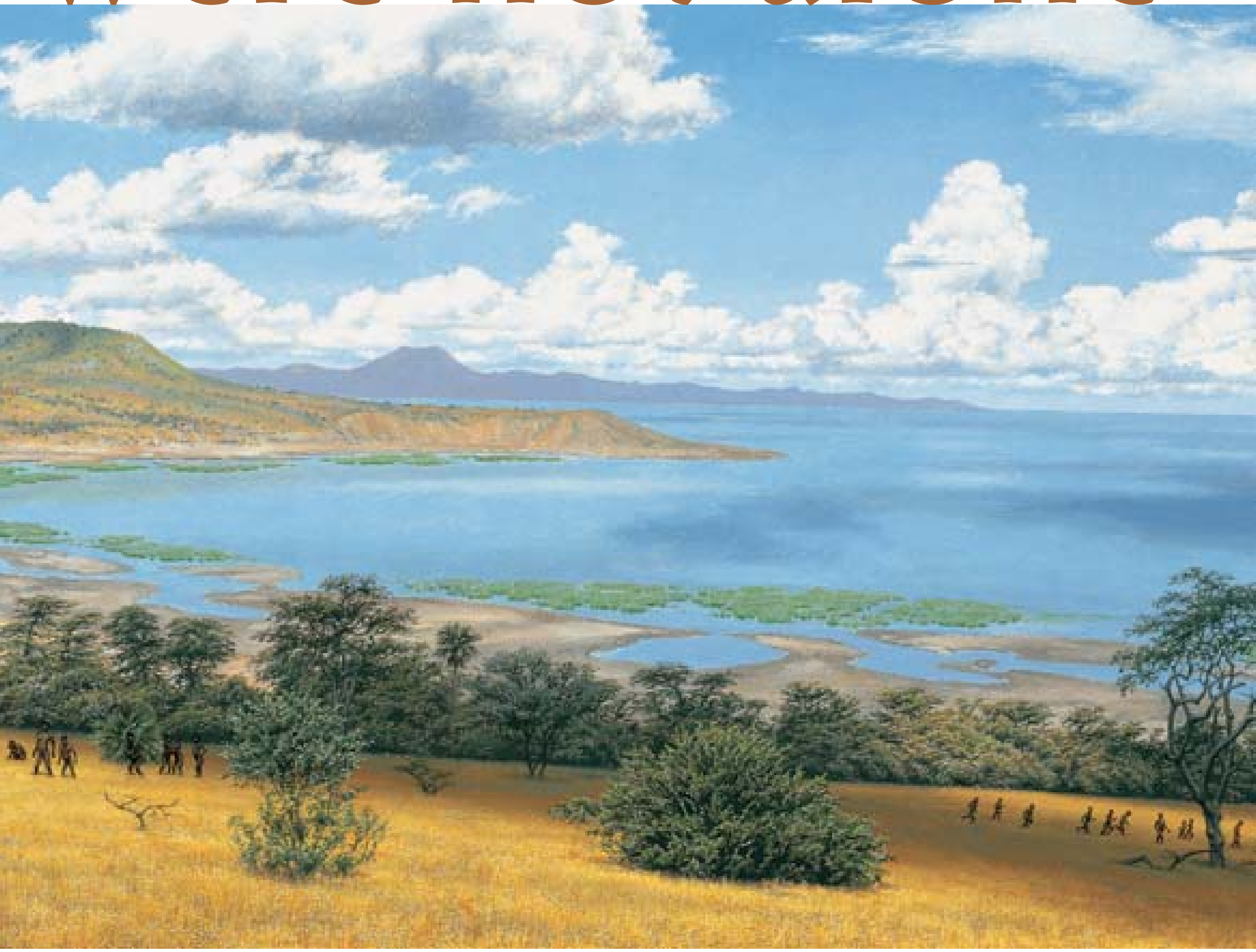


SHARING A SINGLE LANDSCAPE, four kinds of hominids lived about 1.8 million years ago in what is now part of northern Kenya. Although paleoanthropologists have no idea how—or if—these different species interacted, they do know that *Paranthropus boisei, Homo rudolfensis, H. habilis* and *H. ergaster* foraged in the same area around Lake Turkana.

 Updated from the January 2000 issue

IS THE ONLY HOMINID ON EARTH. YET FOR AT LEAST
SHARED THE PLANET. WHAT MAKES US DIFFERENT?

were not alone



By Ian Tattersall • Paintings by Jay H. Matternes

Homo sapiens has had the earth to itself

for the past 25,000 years or so, free and clear of competition from other members of the hominid family. This period has evidently been long enough for us to have developed a profound feeling that being alone in the world is an entirely natural and appropriate state of affairs.

So natural and appropriate, indeed, that during the 1950s and 1960s a school of thought emerged that claimed, in essence, that only one species of hominid could have existed at a time because there was simply no ecological space on the planet for more than one culture-bearing species. The "single-species hypothesis" was never very convincing—even in terms of the rather sparse hominid fossil record of 40 years ago. But the implicit scenario of the slow, single-minded transformation of the bent and benighted ancestral hominid into the graceful and gifted modern *H. sapiens* proved powerfully seductive—as fables of frogs becoming princes always are.

So seductive that it was only in the late 1970s, following the discovery of incontrovertible fossil evidence that hominid species coexisted some 1.8 million years ago in what is now northern Kenya, that the single-species hypothesis was abandoned. Yet even then, paleoanthropologists continued to cleave to a rather minimalist interpretation of the fossil record. Their tendency was to downplay the number of species and to group together distinctively different fossils under single, uninformative epithets such as "archaic *Homo sapiens.*" As a result, they tended to lose sight of the fact that many kinds of hominids had regularly contrived to coexist.

Although the minimalist tendency persists, recent discoveries and fossil reappraisals make clear that the biological history of hominids resembles that of most other successful animal families. It is marked by diversity rather than by linear progression. Despite this rich history—during which hominid species developed and lived together and competed and rose and fell—*H. sapiens* ultimately emerged as the sole hominid. The reasons for this are generally unknowable, but different interactions between the last coexisting hominids—*H. sapiens* and *H. neanderthalensis*—in two distinct geographical regions offer some intriguing insights.

A Suite of Species

FROM THE BEGINNING, almost from the very moment the earliest hominid biped—the first "australopith"—made its initial hesitant steps away from the forest depths, we have evidence for hominid diversity. The oldest-known potential hominid is *Sahelanthropus tchadensis,* represented by a cranium from the central-western country of Chad [*see illustration on page 26*]. Better known is *Australopithecus anamensis,* from sites in northern Kenya that are about 4.2 million years old.

A. anamensis looks reassuringly similar to the 3.8- to 3.0-million-year-old *Australopithecus afarensis,* a small-brained, big-faced bipedal species to which the famous "Lucy" belonged. Many remnants of *A. afarensis* have been found in various eastern African sites, but some researchers have suggested that the mass of fossils described as *A. afarensis* may contain more than one species, and it is only a matter of time

PARANTHROPUS BOISEI had massive jaws, equipped with huge grinding teeth for a presumed vegetarian diet. Its skull is accordingly strongly built, but it is not known if in body size it was significantly larger than the "gracile" australopiths.

HOMO RUDOLFENSIS was a relatively large-brained hominid, typified by the famous KNM-ER 1470 cranium. Its skull was distinct from the apparently smaller-brained *H. habilis*, but its body proportions are effectively unknown.

until the subject is raised again. In any event, *A. afarensis* was not alone in Africa. A distinctive jaw, from an australopith named *A. bahrelghazali,* was found in 1995 in Chad. It is probably between 3.5 and 3.0 million years old and is thus roughly coeval with Lucy, as is the recently named new form *Kenyanthropus platyops.*

In southern Africa, scientists reported evidence in 1999 of another primitive bipedal hominid species. As yet unnamed and undescribed, this distinctive form is 3.3 million years old. At about three million years ago, the same region begins to yield fossils of *A. africanus,* the first australopith to be discovered (in 1924). This species may have persisted until not much more than two million years ago. A 2.5-million-year-old species from Ethiopia, named *Australopithecus garhi* in 1999, is claimed to fall in an intermediate position between *A. afarensis,* on the one hand, and a larger group that includes more recent australopiths and *Homo,* on the other. Almost exactly the same age is the first representative of the "robust" group of australopiths, *Paranthropus aethiopicus.* This early form is best known from the 2.5-million-year-old "Black Skull" of northern Kenya, and in the period between about 2 and 1.4 million years ago the robusts were represented all over eastern Africa by the familiar *P. boisei.* In South Africa, during the period around 1.6 million years ago, the robusts included the distinctive *P. robustus* and possibly a closely related second species, *P. crassidens.*

I apologize for inflicting this long list of names on readers, but in fact it actually underestimates the number of australopith species that existed. What is more, scientists don't know how long each of these creatures lasted. Nevertheless, even if average species longevity was only a few hundred thousand years, it is clear that from the very beginning the continent of Africa was at least periodically—and most likely continually—host to multiple kinds of hominids.

The appearance of the genus *Homo* did nothing to perturb this pattern. The 2.5- to 1.8-million-year-old fossils from eastern and southern Africa that announce the earliest appearance of *Homo* are an oddly assorted lot and probably a lot more diverse than their conventional assignment to the two species *H. habilis* and *H. rudolfensis* indicates. Still, at Kenya's East Turkana, in the period between 1.9 and 1.8 million years ago, these two species were joined not only by the ubiquitous *P. boisei* but by *H. ergaster,* the first hominid of essentially modern body form. Here, then, is evidence for four hominid species sharing not just the same continent but the same landscape [*see illustration on opposite page and below*].

The first exodus of hominids from Africa, presumably in the form of *H. ergaster* or a close relative, opened a vast prospect for further diversification. One could wish for a better record of this movement, and particularly of its dating, but there are indications that hominids of some kind had reached China and Java by about 1.8 million years ago. A lower jaw that may be about the same age from Dmanisi in ex-Soviet Georgia is different from anything else yet found [see "Out of Africa Again … and Again?" by Ian Tattersall, on page 38]. By the million-year mark *H. erectus* was established in both Java and China, and it is possible that a more robust hominid species was present in Java as well. At the other end of the Eurasian continent, the oldest-known European hominid fragments—from about 800,000 years ago—are highly distinctive and have been dubbed *H. antecessor* by their Spanish discoverers.

About 600,000 years ago, in Africa, we begin to pick up evidence for *H. heidelbergensis,* a species also seen at sites in Europe—and possibly China—between 500,000 to 200,000 years ago. As we learn more about *H. heidelbergensis,* we are likely to find that more than one species is actually represented in this group of fossils. In Europe, *H. heidelbergensis* or a relative gave rise to an endemic group of hominids whose best-known representative was *H. neanderthalensis,* a European and western Asian species that flourished between about 200,000 and 30,000 years ago. The sparse record from Africa suggests that at this time independent develop-

HOMO HABILIS ("handy man") was so named because it was thought to be the maker of the 1.8-million-year-old stone tools discovered at Olduvai Gorge in Tanzania. This hominid fashioned sharp flakes by banging one rock cobble against another.

HOMO ERGASTER, sometimes called "African *H. erectus,*" had a high, rounded cranium and a skeleton broadly similar to that of modern humans. Although *H. ergaster* clearly ate meat, its chewing teeth are relatively small. The best specimen of this hominid is that of an adolescent from about 1.6 million years ago known as Turkana boy.

TUC D'AUDOUBERT CAVE in France was entered sometime between perhaps 11,000 and 13,000 years ago by *H. sapiens*, also called Cro Magnons, who sculpted small clay bison in a recess almost a mile underground.

ments were taking place there, too—including the emergence of *H. sapiens*. And in Java, possible *H. erectus* fossils from Ngandong were dated to around 40,000 years ago, implying that this area had its own indigenous hominid evolutionary history for perhaps millions of years as well.

The picture of hominid evolution just sketched is a far cry from the "*Australopithecus africanus* begat *Homo erectus* begat *Homo sapiens*" scenario that prevailed 40 years ago—and it is, of course, based to a great extent on fossils that have been discovered since that time. Yet the dead hand of linear thinking still lies heavily on paleoanthropology, and even today quite a few of my colleagues would argue that this scenario overestimates diversity. There are various ways of simplifying the picture, most of them involving the cop-out of stuffing all variants of *Homo* of the past half a million or even two million years into the species *H. sapiens*.

My own view, in contrast, is that the 20 or so hominid species invoked (if not named) above represent a minimum estimate. Not only is the human fossil record as we know it full of largely unacknowledged morphological indications of diversity, but it would be rash to claim that every hominid species that ever existed is represented in one fossil collection or another. And even if only the latter is true, it is still clear that the story of human evolution has not been one of a lone hero's linear struggle.

Instead it has been the story of nature's tinkering: of repeated evolutionary experiments. Our biological history has been one of sporadic events rather than gradual accretions. Over the past five million years, new hominid species have regularly emerged, competed, coexisted, colonized new environments and succeeded—or failed. We have only the dimmest of perceptions of how this dramatic history of innovation and interaction unfolded, but it is already evident that our species, far from being the pinnacle of the hominid evolutionary tree, is simply one more of its many terminal twigs.

The Roots of Our Solitude

ALTHOUGH THIS is all true, *H. sapiens* embodies something that is undeniably unusual and is neatly captured by the fact that we are alone in the world today. Whatever that something is, it is related to how we interact with the external world: it is behavioral, which

HOMINIDS of modern body form most likely emerged in Africa around 150,000 years ago and coexisted with other hominids for a time before emerging as the only species of our family. Until about 30,000 years ago, they overlapped with *H. neanderthalensis* (*left*) in Europe and in the Levant, and they may have been contemporaneous with the *H. erectus* (*right*) then living in Java.

means that we have to look to our archaeological record to find evidence of it. This record begins some 2.5 million years ago with the production of the first recognizable stone tools: simple sharp flakes chipped from parent "cores." We don't know exactly who the inventor was, but chances are that he or she was something we might call an australopith.

This landmark innovation represented a major cognitive leap and had profound long-term consequences for hominids. It also inaugurated a pattern of highly intermittent technological change. It was a full million years before the next significant technological innovation came along: the creation about 1.5 million years ago, probably by *H. ergaster*, of the hand ax. These symmetrical implements, shaped from large stone cores, were the first tools to conform to a "mental template" that existed in the toolmaker's mind. This template remained essentially unchanged for another million years or more, until the invention of "prepared-core" tools by *H. heidelbergensis* or a relative. Here a stone core was elaborately shaped in such a way that a single blow would detach what was an effectively finished implement.

Among the most accomplished practitioners of prepared-core technology were the large-brained, big-faced and low-skulled Neandertals, who occupied Europe and western Asia until about 30,000 years ago. Because they left an excellent record of themselves and were abruptly replaced by modern humans who did the same, the Neandertals furnish us with a particularly instructive yardstick by which to judge our own uniqueness. The stoneworking skills of the Neandertals were impressive, if somewhat stereotyped, but they rarely if ever made tools from other preservable materials. And many archaeologists question the sophistication of their hunting skills.

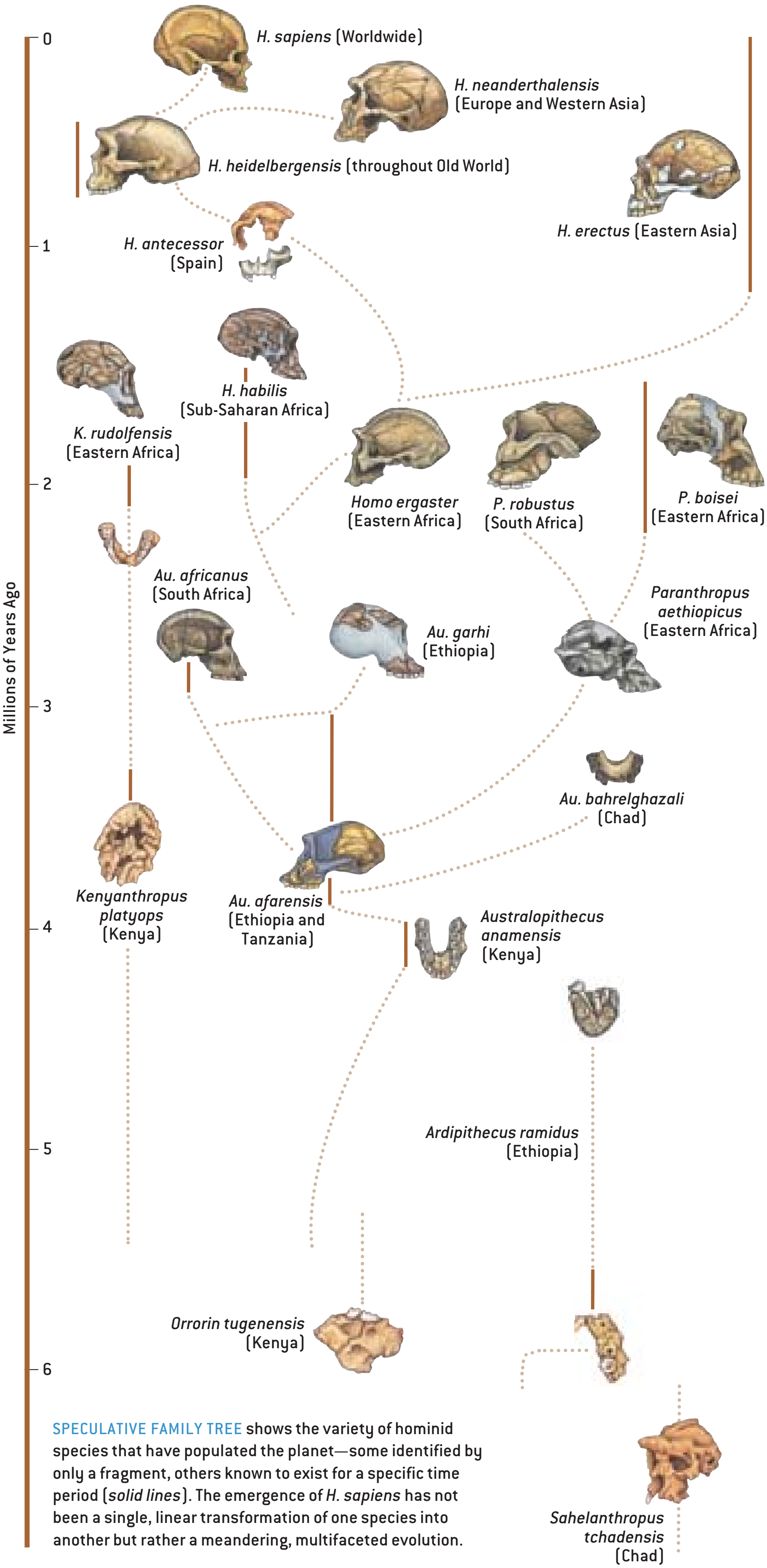
Further, despite misleading early accounts of bizarre Neandertal "bear cults" and other rituals, no substantial evidence has been found for symbolic behaviors among these hominids or for the production of symbolic objects—certainly not before contact had been made with modern humans. Even the occasional Neandertal practice of burying the dead may have been simply a way of discouraging hyenas from making incursions into their living spaces or have a similar mundane explanation. This view arises because Neandertal burials lack the "grave goods" that would attest to ritual and belief in an afterlife. The Neandertals, in other words, though admirable in many ways and for a long time successful in the difficult circumstances of the late ice ages, lacked the spark of creativity that, in the end, distinguished *H. sapiens*.

Although the source of *H. sapiens* as a physical entity is obscure, most evidence points to an African origin perhaps between 150,000 and 200,000 years ago. Modern behavior patterns did not emerge until much later. The best evidence comes from Israel and its surrounding environs, where Neandertals lived about 200,000 years ago or perhaps even earlier. By about 100,000 years ago, they had been joined by anatomically modern *H. sapiens*, and the remarkable thing is that the tools and sites the two hominid species left behind are essentially identical. As far as can be told, these two hominids behaved

THE AUTHOR AND THE ARTIST

IAN TATTERSALL and *JAY H. MATTERNES* have worked together since the early 1990s, notably on the Hall of Human Biology and Evolution at the American Museum of Natural History in New York City and at the Gunma Museum of Natural History in Tomioka, Japan (where the Tuc d'Audoubert mural on the opposite page is installed). Tattersall was born in England and raised in East Africa. He is a curator in the department of anthropology at the American Museum of Natural History. His books include *Becoming Human: Evolution and Human Uniqueness* (Harvest Books, 1999) and *The Last Neanderthal: The Rise, Success, and Mysterious Extinction of Our Closest Human Relatives* (Westview Press, 1999, revised).

Matternes is an artist and sculptor who has for more than 40 years specialized in fossil primates and hominids. In addition to his museum murals, he is well known for his illustrations for books, periodicals and television, including Time/Life Books and *National Geographic*. The research for his depictions has taken him to many parts of the U.S., Canada, Mexico, France, Colombia and Africa.



SPECULATIVE FAMILY TREE shows the variety of hominid species that have populated the planet—some identified by only a fragment, others known to exist for a specific time period (*solid lines*). The emergence of *H. sapiens* has not been a single, linear transformation of one species into another but rather a meandering, multifaceted evolution.

in similar ways despite their anatomical differences. And as long as they did so, they somehow contrived to share the Levantine environment.

The situation in Europe could hardly be more different. The earliest *H. sapiens* sites there date from only about 40,000 years ago, and just 10,000 or so years later the formerly ubiquitous Neandertals were gone. Significantly, the *H. sapiens* who invaded Europe brought with them abundant evidence of a fully formed and unprecedented modern sensibility. Not only did they possess a new "Upper Paleolithic" stoneworking technology based on the production of multiple long, thin blades from cylindrical cores, but they made tools from bone and antler, with an exquisite sensitivity to the properties of these materials.

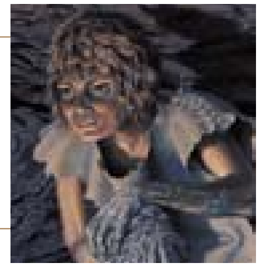
Even more significant, they brought with them art, in the form of carvings, engravings and spectacular cave paintings; they kept records on bone and stone plaques; they made music on wind instruments; they crafted intricate personal adornments; they afforded some of their dead elaborate burials with grave goods (hinting at social stratification in addition to belief in an afterlife, for not all burials were equally fancy); and their living sites were highly organized, with evidence of sophisticated hunting and fishing. The pattern of intermittent technological innovation was gone, replaced by constant refinement. Clearly, these people were *us*.

Competing Scenarios

IN ALL THESE WAYS, early Upper Paleolithic people contrasted dramatically with the Neandertals. Some Neandertals in Europe seem to have picked up new ways of doing things from the arriving *H. sapiens,* but we have no direct clues as to the nature of the interaction between the two species. In light of the Neandertals' rapid disappearance and of the appalling subsequent record of *H. sapiens,* though, we can reasonably surmise that such interactions were rarely happy for the former. Certainly the repeated pattern found at archaeological sites is one of short-term replacement, and there is no convincing biological ev-

PATRICIA J. WYNNE (*drawings*)

The pattern of intermittent technological innovation was gone, replaced by **constant refinement**. *Clearly, these people were* us.



idence of any intermixing of peoples in Europe.

In the Levant, the coexistence ceased—after about 60,000 years or so—at right about the time that Upper Paleolithic–like tools began to appear. About 40,000 years ago the Neandertals of the Levant yielded to a presumably culturally rich *H. sapiens,* just as their European counterparts had.

The key to the difference between the European and the Levantine scenarios lies, most probably, in the emergence of modern cognition—which, it is reasonable to assume, is equivalent to the advent of symbolic thought. Business had continued more or less as usual right through the appearance of modern bone structure, and only later, with the acquisition of fully modern behavior patterns, did *H. sapiens* become completely intolerant of competition from its nearest—and, evidently, not its dearest—co-inhabitors.

To understand how this change in sensibility occurred, we have to recall certain things about the evolutionary process. First, as in this case, all innovations must necessarily arise *within* preexisting species—for where else can they do so? Second, many novelties arise as "exaptations," features acquired in one context before (often long before) being co-opted in a different one. For example, hominids possessed essentially modern vocal tracts for hundreds of thousands of years before the behavioral record gives us any reason to believe that they employed the articulate speech that the peculiar form of this tract permits.

And finally, it is important to bear in mind the phenomenon of emergence—the notion that a chance coincidence gives rise to something totally unexpected. The classic scientific example in this regard is water, whose properties are wholly unpredicted by those of hydrogen and oxygen atoms alone. If we combine these various observations, we can see that, profound as the consequences of achieving symbolic thought may have been, the process whereby it came about was unexceptional.

We have no idea at present how the modern human brain converts a mass of electrical and chemical discharges into what we experience as consciousness. We do know, however, that somehow our lineage passed to symbolic thought from some nonsymbolic precursor state. The only plausible possibility is that with the arrival of anatomically modern *H. sapiens,* existing exaptations were fortuitously linked by a relatively minor genetic innovation to create an unprecedented potential.

Yet even in principle this deduced scenario cannot be the full story, because anatomically modern humans behaved archaically for a long time before adopting modern behaviors. That discrepancy may be the result of the late appearance of some key hardwired innovation not reflected in the skeleton, which is all that fossilizes. But this seems unlikely, because it would have necessitated a wholesale Old World–wide replacement of hominid populations in a very short time, something for which there is no evidence.

It is much more likely that the modern human capacity was born at—or close to—the origin of *H. sapiens,* as an ability that lay fallow until it was activated by a cultural stimulus of some kind. If sufficiently advantageous, this behavioral novelty could then have spread rapidly by cultural contact among populations that already had the potential to acquire it. No population replacement would have been necessary to spread the capability worldwide.

It is impossible to be sure what this innovation might have been, but the best current bet is that it was the invention of language. For language is not simply the medium by which we express our ideas and experiences to one another. Rather it is fundamental to the thought process itself. It involves categorizing and naming objects and sensations in the outer and inner worlds and making associations between resulting mental symbols. It is, in effect, impossible for us to conceive of thought (as we are familiar with it) in the absence of language, and it is the ability to form mental symbols that is the fount of our creativity. Only when we are able to create such symbols can we recombine them and ask such questions as "What if...?"

We do not know exactly how language might have emerged in one local population of *H. sapiens,* although linguists have speculated widely. But we do know that a creature armed with symbolic skills is a formidable competitor—and not necessarily an entirely rational one, as the rest of the living world, including *H. neanderthalensis,* has discovered to its cost. SA

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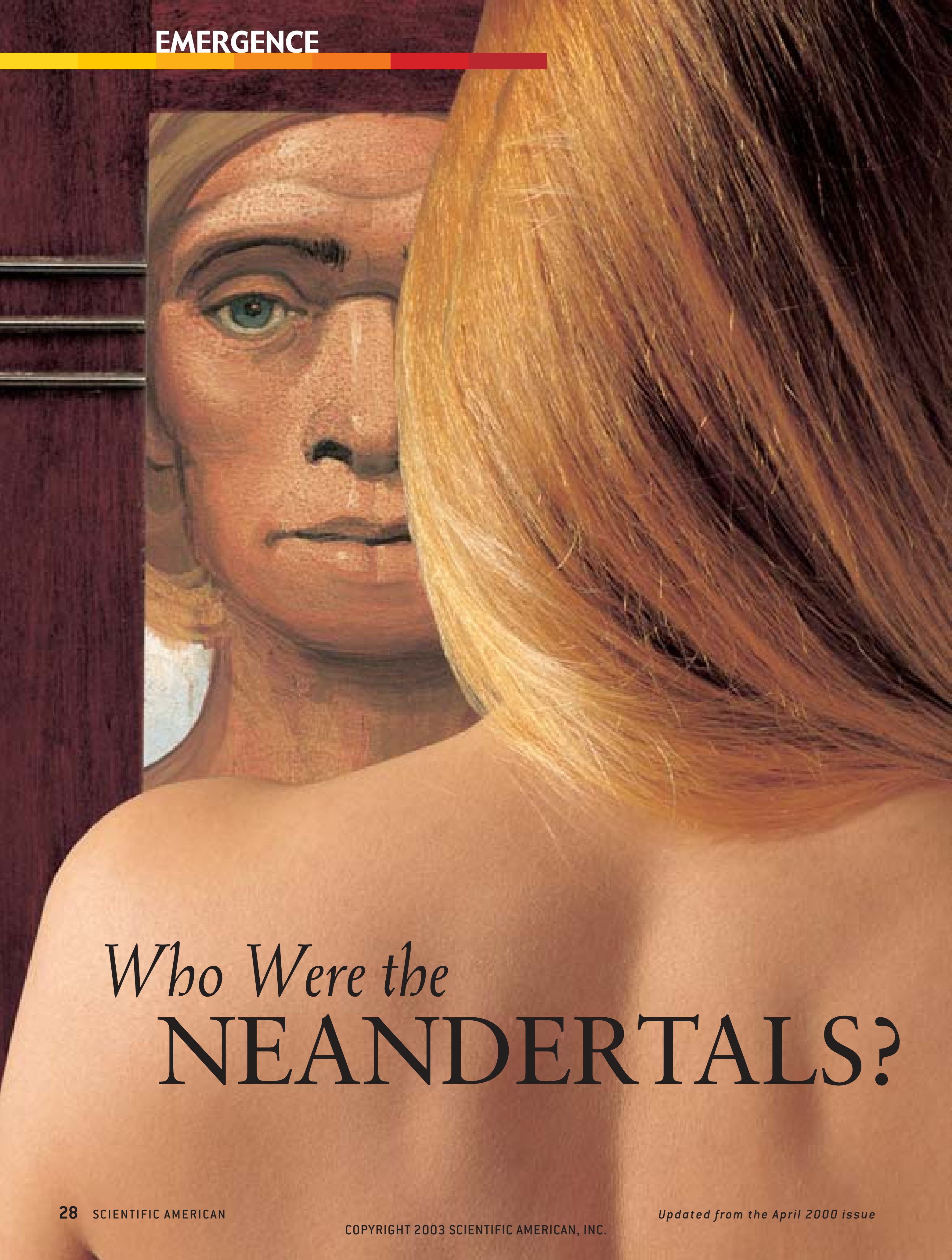


Who Were the NEANDERTALS?

Updated from the April 2000 issue

Controversial evidence indicates that these hominids interbred with anatomically modern humans and sometimes behaved in surprisingly modern ways

By Kate Wong

REFLECTION OF THE PAST reveals a face that is at once familiar and foreign. The 130,000-year-old skull of an adult female from the Krapina rock-shelter in northwestern Croatia inspired this Neandertal reconstruction.

CROATIAN NATURAL HISTORY MUSEUM

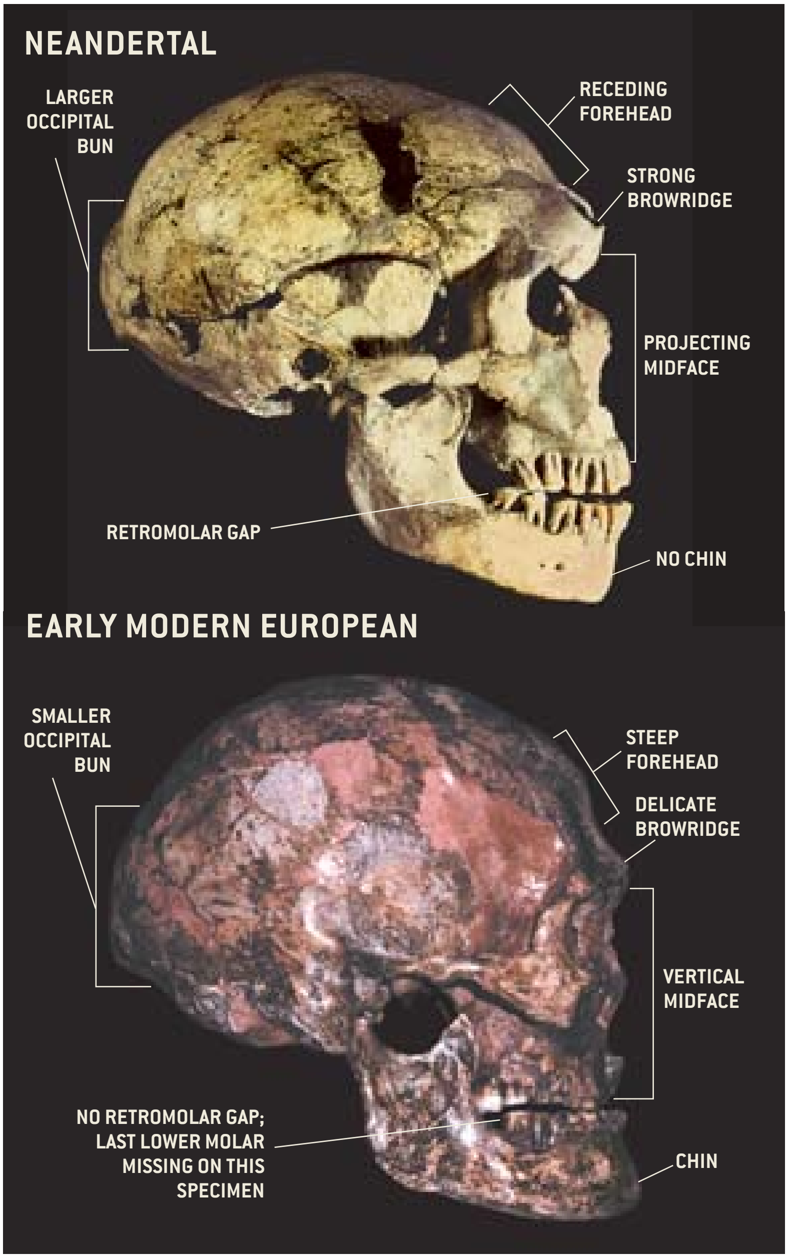
It was such a neat and tidy story.

No match for the anatomically modern humans who swept in with a sophisticated culture and technology, the Neandertals—a separate species—were quickly driven to extinction by the invading moderns. But neat and tidy stories about the past have a way of unraveling, and the saga of the Neandertals, it appears, is no exception. For more than 200,000 years, these large-brained hominids occupied Europe and western Asia, battling the bitter cold of glacial maximums and the daily perils of prehistoric life. Today they no longer exist. Beyond these two facts, however, researchers fiercely debate who the Neandertals were, how they lived and exactly what happened to them.

The steadfast effort to resolve these elusive issues stems from a larger dispute over how modern humans evolved. Some researchers posit that our species arose recently (around 200,000 years ago) in Africa and subsequently replaced archaic hominids around the world, whereas others propose that these ancient populations contributed to the early modern human gene pool. As the best known of these archaic groups, Neandertals are critical to the origins controversy. Yet this is more than an academic argument over certain events of our primeval past, for in probing Neandertal biology and behavior, researchers must wrestle with the very notion of what it means to be fully human and determine what, if anything, makes us moderns unique. Indeed, spurred by recent discoveries, paleoanthropologists and archaeologists are increasingly asking, How much like us were they?

Comparisons of Neandertals and modern humans first captured the attention of researchers when a partial Neandertal skeleton turned up in Germany's Neander Valley in 1856. Those remains—a heavily built skull with the signature arched browridge and massive limb bones—were clearly different, and Neandertals were assigned to their own species, *Homo neanderthalensis* (although even then there was disagreement: several German scientists argued that these were the remains of a crippled Cossack horseman). But it was the French discovery of the famous "Old Man" of La Chapelle-aux-Saints some 50 years later that led to the characterization of Neandertals as primitive protohumans. Reconstructions showed them as stooped, lumbering, apelike brutes, in stark contrast to upright, graceful *Homo sapiens*. The Neandertal, it seemed, represented the ultimate "other," a dim-witted ogre lurking behind the evolutionary threshold of humanity.

Decades later reevaluation of the La Chapelle individual revealed that certain anatomical features had been misinterpreted. In fact, Neandertal posture and movement would have been the same as ours. Since then, paleoanthropologists have struggled to determine whether the morphological features that do characterize Neandertals as a group—such as the robustness of their skeletons, their short limbs and barrel chests, prominent browridges and low, sloping foreheads, protruding midfaces and chinless jaws—warrant designating them as a separate species. Researchers agree that some of these characteristics represent environmental adaptations. The Neandertals' stocky body proportions, for example, would have allowed them to retain heat more effectively in the extremely cold weather brought on by glacial cycles. But other traits, such as the form of the Neander-



CHARACTERISTIC DIFFERENCES are shown between a Neandertal, represented by a French specimen, La Ferrassie 1, and an early modern, Dolní Věstonice 16, from the Czech Republic. Each aspect can be found in both groups, varying in degree and frequency, but they tend to appear as suites of features.

ERIK TRINKAUS/MUSÉE DE L'HOMME (*top*); ARCHEOLOGICKÝ ÚSTAV AVČR (*bottom*)

tal browridge, lack any clear functional significance and seem to reflect the genetic drift typical of isolated populations.

For those scholars who subscribe to the replacement model of modern human origins, the distinctive Neandertal morphology resulted from following an evolutionary trajectory separate from that of moderns. But for years, another faction of researchers has challenged this interpretation, arguing that many of the features that characterize Neandertals are also seen in the early modern Europeans that followed them. "They clearly have a suite of features that are, overall, different, but it's a frequency difference, not an absolute difference," contends David W. Frayer, a paleoanthropologist at the University of Kansas. "Virtually everything you can find in Neandertals you can find elsewhere."

He points to one of the earliest-known modern Europeans, a fossil from a site in southwestern Germany called Vogelherd, which combines the skull shape of moderns with features that are typically Neandertal, such as the distinct space between the last molar and the ascending part of the lower jaw known as a retromolar gap, and the form of the mandibular foramen—a nerve canal in the lower jaw. Additional evidence, according to Frayer and Milford H. Wolpoff of the University of Michigan at Ann Arbor, comes from a group of early moderns discovered in Moravia (Czech Republic) at a site called Mladeč. The Mladeč people, they say, exhibit characteristics on their skulls that other scientists have described as uniquely Neandertal traits.

Although such evidence was once used to argue that Neandertals could have independently evolved into modern Europeans, this view has shifted somewhat. "It's quite clear that people entered Europe as well, so the people that are there later in time are a mix of Neandertals and those populations coming into Europe," says Wolpoff, who believes the two groups differed only as much as living Europeans and aboriginal Australians do. Evidence for mixing also appears in later Neandertal fossils, according to Fred H. Smith, a paleoanthropologist at Loyola University of Chicago. Neandertal remains from Vindija cave in northwestern Croatia reflect "the assimilation of some early modern features," he says, referring to their more modern-shaped browridges and the slight presence of a chin on their mandibles.

Those who view Neandertals as a separate species, however, maintain that the Vindija fossils are too fragmentary to be diagnostic and that any similarities that do exist can be attributed to convergent evolution. These researchers likewise dismiss the mixing argument for the early moderns from Mladeč. "When I look at the morphology of these people, I see robustness, I don't see Neandertal," counters Christopher B. Stringer of the Natural History Museum in London.

Another reason to doubt these claims for interbreeding, some scientists say, is that they contradict the conclusions reached by Svante Pääbo, now at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany, and his colleagues, who in July 1997 announced that they had retrieved and analyzed mitochondrial DNA (mtDNA) from a Neandertal fossil. The cover of the journal *Cell,* which contained their report, was unequivocal: "Neandertals Were Not Our Ancestors." From the short stretch of mtDNA they sequenced, the researchers determined that the difference between the Neandertal mtDNA and living moderns' mtDNA was considerably greater than the differences found among living human populations. But though it seemed on the surface that the species question had been answered, undercurrents of doubt have persisted [see "Ancestral Quandary," by

Kate Wong, News and Analysis, January 1998]. Since then, mtDNA from three more specimens has been retrieved and analyzed, with similarly inconclusive results.

Recent fossil evidence from western Europe has intensified interest in whether Neandertals and moderns mixed. In January 1999 researchers announced the discovery in central Portugal's Lapedo Valley of a largely complete skeleton from a four-year-old child buried 24,500 years ago in the Gravettian style known from other early modern Europeans. According to Erik Trinkaus of Washington University, Cidália Duarte of the Portuguese Institute of Archaeology in Lisbon and their colleagues, the specimen, known as Lagar Velho 1, bears a combination of Neandertal and modern human traits that could only have resulted from extensive interbreeding between the two populations [see "The Hybrid Child from Portugal," on the next page].

If the mixed-ancestry interpretation for Lagar Velho 1 holds up after further scrutiny, the notion of Neandertals as a variant of our species will gain new strength. Advocates of the

GUIDE TO TERMINOLOGY

Neandertal can also be spelled Neanderthal. Around 1900 German orthography changed, and the silent "h" in certain words, such as "thal" (meaning "valley"), was dropped. The designation *Homo neanderthalensis* remains the same, but the common name can be spelled either way.

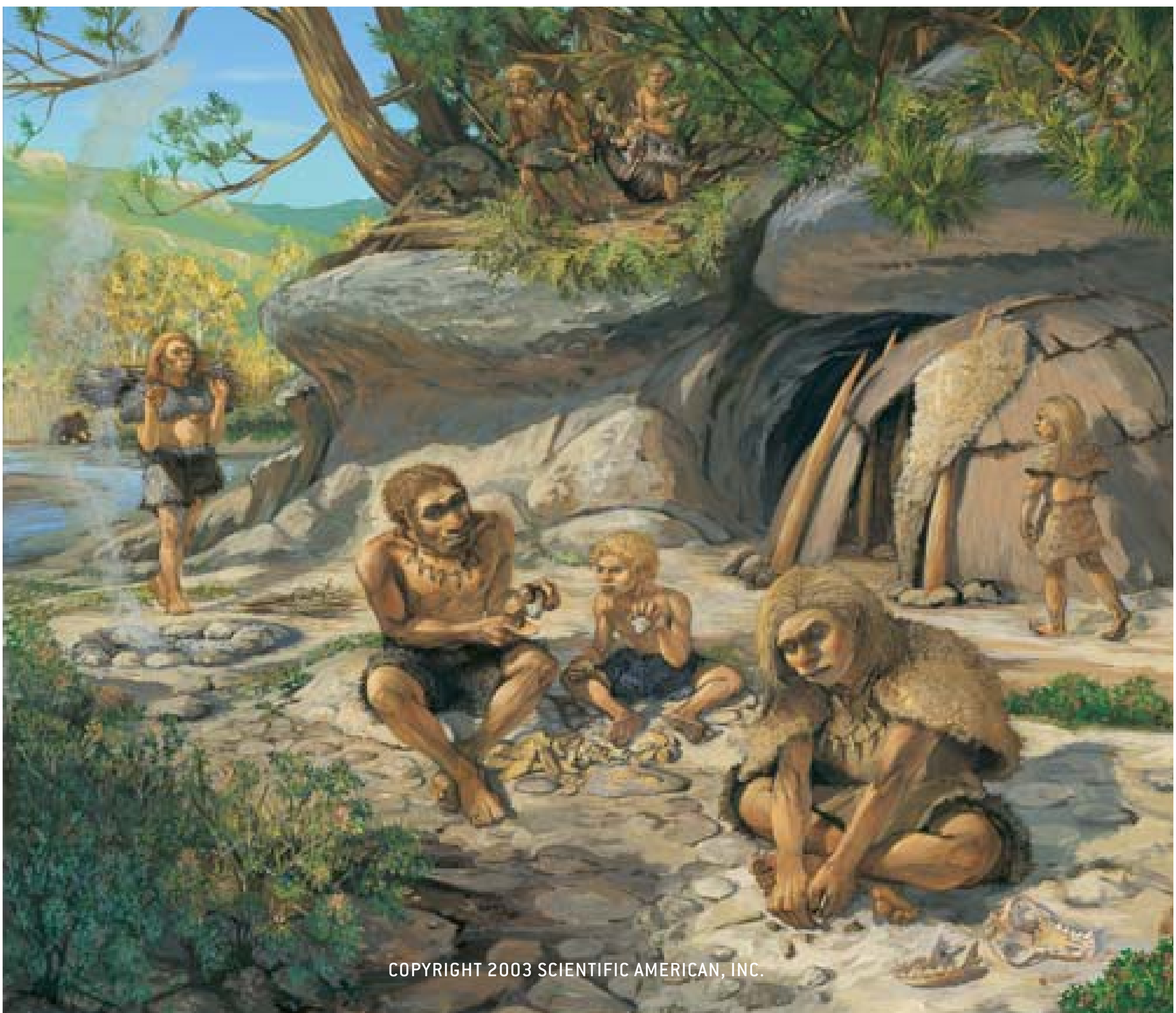
Paleolithic, or Old Stone Age, is the period ranging from the beginning of culture to the end of the last glaciation. It is subdivided into Lower, Middle and Upper stages.

Mousterian is a Middle Paleolithic stone tool–based cultural tradition associated with Neandertals and with early moderns in the Near East.

Aurignacian is an Upper Paleolithic cultural tradition associated with moderns that includes advanced tools and art objects.

Châtelperronian is an Upper Paleolithic cultural tradition associated with Neandertals. It resembles both the Mousterian and the Aurignacian.

DAY IN THE LIFE of Neandertals at the Grotte du Renne in France is imagined here. The Châtelperronian stratigraphic levels have yielded a trove of pendants and advanced bone and stone tools. Such items, along with evidence of huts and hearths, were once linked to modern humans alone, but the Grotte du Renne remains suggest that some Neandertals were similarly industrious.



MICHAEL ROTHMAN

THE HYBRID CHILD FROM PORTUGAL BY ERIK TRINKAUS AND CIDÁLIA DUARTE

ON A CHILLY AFTERNOON in late November 1998, while inspecting the Abrigo do Lagar Velho rock-shelter in central Portugal's Lapedo Valley, two archaeology scouts spotted loose sediment in a rodent hole along the shelter's back wall. Knowing that burrowing animals often bring deeper materials to the surface, one of the scouts reached in to see what might have been unearthed. When he withdrew his hand, he held in it something extraordinary: bones of a human child buried nearly 25,000 years ago.

Subsequent excavation of the burial, led by one of us (Duarte), revealed that the four-year-old had been ceremonially interred—covered with red ocher and laid on a bed of burnt vegetation, along with pierced deer teeth and a marine shell—in the Gravettian style known from modern humans of that time across Europe. Based on the abrupt cultural transition seen in archaeological remains from the Iberian Peninsula, it seemed likely that when moderns moved into the area after 30,000 years ago, they rapidly replaced the native Neandertals. So it stood to reason that this specimen, called Lagar Velho 1, represented an early modern child. In fact, it didn't occur to us at first that it could be anything else.

This wonderfully complete skeleton does have a suite of features that align it predominantly with early modern Europeans. These include a prominent chin and other details of the mandible (lower jaw), small front teeth, a short face, the nose shape, minimal brow development, muscle markings on the thumb bone, the narrowness of the front of the pelvis, and several aspects of the shoulder blade and forearm bones.

Yet intriguingly, a number of features also suggest certain Neandertal affinities. Specifically, the front of the mandible slopes backward despite the chin, there is a porous depression above the neck muscles, the pectoral muscles are strongly developed, and the lower legs are short and stout. Thus, the Lagar Velho child exhibits a complex mosaic of Neandertal and early modern human features.

This anatomical amalgam is not the result of any abnormalities. Taking normal human growth patterns into consideration, our analysis indicates that except for a bruised forearm, a couple of lines on the bones indicating times when growth was trivially arrested (by sickness or lack of food) and the fact that it died as a child, Lagar Velho 1 developed normally. The combination can only have resulted from a mixed ancestry—something that had not been previously documented for western Europe. We therefore conclude that Lagar Velho 1 resulted from interbreeding between indigenous Iberian Neandertals and early modern humans dispersing throughout Iberia sometime after 30,000 years ago. Because the child lived several millennia after Neandertals are thought to have disappeared, its anatomy probably reflects a true mixing of these populations during the period when they coexisted and not a rare chance mating between a Neandertal and an early modern human.

Fieldwork conducted in 1999 yielded major pieces of the skull and most of the remaining teeth. An international team then assembled to fully interpret this remarkable specimen. Aside from detailed comparative analyses of individual portions of the skeleton, all the remains were CT scanned and a virtual, computer-assisted reconstruction of the skull was undertaken.

Such rigorous technological study is

MORPHOLOGICAL MOSAIC found on this 24,500-year-old skeleton from Portugal indicates that Neandertals and modern humans are members of the same species who interbred freely. The child—called Lagar Velho 1—is modern overall but bears some Neandertal traits, such as short lower-limb bones and a backward-sloping mandible.

replacement model do allow for isolated instances of interbreeding between moderns and the archaic species, because some other closely related mammal species interbreed on occasion. But unlike central and eastern European specimens that are said to show a combination of features, the Portuguese child dates to a time when Neandertals are no longer thought to have existed. For Neandertal features to have persisted thousands of years after those people disappeared, Trinkaus and Duarte say, coexisting populations of Neandertals and moderns must have mixed significantly.

Their interpretation has not gone unchallenged. In a commentary accompanying the team's report in the *Proceedings of the National Academy of Sciences USA* in June 1999, paleoanthropologists Ian Tattersall of the American Museum of Natural History in New York City and Jeffrey H. Schwartz of the University of Pittsburgh argued that Lagar Velho 1 is most likely "a chunky Gravettian child." The robust body proportions that Trinkaus and his colleagues view as evidence for Neandertal ancestry, Stringer says, might reflect adaptation to Portugal's then cold climate. But this interpretation is problematic, according to Jean-Jacques Hublin of France's CNRS, who points out that although some cold-adapted moderns exhibit such proportions, none are known from that period in Europe. For his part, Hublin is troubled that Lagar Velho 1 represents a child, noting that "we do not know anything about the variation in children of a given age in this range of time."

Survival Skills

TAXONOMIC ISSUES ASIDE, much research has focused on Neandertal behavior, which remained largely misunderstood until relatively recently. Neandertals were often portrayed as incapable of hunting or planning ahead, recalls archaeologist John J. Shea of the State University of New York at Stony Brook. "We've got reconstructions of Neandertals as people who couldn't survive a single winter, let alone a quarter of a million years in the worst environments in which humans ever lived," he observes. Analysis of animal remains from the Croatian site of Krapina, however, indicates that Neandertals were

necessary because the discovery of an individual with such a mosaic of features has profound implications. First, it rejects the extreme Out of Africa model of modern human emergence, which proposes that early moderns originating in Africa subsequently displaced all archaic humans in other regions. Instead the Lagar Velho child's anatomy supports a scenario that combines a dispersal of anatomically modern humans out of Africa with mixing between that population and the archaic populations it encountered. (For example, the African ancestry of early modern Europeans is reflected in their relatively long lower-leg bones, a tropical adaptation. Lagar Velho 1, however, has the short shins of the cold-adapted Neandertals.)

Lagar Velho 1 also provides insights into the behavioral similarities of Neandertals and early modern humans. Despite the paleontological evidence indicating anatomical differences between these two groups, their overall adaptive patterns, social behaviors and means of communication (including language) cannot have contrasted greatly. To their contemporaries, the Neandertals were just another group of Pleistocene hunter-gatherers, fully as human as themselves.

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JOSÉ PAULO B. RUAS/PORTUGUESE INSTITUTE OF ARCHAEOLOGY

skilled hunters capable of killing even large animals such as rhinoceroses, according to University of Cambridge archaeologist Preston T. Miracle. And Shea's studies suggest that some Neandertals employed sophisticated stone-tipped spears to conquer their quarry—a finding supported in 1999, when researchers reported the discovery in Syria of a Neandertal-made stone point lodged in a neckbone of a prehistoric wild ass. Moreover, additional research conducted by Shea and investigations carried out by University of Arizona archaeologists Mary C. Stiner and Steven L. Kuhn have shown that Neandertal subsistence strategies varied widely with the environment and the changing seasons.

Such demonstrations refute the notion that Neandertals perished because they could not adapt. But it may be that moderns were better at it. One popular theory posits that modern humans held some cognitive advantage over Neandertals, perhaps a capacity for the most human trait of all: symbolic thought, including language. Explanations such as this one arose from observations that after 40,000 years ago, whereas Neandertal culture remained relatively static, that of modern Europeans boasted a bevy of new features, many of them symbolic. It appeared that only moderns performed elaborate burials, expressed themselves through body ornaments, figurines and cave paintings, and crafted complex bone and antler tools—an industry broadly referred to as Upper Paleolithic. Neandertal assemblages, in contrast, contained only Middle Paleolithic stone tools made in the Mousterian style.

A CASE FOR NEANDERTAL CULTURE

BY JOÃO ZILHÃO AND FRANCESCO D'ERRICO

EVER SINCE THE DISCOVERY nearly 150 years ago of the specimen that defined the Neandertals, researchers have tended to deny Neandertals the behavioral capabilities of modern humans, such as the use of symbols or of complex techniques for tool manufacture. Instead Neandertals were characterized as subhuman, stuck in primitive technical traditions impervious to innovation. And when sophisticated cultural remains were linked to late Neandertals at several sites in western Europe, the evidence was explained away. The most spectacular of these sites, a cave in north-central France named Grotte du Renne (one in a string of sites collectively known as the Arcy-sur-Cure caves), yielded a wealth of complex bone and stone tools, body ornaments and decorated objects, found in association with Neandertal remains. Other sites in France and along the Cantabrian and Pyrenean mountain ranges bore similar artifacts made in this tradition, called the Châtelperronian.

Because early modern Europeans had a comparable industry known as Aurignacian—which often appears at the same sites that contain Châtelperronian materials—some researchers have suggested that the archaeological layers were disrupted, mixing Aurignacian artifacts into the Neandertal-associated levels. Other scholars have interpreted this to mean that Neandertals picked up these ideas from moderns, either collecting or trading for items manufactured by moderns or imitating the newcomers' practices without really grasping the underlying symbolic nature of some of the objects.

Our reassessment of the evidence from the Grotte du Renne shows that the Neandertal-associated ornaments and tools found there did not result from a mixing of the strata, as demonstrated by the presence of finished objects and the by-products of their manufacture in the same stratigraphic level. Moreover, the Châtelperronian artifacts recovered at the Grotte du Renne and other sites, such as Quinçay, in the Poitou-Charentes region of France, were created using techniques different from those favored by Aurignacians. With regard, for example, to the pendants—modified bear, wolf and deer teeth, among others—Neandertals carved a furrow around the tooth root so that a string of some sort could be tied around it for suspension, whereas Aurignacians pierced their pendants. As archaeologist François Lévêque and a colleague have described, even when, as they did on occasion, Neandertals put a hole through a tooth, they took an unusual approach, puncturing the tooth. Moderns preferred to scrape the tooth thin and then pierce it.

Similarly, the new knapping techniques and tool types that appear among late Neandertals at other sites in France, Italy and Spain fail to show any influence from the Aurignacian. Instead they maintain affinities with the preceding local traditions, of which they seem to represent an autonomous development.

If the Neandertals' Châtelperronian culture was an outcome of contact with moderns, then the Aurignacian should predate the Châtelperronian. Yet our reanalysis of the radiometric dates for the archaeological sequences reveals that apart from a few debatable instances of mixture, wherever both cultures are

Yet hints that Neandertals thought symbolically had popped up. Neandertal burials, for example, are well known across Europe, and several, it has been argued, contain grave goods. (Other researchers maintain that for Neandertals, interment merely constituted a way of concealing the decomposing body, which might have attracted unwelcome predators. They view the purported grave goods as miscellaneous objects that happened to be swept into the grave.) Evidence for art, in the form of isolated pierced teeth and engraved bone fragments, and red and yellow ocher, has been reported from a few sites, too, but given their relative rarity, researchers tend to assign alternative explanations to these items.

The possibility that Neandertals might have engaged in modern practices was taken more seriously in 1980, when researchers reported a Neandertal from the Saint-Césaire rock-shelter in Charente-Maritime, France, found along with stone tools manufactured according to a cultural tradition known as the Châtelperronian, which was assumed to have been the handiwork of moderns. Then, in 1996, Hublin and his co-workers made a startling announcement. Excavations that began in the 1940s at the Grotte du Renne at Arcy-sur-Cure near Auxerre, France, had yielded numerous blades, body ornaments and bone tools and revealed evidence of huts and hearths—all hallmarks of the Upper Paleolithic. The scant human remains found amid the artifacts were impossible to identify initially, but using computed tomography to examine the hidden inner-ear region preserved inside an otherwise uninformative skull fragment, Hublin's team identified the specimen as Neandertal.

In response, a number of scientists suggested that Neandertals had acquired the modern-looking items by stealing them, collecting artifacts discarded by moderns or perhaps trading for them. But this view has come under fire, most recently from archaeologists Francesco d'Errico of the University of Bordeaux and João Zilhão of the University of Lisbon, who argue that the represented at the same site, the Châtelperronian always underlies the Aurignacian, suggesting its priority. Furthermore, consideration of the hundreds of datings available from this period in Europe and the Near East shows that wherever the context of the dated samples is well known, the earliest occurrences of the Aurignacian are apparently from no earlier than around 36,500 years ago. The same radiometric data, however, indicate that by then Neandertals were already moving toward modernity on their own. In other words, the Châtelperronian and other late Neandertal cultures, such as the Uluzzian of Italy, emerged in Europe around 40,000 years ago, long before any moderns established themselves in those areas.

That this autonomous development included the manufacture and use of symbolic objects created for visual display on the body, as are often observed in traditional societies, reflects various social roles within Neandertal cultures. Thus, "modern" behavior seems to have emerged in different regions and among different groups of humans, as would happen later in history with the invention of agriculture, writing and state society.

An alternative explanation, taking into account the broadly simultaneous appearance of personal ornaments in many parts of the Old World, is that contacts between modern and archaic humans challenged each group's personal, social and biological identities, igniting an explosion of production of symbolic objects by all those involved. On the strength of the available data, however, we favor the hypothesis of independent invention.

Regardless of which is eventually proved correct, the behavioral barrier that seemed to separate moderns from Neandertals and gave us the impression of being a unique and particularly gifted human type—the ability to produce symbolic cultures—has definitively collapsed.

PENDANTS, BONE TOOLS AND KNIVES from the Grotte du Renne site seem to be the handiwork of Neandertals. That the advanced items underlie early modern human cultural remains from the same site and are manufactured according to methods different from those favored by the moderns suggests that some Neandertals independently developed a modern culture.

COURTESY OF DOMINIQUE BAFFIER (*left and right panels*), FROM "LES DERNIERS NÉANDERTALIENS," LA MAISON DES ROCHES, 1999; FRANCESCO D'ERRICO (*center panel*)

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FRANCESCO D'ERRICO is a CNRS researcher at the Institute of Prehistory and Quaternary Geology, University of Bordeaux, in France.

Châtelperronian artifacts at the Grotte du Renne and elsewhere, though superficially similar to those from the Aurignacian, reflect an older, different method of manufacture [see "A Case for Neandertal Culture," above].

Most researchers are now convinced that Neandertals manufactured the Châtelperronian tools and ornaments, but what prompted this change after hundreds of thousands of years is unclear. Cast in this light, "it's more economical to see that as a result of imitation or acculturation from modern humans than to assume that Neandertals invented it for themselves," reasons Cambridge archaeologist Paul A. Mellars. "It would be an extraordinary coincidence if they invented all these things shortly before the modern humans doing the same things arrived." Furthermore, Mellars disagrees with d'Errico and Zilhão's proposed order of events. "The dating evidence proves to me that [Neandertals] only started to do these things after the modern humans had arrived in western Europe or at least in northern Spain," he asserts. Unfortunately, because scientists have been unable to date these sites with sufficient precision, researchers can interpret the data differently.

From his own work on the Grotte du Renne body ornaments, New York University archaeologist Randall White argues that these artifacts reflect manufacturing methods known—albeit at lower frequencies—from Aurignacian ornaments. Given the complicated stratigraphy of the Grotte du Renne site, the modern-looking items might have come from overlying Aurignacian levels. But more important, according to White, the Châtelperronian does not exist outside of France, Belgium, Italy and northern Spain. Once you look at the Upper Paleolithic from a pan-European perspective, he says, "the Châtelperronian becomes post-Aurignacian by a long shot."

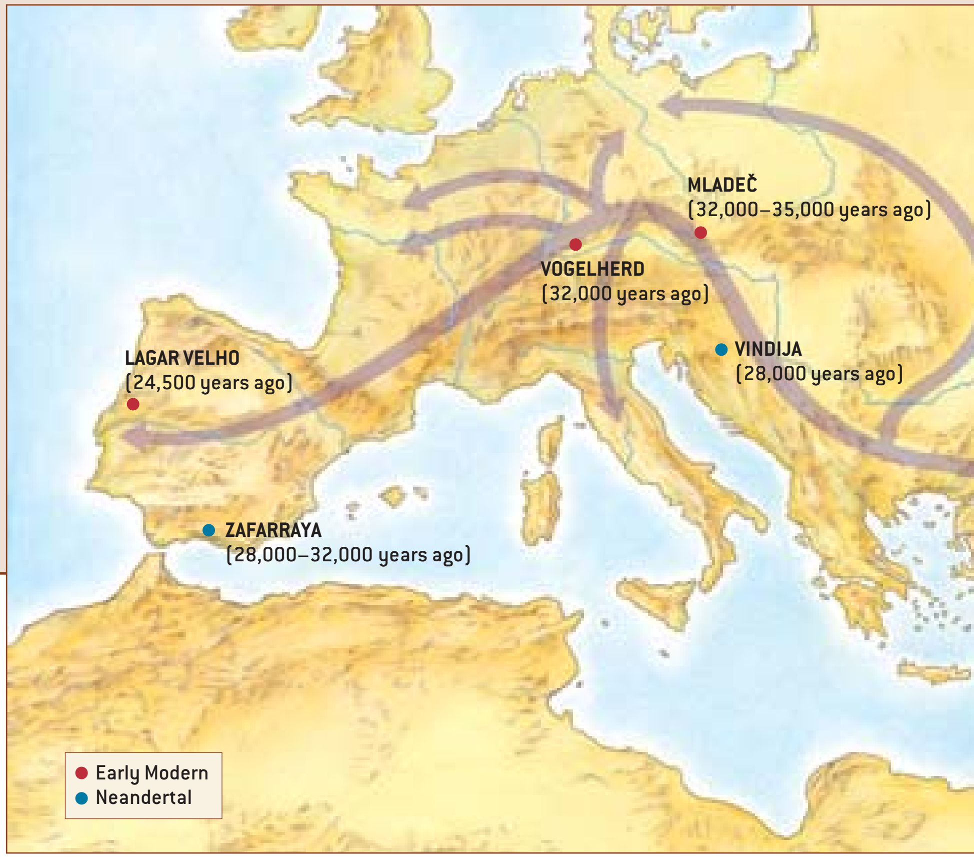
Still, post-Aurignacian does not necessarily mean after contact with moderns. The earliest Aurignacian sites do not in-

THE FATE OF THE NEANDERTALS BY FRED H. SMITH

STRONG EVIDENCE has accumulated in recent years that the emergence of modern humans in Europe resulted largely from the immigration of peoples into the continent, probably from the Near East, starting sometime between 40,000 and 30,000 years ago. Most researchers envisioned these early modern populations as having moved into Anatolia and the Balkans, then up through the plains and valleys of central Europe, and finally into northern and western Europe. Meanwhile the indigenous Neandertals, it was thought, were systematically pushed into more peripheral and undesirable parts of the landscape by these expanding populations of moderns. The Neandertals' last bastion appeared to have been the Iberian Peninsula, where fossils from a Spanish site called Zafarraya have been dated to 32,000 years ago and tools attributed to Neandertals have been dated to around 28,000 years ago.
A number of scholars argued that after this time no traces of Neandertals remained in Europe and that the Neandertals did not make any biological contributions to early modern humans. It seemed that the Neandertals were sent into complete extinction by a superior human species—us.

Evidence from an important site in northwestern Croatia calls aspects of this conventional wisdom into question. By performing accelerator mass spectrometry dating directly on two Neandertal specimens from Vindija cave, my colleagues and I have demonstrated that Neandertals were living in some of the most desirable real estate in central Europe as late as 28,000 years ago. These dates, the most recent known for Neandertal fossils, show that these humans were not quickly relegated to the periphery; they competed quite well with intruding modern populations for a long time.

This overlap of Neandertal and early modern peoples for several millennia in the heart of Europe allowed considerable



clude any human remains. Researchers have assumed that they belonged to moderns because moderns are known from younger Aurignacian sites. But "who the Aurignacians were biologically between 40,000 and 35,000 years ago remains very much an unanswered question," White notes.

He adds that if you look at the Near East around 90,000 years ago, anatomically modern humans and Neandertals were both making Mousterian stone tools, which, though arguably less elaborate than Aurignacian tools, actually require a considerable amount of know-how. "I cannot imagine that Neandertals were producing these kinds of technologically complex tools and passing that on from generation to generation without talking about it," White declares. "I've seen a lot of people do this stuff, and I can't stand over somebody's shoulder and learn how to do it without a lot of verbal hints." Thus, White and others do not buy the argument that moderns were somehow cognitively superior, especially if Neandertals' inferiority meant that they lacked language. Instead it seems that moderns invented a culture that relied more heavily on material symbols.

Researchers have also looked to brain morphology for clues to cognitive ability. According to Ralph L. Holloway of Columbia University, all the brain asymmetries that characterize modern humans are found in Neandertals. "To be able to discriminate between the two," he remarks, "is, at the moment, impossible." As to whether Neandertal anatomy permitted speech, studies of the base of the skull conducted by Jeffrey T. Laitman of the Mount Sinai School of Medicine suggest that if they talked, Neandertals had a limited vocal repertoire. The significance of such physical constraints, however, is unclear.

Fading Away

IF NEANDERTALS POSSESSED basically the same cognitive ability as moderns, it makes their disappearance additionally puzzling. But the recent redating of Neandertal remains from Vindija cave in Croatia emphasizes that this did not happen overnight. Loyola's Smith and his colleagues have demonstrated

SUSAN CARLSON

opportunity for various interactions, and Vindija may reflect some of them. Work by my Croatian colleagues Ivor Karavanić of the University of Zagreb and Jakov Radovčić of the Croatian Natural History Museum has revealed a combination of Mousterian and Aurignacian tools in the same stratigraphic level as the dated Neandertal fossils, indicating that Neandertals either made advanced implements or traded with moderns for them. Morphologically, the Vindija Neandertals look more modern than do most other Neandertals, which suggests that their ancestors interbred with early moderns.

The likelihood of gene flow between the groups is also supported by evidence that Neandertals left their mark on early modern Europeans. Fossils representing early modern adults from central European sites such as Vogelherd in southwestern Germany and Mladeč in Moravia (Czech Republic) have features that are difficult to explain unless they have some Neandertal contribution to their ancestry.

For example, Neandertals and early modern Europeans virtually all exhibit a projection of the back of the skull called an occipital bun (aspects of the shape and position of the buns differ between them because the overall skull shapes are not the same). Yet fossils from the Near Eastern sites of Skhūl and Qafzeh, which presumably represent the ancestors of early modern Europeans, do not have this morphology. It is hard to explain how the growth phenomenon responsible for this bunning could reappear independently and ubiquitously in early modern Europeans. Instead it is far more logical to recognize this morphology as a link to the Neandertals. The Portuguese child discovered late in 1998 in the Lapedo Valley offers more intriguing clues [see "The Hybrid Child from Portugal," on page 32].

I believe the evidence shows that the behavioral and biological interactions between Neandertal and early modern human populations were very complex—too complex for the origins of modern humans in Europe to have involved a simple, complete biological replacement of the Neandertals. Neandertals as organisms no longer exist, and Neandertal genes may not have persisted to the present day, but those genes were there in the beginnings of modern European biological history.

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MOVEMENT OF MODERNS (*purple*) into Europe did not displace the Neandertals, who were still living in central and western Europe 28,000 years ago. A number of the early modern European specimens bear some Neandertal features, which suggests that during the long period of overlap the two populations mixed.

that Neandertals still lived in central Europe 28,000 years ago, thousands of years after moderns had moved in [see "The Fate of the Neandertals," above]. Taking this into consideration, Stringer imagines that moderns, whom he views as a new species, replaced Neandertals in a long, slow process. "Gradually the Neandertals lost out because moderns were a bit more innovative, a bit better able to cope with rapid environmental change quickly, and they probably had bigger social networks," he supposes.

On the other hand, if Neandertals were an equally capable variant of our own species, as Smith and Wolpoff believe, long-term overlap of Neandertals and the new population moving into Europe would have left plenty of time for mingling, hence the mixed morphology that these scholars see in late Neandertals and early moderns in Europe. And if these groups were exchanging genes, they were probably exchanging cultural ideas, which might account for some of the similarity between, say, the Châtelperronian and the Aurignacian. Neandertals as entities disappeared, Wolpoff says, because they were outnumbered by the newcomers. Thousands of years of interbreeding between the small Neandertal population and the larger modern human population, he surmises, diluted the distinctive Neandertal features, which ultimately faded away.

"If we look at Australians a thousand years from now, we will see that the European features have predominated [over those of native Australians] by virtue of many more Europeans," Wolpoff asserts. "Not by virtue of better adaptation, not by virtue of different culture, not by virtue of anything except many more Europeans. And I really think that's what describes what we see in Europe—we see the predominance of more people."

From the morass of opinions in this contentious field, one consensus emerges: researchers have retired the vision of the shuffling, cultureless Neandertal. But whether these ancient hominids were among the ancestors of living people or a closely related species that competed with our own for the Eurasian territory and lost remains to be seen. In either case, the details will be extraordinarily complicated. "The more we learn, the more questions arise, the knottier it gets," muses archaeologist Lawrence G. Straus of the University of New Mexico. "That's why simple explanations just don't cut it." SA

Kate Wong is editorial director of ScientificAmerican.com

out of afr

Africa is the birthplace of species evolved there? And when

It all used to seem so simple. The human lineage evolved in Africa. Only at a relatively late date did early humans finally migrate from the continent of their birth, in the guise of the long-known species *Homo erectus*, whose first representatives had arrived in eastern Asia by around one million years ago. All later kinds of humans were the descendants of this species, and almost everyone agreed that all should be classified in our own species, *H. sapiens*. To acknowledge that some of these descendants were strikingly different from ourselves, they were referred to as "archaic *H. sapiens*," but members of our own species they were nonetheless considered to be.

Such beguiling simplicity was, alas, too good to last, and over the past few years it has become evident that the later stages of human evolution have been a great deal more eventful than conventional wisdom for so long had it. This is true for the earlier stages, too, although there is still no reason to believe that humankind's birthplace was elsewhere than in Africa. Indeed, for well over the first half of the documented existence of the hominid family (which includes all upright-walking primates), there is no record at all outside that continent. But recent evidence does seem to indicate that it was not necessarily *H. erectus* who migrated from Africa—and that these peregrinations began earlier than we had thought.

A Confused Early History

RECENT DISCOVERIES in Kenya of fossils attributed to the new species *Australopithecus anamensis* have pushed back the undoubted record of upright-walking hominids to about 4.2 to 3.9 million years ago. The most recent finds in Kenya and Chad may push this back to six million years ago or more. The *A. anamensis* fossils bear a strong resemblance to the later and far better known species *Australopithecus afarensis*, found at sites in Ethiopia and Tanzania in the 3.9- to 3.0-million-year range and most famously represented by the "Lucy" skeleton from Hadar, Ethiopia.

Lucy and her kind were upright walkers, as the structures of their pelvises and knee joints particularly attest, but they retained many ancestral features, notably in their limb proportions and in their hands and feet, that would have made them fairly adept tree climbers. Together with ape-size brains and large, protruding faces, these characteristics have led many to call such creatures "bipedal chimpanzees." This is proba-

"LUCY" SKELETON represents the best-known species of early hominid, or human precursor, *Australopithecus afarensis*, often characterized as a "bipedal chimpanzee." The 3.18-million-year-old skeleton is from the Hadar region of Ethiopia.

Updated from the April 1997 issue

By Ian Tattersall

ica
again . . . and again?

humanity. But how many human
did they emigrate?

PHOTOGRAPH BY D. FINNIN AND J. BECKETT, FROM CAST ON DISPLAY AT THE AMERICAN MUSEUM OF NATURAL HISTORY (*these two pages*)

bly a fairly accurate characterization, especially given the increasing evidence that early hominids favored quite heavily wooded habitats. Their preferred way of life was evidently a successful one, for although these primates were less adept arborealists than the living apes and less efficient bipeds than later hominids, their basic "eat your cake and have it" adaptation endured for well over two million years, even as species of this general kind came and went in the fossil record.

It is not even clear to what extent lifestyles changed with the invention of stone tools, which inaugurate our archaeological record at about 2.5 million years ago. No human fossils are associated with the first stone tools known, from sites in Kenya and Ethiopia. Instead there is a motley assortment of hominid fossils from the period following about two million years ago, mostly associated with the stone tools and butchered mammal bones found at Tanzania's Olduvai Gorge and in Kenya's East Turkana region. By one reckoning, at least some of the first stone toolmakers in these areas were hardly bigger or more advanced in their body skeletons than the tiny Lucy; by another, the first tools may have been made by taller, somewhat larger-brained hominids with more modern body structures. Exactly how many species of early hominids there were, which of them made the tools, and how they walked remain among the major conundrums of human evolution.

Physically, at least, the picture becomes clearer after about 1.9 million years ago, when the first good evidence occurs in northern Kenya of a species that is recognizably like ourselves. Best exemplified by the astonishingly complete 1.6-million-year-old skeleton known as the Turkana Boy, discovered in 1984, these humans possessed an essentially modern body structure, indicative of modern gait, combined with moderately large-faced skulls that contained brains double the size of those of apes (though not much above half the modern human average). The Boy himself had died as an adolescent, but it is estimated that had he lived to maturity he would have attained a height of six feet, and his limbs were long and slender, like those of people who live today in hot, arid African climates, although this common adaptation does not, of course, indicate any special relationship. Here at last we have early hominids who were clearly at home on the open savanna.

A long-standing paleoanthropological tradition seeks to minimize the num-

"TURKANA BOY," an adolescent *Homo ergaster* dated to about 1.6 million years ago, is representative of the first hominids with an effectively modern body skeleton.

NEWLY DISCOVERED SPECIES: *Australopithecus anamensis* is the earliest well-documented hominid. This lower jaw from Kanapoi, Kenya, seen as it was found in the field, has been dated to around four million years ago. *A. anamensis* closely resembles *A. afarensis* in dental details, and a partial tibia (shinbone) indicates that it walked upright.

PHOTOGRAPH BY ROBERT CAMPBELL; COURTESY OF MEAVE LEAKEY

ber of species in the human fossil record and to trace a linear, progressive pattern of descent among those few that are recognized. In keeping with this practice, the Boy and his relatives were originally assigned to the species *H. erectus*. This species was first described from a skullcap and thighbone found in Java a century ago. Fossils later found in China—notably the now lost 500,000-year-old "Peking Man"—and elsewhere in Java were soon added to the species, and eventually *H. erectus* came to embrace a wide variety of hominid fossils, including a massive braincase from Olduvai Gorge known as OH9. The latter has been redated to about 1.4 million years, although it was originally thought to have been a lot younger. All these fossil forms possessed brains of moderate size (about 900 to 1,200 milliliters in volume, compared with an average of around 1,400 milliliters for modern humans and about 400 milliliters for apes), housed in long, low skull vaults with sharp angles at the back and heavy brow ridges in front. The few limb bones known were robust but essentially like our own.

Whether *H. erectus* had ever occupied Europe was vigorously debated, the alternative being to view all early human fossils from that region (the earliest of them being no more than about 500,000 years old) as representatives of archaic *H. sapiens*. Given that the Javan fossils were conventionally dated in the range of one million to 700,000 years and younger and that the earliest Chinese fossils were reckoned to be no more than one million years old, the conclusion appeared clear: *H. erectus* (as exemplified by OH9 and also by the earlier Turkana Boy and associated fossils) had evolved in Africa and had exited that continent not much more than one million years ago, rapidly spreading to eastern Asia and spawning all subsequent developments in human evolution, including those in Europe.

Yet on closer examination the specimens from Kenya turned out to be distinctively different in braincase construction from those of classic eastern Asian *H. erectus*. In particular, certain anatomical features that appear specialized in the eastern Asian *H. erectus* look ancestral in the African fossils of comparable age. Many researchers began to realize that we are dealing with two kinds of early human here, and the earlier Kenyan form is now increasingly placed in its own species, *H. ergaster*. This species makes a plausible ancestor for all subsequent humans, whereas the cranial specializations of *H. erectus* suggest that this species, for so long regarded as the standard-issue hominid of the 1- to 0.5-million-year period, was in fact a local (and, as I shall explain below, ultimately terminal) eastern Asian development.

An Eastern Asian Cul-de-Sac

THE PLOT THICKENED in early 1994, when Carl C. Swisher of the Berkeley Geochronology Center and his colleagues applied the newish argon/argon dating method to volcanic rock samples taken from two hominid sites in Java. The results were 1.81 and 1.66 million years: far older than anyone had really expected, although the earlier date did confirm one made many years before. Unfortunately, the fossils from these two sites are rather undiagnostic as to species: the first is a braincase of an infant (juveniles never show all the adult characteristics on which species are defined), and the second is a horrendously crushed and distorted cranium that has never been satisfactorily reconstructed. Both specimens have been regarded by most as *H. erectus*, more for reasons of convenience than anything else. Over the decades,

"PEKING MAN" is the name given to this skull of a male *H. erectus* from Zhoukoudian, near Beijing. The skull was reconstructed from fragments of various individuals, all probably around 500,000 years old.

PHOTOGRAPH BY CRAIG CHESEK, FROM A CAST AT THE AMERICAN MUSEUM OF NATURAL HISTORY

PHOTOGRAPHS BY WILLARD WHITSON

REPLICA OF OLDOWAN BASALT CORE illustrates how sharp flakes were struck from the core to provide cutting implements. Tools of this kind were first made around 2.5 million years ago.

TWO ACHEULEAN TOOLS, from St. Acheul, France, are probably around 300,000 years old, but implements of this kind began to be made in Africa as many as 1.5 million years ago. On the left is a pointed hand ax and on the right a blunt-ended cleaver.

sporadic debate has continued regarding whether the Javan record contains one or more species of early hominid. Further, major doubt has been cast on whether the samples that yielded the older date were actually obtained from the same spot as the infant specimen. Still, these dates do fit with other evidence pointing to the probability that hominids of some kind were around in eastern Asia much earlier than anyone had thought.

Independent corroboration of this scenario comes, for instance, from the Dmanisi site in the former Soviet republic of Georgia, where in 1991 a hominid lower jaw that its describers allocated to *H. erectus* was found. Three different methods indicated that this jaw was as old as 1.8 million years, and with four crania from the site now in hand, there is ample evidence of an unexpectedly early hominid exodus from Africa. Even the most parsimonious reading of the admittedly imperfect record suggests that these pioneering emigrants must have been *H. ergaster* or something very much like it.

A very early hominid departure from Africa has the advantage of explaining an apparent anomaly in the archaeological record. The stone tools found in sediments coeval with the earliest *H. ergaster* (just under two million years ago) are essentially identical with those made by the first stone toolmakers many hundreds of thousands of years before. These crude tools consisted principally of sharp flakes struck with a stone "hammer" from small cobbles. Effective cutting tools though these may have been (experimental archaeologists have shown that even elephants can be quite efficiently butchered using them), they were not made to a standard form but were apparently produced simply to obtain a sharp cutting edge. Following about 1.5 million years ago, however, standardized stone tools began to be made in Africa, typified by the hand axes and cleavers of the Acheulean industry (first identified in the mid-19th century from St. Acheul in France). These were larger implements, carefully shaped on both sides to a teardrop form. Oddly, stone tool industries in eastern Asia lacked such utensils, which led many to wonder why the first human immigrants to the region had not brought this technology with them, if their ancestors had already wielded it for half a million years. The new dates suggest, however, that the first emigrants had left Africa before the invention of the Acheulean technology, in which case there is no reason why we should expect to find this technology in eastern Asia. Interestingly, in 1989 Robin W. Dennell of the University of Sheffield in England caused quite a stir by reporting very crude stone tools from Riwat in Pakistan that are older than 1.6 million years. Their great age is now looking decreasingly anomalous.

Of course, every discovery raises new questions, and in this case the problem is to explain what it was that enabled human populations to expand beyond Africa for the first time. Most scholars had felt that it was technological advances that allowed the penetration of the cooler continental areas to the north. If, however, the first emigrants left Africa equipped with only the crudest of stone-

DRAWINGS BY DON McGRANAGHAN

SKULLCAP known as Olduvai Hominid 9 (OH9) was dated to 1.4 million years old; it was originally believed to have been much younger. Its affinities are still being debated.

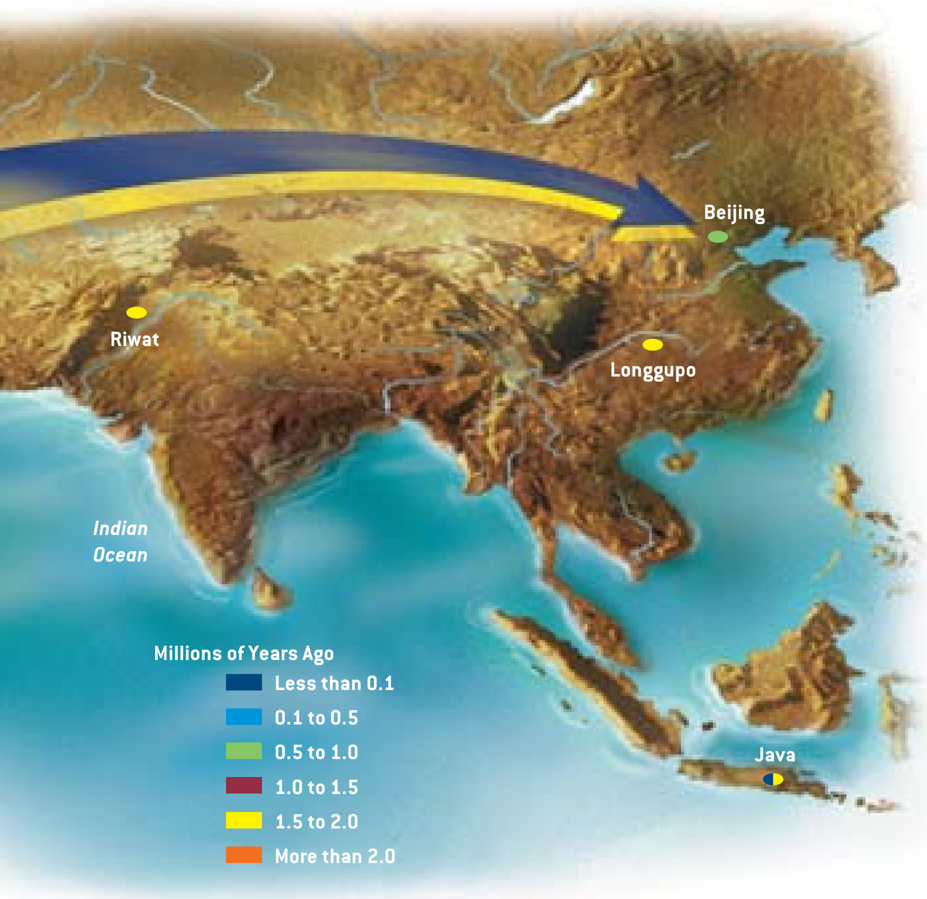
SUCCESSIVE WAVES of early humans exited from Africa to all parts of the Old World. The record of these emigrations is incomplete, but it is evident that this history is much longer and more complex than has traditionally been believed.

working technologies, we have to look to something other than technological prowess for the magic ingredient. And because the first human diaspora apparently followed hard on the heels of the acquisition of more or less modern body form, it seems reasonable to conclude that the typically human wanderlust emerged in concert with the emancipation of hominids from the forest edges that had been their preferred habitat. Of course, the fact that the Turkana Boy and his kin were adapted in their body proportions to hot, dry environments does nothing to explain why *H. ergaster* was able to spread rapidly into the cooler temperate zones beyond the Mediterranean; evidently the new body form that made possible remarkable endurance in open habitats was in itself enough to make the difference.

The failure of the Acheulean ever to diffuse as far as eastern Asia reinforces the notion, consistent with the cranial specializations of *H. erectus*, that this part of the world was a kind of paleoanthropological cul-de-sac. In this region, ancient human populations largely followed their own course, independent of what was going on elsewhere in the world. Further datings tend to confirm this view. Swisher and his colleagues reported in 1996 dates for the Ngandong *H. erectus* site in Java that center on only about 40,000 years ago. These dates, though very carefully obtained, have aroused considerable skepticism; but, if accurate, they have considerable implications for the overall pattern of human evolution. For they are so recent as to suggest that the long-lived *H. erectus* might even have suffered a fate similar to that experienced by the Neandertals in Europe: extinction at the hands

FOSSILS FROM LONGGUPO, such as the lower jaw fragment (*side and top views at left*), may indicate the presence of hominids in China as many as 1.9 million years ago.

PHOTOGRAPHS COURTESY OF RUSSELL CIOCHON *University of Iowa*



LAURIE GRACE AND JANA BRENNING

of late-arriving *H. sapiens*. Here we find reinforcement of the gradually emerging picture of human evolution as one of repeated experimentation, with regionally differentiated species, in this case on opposite sides of the Eurasian continent, being ultimately replaced by other hominid lineages that had evolved elsewhere.

At the other end of the scale, in 1996 an international group led by Huang Wanpo of Academia Sinica in Beijing reported a remarkably ancient date for Longgupo Cave in China's Sichuan Province. This site had previously yielded an incisor tooth and a tiny lower jaw fragment with two teeth that were initially attributed to *H. erectus*, plus a few very crude stone artifacts. Huang and his colleagues concluded that the fossils and tools might be as many as 1.9 million years old, and their reanalysis of the fossils suggested to them a closer resemblance to the earliest African *Homo* species than to *H. erectus*.

This latter claim has not gone unexamined. As my colleague Jeffrey H. Schwartz of the University of Pittsburgh and I pointed out, for instance, the teeth in the jaw fragment resemble African *Homo* in primitive features rather than in the specialized ones that indicate a special relationship. What is more, they bear a striking resemblance to the teeth of an orangutan-related hominoid known from a much later site in Vietnam. And although the incisor appears hominid, it is fairly generic, and there is nothing about it that aligns it with any particular human species. Future fossil finds from Longgupo will, with luck, clarify the situation; meanwhile the incisor and stone tools are clear evidence of the presence of humans in China at what may be a very early date indeed. These ancient eastern Asians were the descendants of the first emigrants from Africa, and, whatever the hominids of Longgupo eventually turn out to have been, it is a good bet that Huang and his colleagues are right in guessing that they represent a precursor form to *H. erectus* rather than that species itself.

All this makes sense, but one anomaly remains. If *H. erectus* was an indigenous eastern Asian development, then we have to consider whether we have correctly identified the Olduvai OH9 braincase as belonging to this species. If we have, then *H. erectus* evolved in eastern Asia at quite an early date (remember, OH9 is now thought to be almost 1.4 million years old), and one branch of the species migrated back to Olduvai in Africa. But if these new Asian dates are accurate, it seems more probable that as we come to know more about OH9 and its kind we will find that they belonged to a different species of hominid altogether.

The opposite end of the Eurasian continent was, as I have hinted, also isolated from the human evolutionary mainstream. As we saw, humans seem to have arrived in Europe fairly late. In this region, the first convincing archaeological sites, with rather crude tools, show up at about 800,000 years ago or thereabouts (although in the Levant, within hailing distance of Africa, the site of 'Ubeidiya has yielded Acheulean tools dated to


COURTESY OF ERIC DELSON

PARTIAL MANDIBLE (*top and side views*) from Dmanisi, in former Soviet Georgia, may be as old as 1.8 million years. Although it was initially assigned to *H. erectus*, its species is still uncertain.

THE AUTHOR

IAN TATTERSALL was born in England and raised in East Africa. He is chair of the department of anthropology at the American Museum of Natural History in New York City. His latest books include *The Monkey in the Mirror: Essays on the Science of What Makes Us Human* (Harvard Books, 2003), *Becoming Human: Evolution and Human Uniqueness* (Harcourt, 1998) and *The Fossil Trail: How We Know What We Think We Know about Human Evolution* (Oxford University Press, 1995).

around 1.4 million years ago, just about as early as any found to the south). The problem has been the lack of a sign of the toolmakers themselves.

This gap began to be filled by finds made by Eudald Carbonell of the University of Tarragona in Spain and his coworkers at the Gran Dolina Cave site in the Atapuerca Hills of northern Spain. In 1994 excavations at that site produced numerous simple stone tools, plus quite a few human fossil fragments, the most complete of which is a partial upper face of an immature individual. All came from a level that was dated to more than 780,000 years ago. No traces of Acheulean technology were found among the tools, and the investigators noted various primitive traits in the fossils, which they provisionally attributed to *H. heidelbergensis*. This is the species into which specimens formerly classified as archaic *H. sapiens* are increasingly being placed. Carbonell and his colleagues see their fossils as the starting point of an indigenous European lineage that gradually evolved into the Neandertals. These latter, large-brained hominids are known only from Europe and western Asia, where they flourished in the period between about 200,000 years and 30,000 years ago, when they were extinguished in some way by invading *H. sapiens*.

GRAN DOLINA CAVE in the Atapuerca Hills of northern Spain has produced the earliest human fossils yet found in Europe. These fossils, dated to about 780,000 years ago and initially attributed to *H. heidelbergensis,* may in fact represent a distinct form. The mature cranium (*below*) is from Sima de los Huesos, about one kilometer from Gran Dolina, where a huge trove of mostly fragmentary but exquisitely preserved human fossils is dated to about 300,000 years ago.

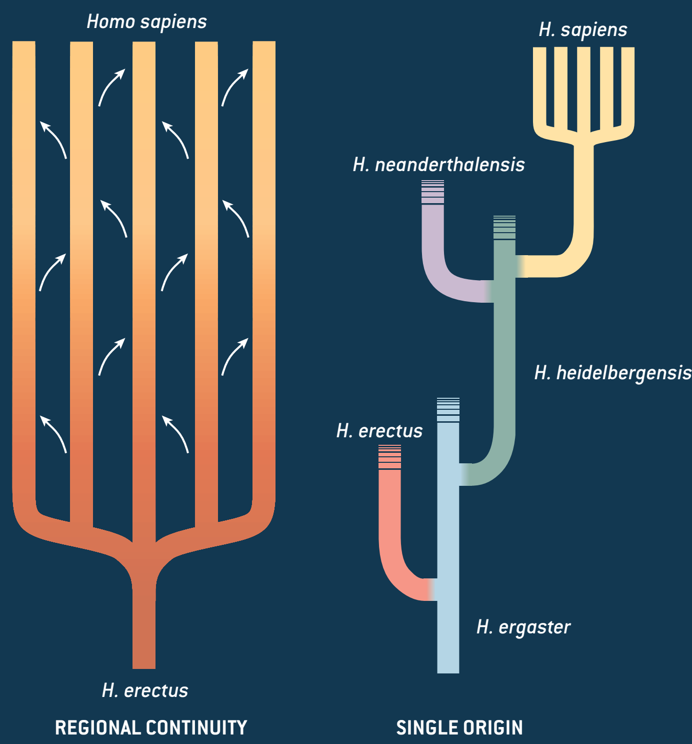
JAVIER TRUEBA *Madrid Scientific Films*

This is not the only possibility, however. With only a preliminary description of the very fragmentary Gran Dolina fossils available, it is hard to be sure, but it seems at least equally possible that they are the remains of hominids who made an initial foray out of Africa into Europe but failed to establish themselves there over the long term. Representatives of *H. heidelbergensis* are known in Africa as well, as long ago as 600,000 years ago, and this species quite likely recolonized Europe later on. There it would have given rise to the Neandertals, whereas a less specialized African population founded the lineage that ultimately produced *H. sapiens.*

At another site, just a kilometer from Gran Dolina, Juan-Luis Arsuaga of Complutense University in Madrid and his colleagues have discovered a huge cache of exquisitely preserved human fossils, about 400,000 years old. These are said to anticipate the Neandertals in certain respects, but they are not fully Neandertal by any means. And although they emphasize that the Neandertals (and possibly other related species) were an indigenous European development, these fossils from Sima de los Huesos ("Pit of the Bones") do not establish an unequivocal backward connection to their Gran Dolina neighbors.

Born in Africa

EVERY LONGTIME READER of *Scientific American* will be familiar with the competing models of "regional continuity" and "single African origin" for the emergence of our own species, *H. sapiens* [see "The Multiregional Evolution of Humans," on page 46; and "The Recent African Genesis of Humans," on page 54]. The first of these models holds that the highly archaic *H. erectus* (including *H. ergaster*) is nothing more than an ancient variant of *H. sapiens* and that for the past two million years the history of our lineage has been one of a braided stream of evolving populations of this species in all areas of the Old World, each adapting to local conditions, yet all consistently linked by gene exchange. The variation we see today among the major geographical populations of humans is, by this reckoning, simply the latest permutation of this lengthy process.



LEADING THEORIES of the origins of modern humans are contrasted in these diagrams. According to the notion of "regional continuity," all modern human populations trace their beginnings to *H. erectus,* but each regional population evolved along its own distinctive lines, exchanging enough genes with its neighbors (*arrows represent gene exchange*) to remain part of the same species; all eventually became *H. sapiens.* The "single origin" theory holds that *H. sapiens* descended from a single ancestral population that emerged in one place, probably Africa.

The other notion, which happens to coincide much better with what we know of evolutionary processes in general, proposes that all modern human populations are descended from a single ancestral population that emerged in one place at some time between about 150,000 and 100,000 years ago. The fossil evidence, thin as it is, suggests that this place of origin was somewhere in Africa (although the neighboring Levant is an alternative possibility); proponents of this scenario point to the support afforded by comparative molecular studies for the notion that all living humans are descended from an African population.

In view of what I have already said about the peripheral roles played in human evolution by early populations both in eastern Asia and Europe, it should come as no surprise that between these two possibilities my strong preference is for a single and comparatively recent origin for *H. sapiens*, very likely in Africa—the continent that, from the beginning, has been the engine of mainstream innovation in human evolution. The rise of modern humans is a recent drama that played out against a long and complex backdrop of evolutionary diversification among hominids, but the fossil record shows that from the earliest times, Africa was consistently the center from which new lineages of hominids sprang. Clearly, interesting evolutionary developments occurred in both Europe and eastern Asia, but they involved populations that were not only derived from but also eventually supplanted by emigrants from Africa. In Africa our lineage was born, and ever since its hominids were first emancipated from the forest edges, that continent has pumped out successive waves of emigrants to all parts of the Old World. What we see in the human fossil record as it stands today is without doubt a shadowy reflection at best of what must have been a complex sequence of events.

Most important, the new dates from eastern Asia show that human-population mobility dates right back to the origins of effectively modern bodily form. Finds from Europe demonstrate that although distinctive regional variants evolved there, the history of occupation of that region may itself not have been at all a simple one. As ever, though, new evidence of the remote human past has served principally to underline the complexity of events in our evolution. We can only hope that an improving fossil record will flesh out the details of what was evidently a richly intricate process of hominid speciation and population movement over the past two million years. SA

MORE TO EXPLORE

Three New Human Skulls from the Sima de los Huesos Middle Pleistocene Site in Sierra de Atapuerca, Spain. J.-L. Arsuaga et al. in *Nature,* Vol. 362, No. 6420, pages 534–537; April 8, 1993.

Age of the Earliest Known Hominids in Java, Indonesia. C. C. Swisher III et al. in *Science,* Vol. 263, No. 5150, pages 1118–1121; February 25, 1994.

Early *Homo* and Associated Artefacts from Asia. W. Huang et al. in *Nature,* Vol. 378, No. 6554, pages 275–278; November 16, 1995.

Whose Teeth? J. H. Schwartz and I. Tattersall in *Nature,* Vol. 381, No. 6579, pages 201–202; May 16, 1996.

Latest *Homo erectus* of Java: Potential Contemporaneity with *Homo sapiens* in Southeast Asia. C. C. Swisher III et al. in *Science,* Vol. 274, No. 5294, pages 1870–1874; December 13, 1996.

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

LAURIE GRACE; SOURCE: *THE LAST NEANDERTHAL,* BY IAN TATTERSALL (MACMILLAN, 1995)

the multiregional evolution of humans

By Alan G. Thorne and Milford H. Wolpoff

Both fossil and genetic evidence argues that ancient ancestors of various human groups lived where they are found today

Three decades ago the paleoanthropological community was locked in a debate about the origin of the earliest humans. The disagreement centered on whether the fossil *Ramapithecus* was an early human ancestor or ancestral to both human and ape lineages. Molecular biologists entered that discussion and supported the minority position held by one of us (Wolpoff) and his students that *Ramapithecus* was not a fossil human, as was then commonly believed. Their evidence, however, depended on a date for the chimpanzee-human divergence that was based on a flawed "molecular clock." We therefore had to reject their support.

Paleoanthropologists are again engaged in a debate, this time about how, when and where modern humans originated. On one side stand some researchers, such as ourselves, who maintain there is no single home for modern humanity—the idea that humans originated in Africa and then developed their modern forms in every area of the Old World. On the other side are researchers who claim that Africa alone gave birth to a new species of modern humans within the past 200,000 years. Once again the molecular geneticists have entered the fray, attempting to resolve it in favor of the African hypothesis with a molecular clock. Once again their help must be rejected because their reasoning is flawed.

Genetic research has undeniably provided one of the great insights of 20th-century biology: that all living people are extremely closely related. Our DNA similarities are far greater than the disparate anatomical variations of humanity might suggest. Studies of the DNA carried by the cell organelles called mitochondria, which are inherited exclusively from one's mother and are markers for maternal lineages, now play a role in the development of theories about the origin of modern humans across the globe.

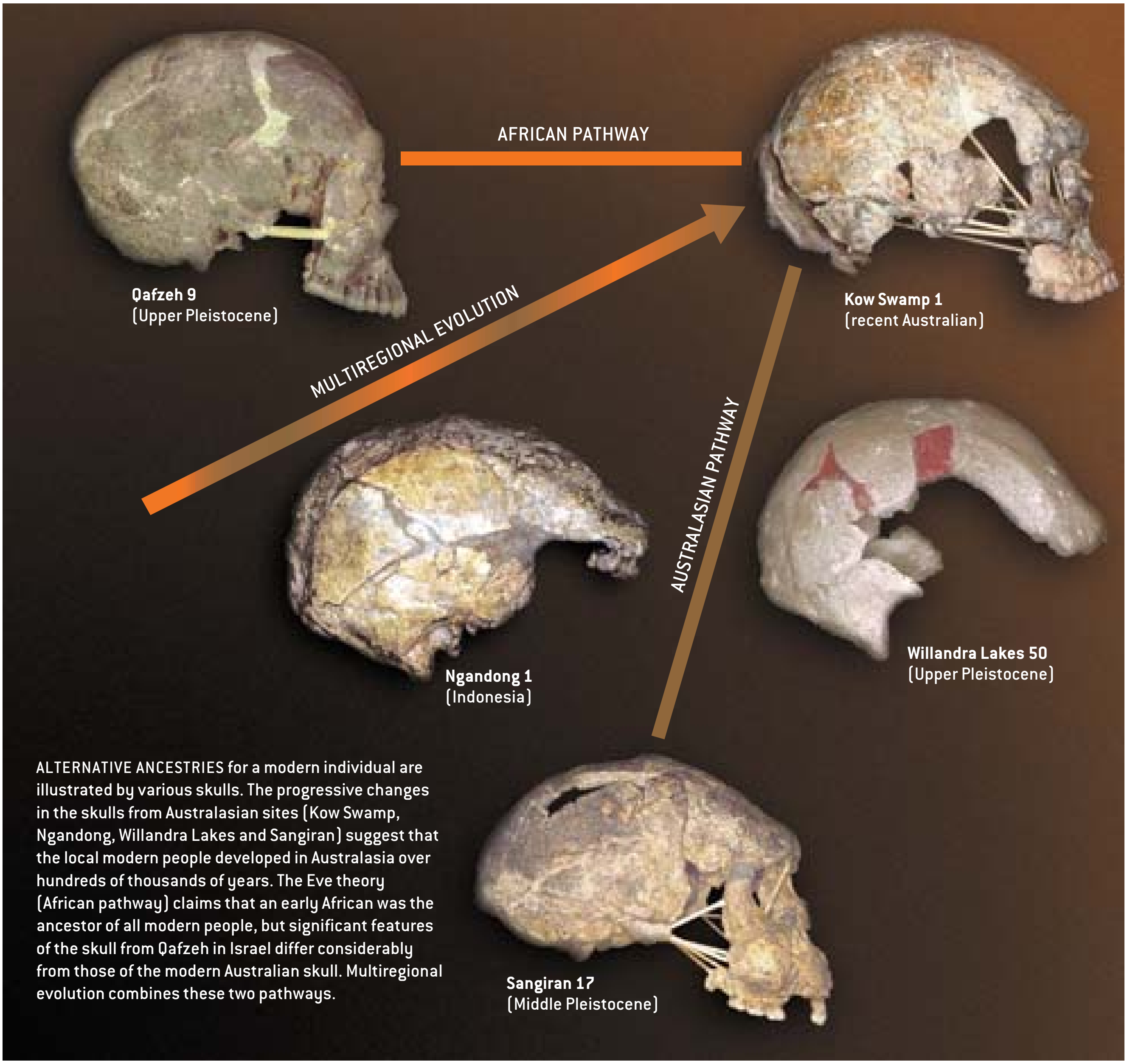
POINT-COUNTERPOINT: For an opposing view of how humankind arose around the globe, see "The Recent African Genesis of Humans," on page 54.

Nevertheless, mitochondrial DNA is not the only source of information we have on the subject. Fossil remains and artifacts also represent a monumental body of evidence—and, we maintain, a considerably more reliable one. The singular importance of the DNA studies is that they show that one of the origin theories discussed by paleontologists must be incorrect.

With Wu Xinzhi of the Institute of Vertebrate Paleontology and Paleoanthropology in Beijing, we developed an explanation for the pattern of human evolution that we described as multiregional evolution. We learned that some of the features that distinguish major human groups, such as Asians, Australian Aborigines and Europeans, evolved over a long period, roughly where these peoples are found today, whereas others spread throughout the human species because they were adaptive.

Multiregional evolution traces all modern populations back to when humans first left Africa almost two million

Updated from the April 1992 issue



ALTERNATIVE ANCESTRIES for a modern individual are illustrated by various skulls. The progressive changes in the skulls from Australasian sites (Kow Swamp, Ngandong, Willandra Lakes and Sangiran) suggest that the local modern people developed in Australasia over hundreds of thousands of years. The Eve theory (African pathway) claims that an early African was the ancestor of all modern people, but significant features of the skull from Qafzeh in Israel differ considerably from those of the modern Australian skull. Multiregional evolution combines these two pathways.

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years ago, through an interconnected web of ancient lineages in which the genetic contributions to all living peoples varied regionally and temporally. Today distinctive populations maintain their physical differences despite interbreeding and population movements; this situation has existed ever since humans first colonized Europe and Asia. Modern humanity originated within these widespread populations, and the modernization of our ancestors has been an ongoing process.

An alternative theory, developed by paleontologist William W. Howells of Harvard University as the "Noah's ark" model, posited that modern people arose recently in a single place and that they subsequently spread around the world, replacing other human groups. That replacement, recent proponents of the theory believe, must have been complete. From their genetic analyses, Allan C. Wilson and his colleagues at the University of California at Berkeley concluded that the evolutionary record of mitochondrial DNA could be traced back to a single female, dubbed "Eve" in one of Wilson's first publications on the subject, who lived in Africa approximately 200,000 years ago. Only mitochondrial DNA that can be traced to Eve, these theorists claim, is found among living people.

Paddling in a Pool

HOW COULD THIS BE? If Eve's descendants mixed with other peoples as their population expanded, we would expect to find other mitochondrial DNA lines present today, especially outside Africa, where Eve's descendants were invaders. The explanation offered for the current absence of other mitochondrial

SERIES OF CHINESE SKULLS shows continuity in form without evidence of a replacement by African characteristics. From left to right, the male skulls are from the Zhoukoudian Lower Cave (Middle Pleistocene period), Dali site (early Upper Pleistocene period) and Zhoukoudian Upper Cave (late Upper Pleistocene).

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DNA lineages is that none of the local women mixed with the invading modern men from Africa—which means that Eve founded a new species. Wilson's reconstruction of the past demands that over a period of no more than 150,000 years there was a complete replacement of all the preexisting hunter-gatherers in Africa and the rest of the then inhabited world; later, the original African features of the invading human species presumably gave way to the modern populational features we see in other regions.

An analogy can highlight the difference between our multiregional evolution theory and Wilson's Eve theory. According to multiregional evolution, the pattern of modern human origins is like several individuals paddling in separate corners of a pool; over time, they influence one another with the spreading ripples they raise (which are the equivalent of genes flowing between populations). In contrast, the total replacement requirement of the Eve theory dictates that a new swimmer must jump into the pool with such a splash that it drowns all the other swimmers. One of these two views of our origin must be incorrect.

Mitochondrial DNA is useful for guiding the development of theories, but only fossils provide the basis for refuting one idea or the other. At best, the genetic information explains how modern humans might have originated if the assumptions used in interpreting the genes are correct, but those conditions are only hypothetical, and one theory cannot be used to test another. The fossil record is the real evidence for human evolution, and it is rich in both human remains and archaeological sites stretching back for two million years. Unlike the genetic data, fossils can be matched to the predictions of theories about the past without relying on a long list of assumptions.

The Eve theory makes five predictions that the fossil evidence should corroborate. The first and major premise is that modern humans from Africa must have completely replaced all other human groups. Second, implicit within this idea is that the earliest modern humans appeared in Africa. Third, it also follows that the earliest modern humans in other areas should have African features. Fourth, modern humans and the people that they replaced should never have mixed or interbred. Fifth, outside of Africa an anatomical discontinuity should be evident between the human fossils before and after the replacement.

No Trace of Invasion

WE ARE SURPRISED by the allegation that beginning about 200,000 years ago one group of hunter-gatherers totally replaced all others worldwide. Although it is not uncommon for one animal species to replace another locally in a fairly short time, the claim that a replacement could occur rapidly in every climate and environment is unprecedented.

We would expect native populations to have an adaptive and demographic advantage over newcomers. Yet according to the Eve theory, it was the newcomers who had the upper hand. To use a modern analogy, however, despite the overwhelming forces of destructive technologies and infectious diseases, most American and Australian indigenous populations and their genes have continued to persist through adaptation and interbreeding.

If a worldwide invasion and complete replacement of all native peoples by Eve's descendants actually took place, we would expect to find at least some archaeological traces of the behaviors that made them successful. Yet examining the archaeology of Asia, we can find none. For instance, whereas the hand ax was a very common artifact in Africa, the technologies of eastern Asia did not include that tool either before or after the Eve period. There is no evidence for the introduction of a novel technology.

Geoffrey G. Pope of William Paterson University has pointed out that six decades of research on the Asian Paleolithic record have failed to unearth any indication of intrusive cultures or technologies. Types of artifacts found in the earliest Asian Paleolithic assemblages continue to appear into the very late Pleistocene. If invading Africans replaced the local Asian populations, they must have adopted the cultures and technologies of the people they replaced and allowed their own to vanish without a trace.

Archaeological evidence for an invasion is also lacking in western Asia, where Christopher B. Stringer of the Natural History Museum in London and a few other researchers believe the earliest modern humans outside of Africa can be found at the Skhūl and Qafzeh sites in Israel. The superb record at Qafzeh shows, however, that these "modern" people had a culture identical to that of their local Neandertal contemporaries: they made the same types of stone tools with the same technologies and at the same frequencies; they had the same stylized burial customs, hunted the same game and even used the same butchering procedures. Moreover, no evidence from the time when Eve's descendants are supposed to have left Africa suggests that any new African technology emerged or spread to other continents. All in all, as we understand them, the Asian data re-

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fute the archaeological predictions implied by the Eve theory.

Perhaps that refutation explains why Wilson turned to a different advantage, asserting that the invasion was successful because Eve's descendants carried a mitochondrial gene that conferred language ability. This proposal is yet to be widely accepted. Not only does it conflict with paleoneurology about the language abilities of archaic humans, but if it were true, it would violate the assumption required of Wilson's clock that mitochondrial mutations are neutral.

The remaining predictions of the Eve theory relate to abrupt anatomical changes and whether the earliest recognizably modern humans resembled earlier regional populations or Africans. With the fossil evidence known at this time, these questions can be resolved in at least two and possibly three regions of the world. The most convincing data are from southern and northern Asia.

The hominid fossils from Australasia (Indonesia, New Guinea and Australia) show an anatomical sequence during the Pleistocene that is uninterrupted by a new African species at any time. The distinguishing features of the earliest of these Javan remains, dated to more than one million years ago, show that they had developed when the region was first inhabited.

Compared with human fossils from other areas, the Javan people have thick skull bones, with strong continuous browridges forming an almost straight bar of bone across their eye sockets and a second well-developed shelf of bone at the back of the skull for the neck muscles. Above and behind the brows, the forehead is flat and retreating. These early Indonesians also have large projecting faces with massive rounded cheekbones. Their teeth are the largest known in archaic humans from that time.

A series of small but important features can be found on the most complete face and on other facial fragments that are preserved. These include such things as a rolled ridge on the lower edge of the eye sockets, a distinctive ridge on the cheekbone and a nasal floor that blends smoothly into the face.

Most of this unique morphology was retained for at least 700,000 years while other modern characteristics continued to evolve in the Javan people. For example, the large fossil series from Ngandong, which evidence suggests is as old as 200,000 years, offers striking proof that the Javans of that time had brain sizes similar to modern Australian populations but were otherwise remarkably similar to much earlier individuals in the region.

Australians and Eve

THE FIRST INHABITANTS of Australia arrived more than 60,000 years ago, and their behavior and anatomy were clearly those of modern human beings. Some of their skeletons show the Javan complex of features, along with further braincase expansions and other modernizations. Several dozen well-preserved fossils from the late Pleistocene and early Holocene demonstrate that the same combination of features that distinguished those Indonesian people from their contemporaries distinguishes some ancestors of indigenous Australians from other living peoples.

If the earliest Australians were all descendants of Africans, as the Eve theory requires, the continuity of fossil features would have to be no more than apparent. All the features of the early Javans would need to have evolved a second time in the population of invaders. The repeated evo-

THE AUTHORS

ALAN G. THORNE and *MILFORD H. WOLPOFF* have extensively studied the original fossil material on the origins of *Homo sapiens*. Thorne is adjunct fellow in the department of archaelogy and natural history at the Australian National University. He graduated from the University of Sydney in 1963 and later taught human anatomy at the medical school there. Thorne's excavations at Kow Swamp and Lake Mungo produced most of the Pleistocene human remains in Australia. Wolpoff is professor of anthropology at the University of Michigan at Ann Arbor, where he directs the paleoanthropology laboratory. He received his Ph.D. in 1969 from the University of Illinois at Urbana-Champaign. Wolpoff would like to thank lecturer Rachel Caspari of the University of Michigan for her help in drafting the epilogue.

lution of an individual feature would be conceivable but rare; the duplication of an entire set of unrelated features would be unprecedentedly improbable.

Northern Asia also harbors evidence linking its modern and ancient inhabitants. Moreover, because the similarities involve features that are different from those significant in Australasia, they compound the improbability of the Eve theory by requiring that a second complete set of features was duplicated in another population.

The very earliest Chinese fossils, about one million years old, differ from their Javan counterparts in many ways that parallel the differences between north Asians and Australians today. Our research with Wu Xinzhi and independent research by Pope demonstrated that the Chinese fossils are less robust, have smaller and more delicately built flat faces, smaller teeth and rounder foreheads separated from their arched browridges. Their noses are less prominent and more flattened at the top. Perhaps the most telling indication of morphological continuity concerns a peculiarity of tooth shapes. Prominently "shoveled" maxillary incisors, which curl inward along their internal edges, are found with unusually high frequency in living east Asians and in all the earlier human remains from that area. Studies by Tracey L. Crummett of San José State University show that the form of prehistoric and living Asian incisors is unique to the region.

This combination of traits is also exhibited at the Zhoukoudian Cave area in northern China, where fully a quarter of all known human remains from the Middle Pleistocene have been found. As Wu Rukang and Zhang Yinyun of the Chinese Academy of Sciences have pointed out, even within the 150,000 or more years spanned by the Zhoukoudian individuals, evolutionary changes in the modern direction, including increases in brain size and decreases in tooth size, can be seen. Our examinations of the Chinese specimens found no anatomical evidence that typically African features ever replaced those of the ancient Chinese in these regions. Instead there is a smooth transformation of the ancient populations into the living peoples of east Asia and the Americas.

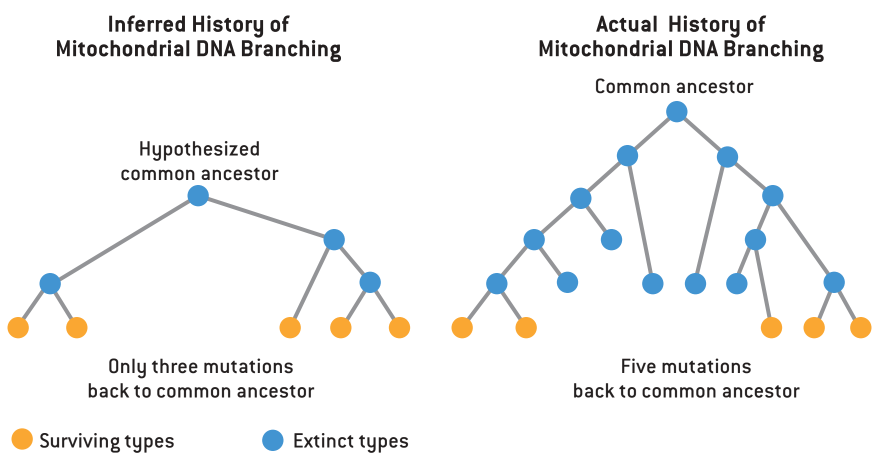
Paleontologists have long thought Europe would be the best source of evidence for the replacement of one group, Neandertals, by more modern humans. Even there, however, the fossil record shows that any influx of new people was neither complete nor without mixture. The most recent known Neandertal skull, from Saint-Césaire in France, apparently had the behavioral characteristics of the people who succeeded the Neandertals in Europe. The earliest post-Neandertal Europeans did not have a pattern of either modern or archaic African features, and many have been described as mixtures. Clearly, the European Neandertals were not completely replaced by Africans or by people from any other region.

Instead the evidence suggests that Neandertals either evolved into later humans or interbred with them, or both. David W. Frayer of the University of Kansas and Fred H. Smith, now at Loyola University of Chicago, have discovered that many allegedly unique Neandertal features are found in the Europeans who followed the Neandertals—the Upper Paleolithic, Mesolithic and later peoples. In fact, only a few Neandertal features completely disappear from the later European skeletal record.

Features that persist range from highly visible structures, such as the prominent shape and size of the nose of Neandertals and later Europeans, to much more minute traits, such as the form of the back of the skull and the details of its surface. A good example is the shape of the opening in the mandibular nerve canal, a spot on the inside of the lower jaw where dentists often give a pain-blocking injection. The upper part of the opening is covered by a broad bony bridge in many Neandertals, but in others the bridge is absent. In European fossils, 53 percent of the known Neandertals have the bridged form; 44 percent of their earliest Upper Paleolithic successors do, too, but in later Upper Paleolithic, Mesolithic and recent groups, the incidence drops to less than 6 percent.

In contrast, the bridged form is seen rarely in fossil or modern people from Asia and Australia. In Africa the few jaws that date from the suggested Eve period do not have it. This mandibular trait and others like it on the skull and the skeleton must have evolved twice in Europe for the Eve theory to be correct.

In sum, the evolutionary patterns of three different regions—Australasia, China and Europe—show that their earliest modern inhabitants do not have the complex of features that characterize Africans. There is no evidence that Africans completely replaced local groups. Contrary to the Eve theory predictions, the evidence points indisputably toward the continuity of various skeletal features between



MATERNAL LINEAGE RECONSTRUCTIONS based solely on the mitochondrial DNA types found today are inherently flawed. A hypothetical tree inferred from only five surviving types (*left*) leaves out the branches and mutational histories of extinct lines (*right*). Consequently, it sets the date for a common ancestor much too recently by presenting evidence of too few mutations.

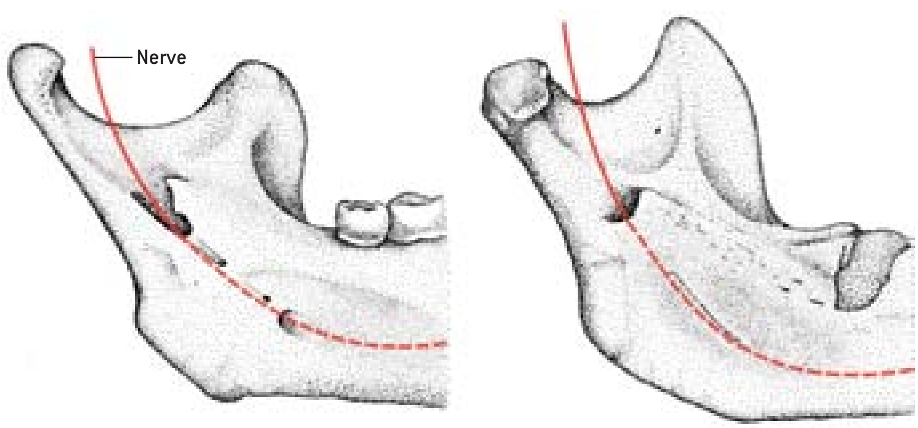
LAURIE GRACE

the earliest human populations and living peoples in different regions. Like genetic variation, human anatomical variation reflects significant differences in occurrence for characteristics found in all populations.

Focus on Features

IF AFRICA REALLY WAS the "Garden of Eden" from which all living people emerged, one would expect to find evidence for the transition from archaic to modern forms there—and only there. Following the lead of German researcher Reiner Protsch von Zieten of Goethe University in Frankfurt, Germany, some paleontologists did argue that modern *Homo sapiens* originated in Africa because they believed the earliest modern-looking humans were found there and that modern African features can be seen in these fossils. But the African evidence is similar to other regions in that modern *features* and not modern *populations* appear gradually and at about the same time as they appear elsewhere.

The African record differs from other regions in that the earlier, archaic populations are more variable and have no specifically African features. Modern-appearing humans and technologies first arise during the time between the last two glaciations. The technologies seem regional and impermanent, not continent-wide, but anatomical features are more widespread. We believe the main reason that Africa differs from the rest of the world at this time is that it is much more heavily populated—many, if not most, people lived there—and more population movement is outward than inward. The key specimens addressing modernity span the continent, from Omo Kibish in Ethiopia to Klasies River Mouth Cave in South Africa. The three Omo Kibish crania date roughly to between 100,000 and 200,000 years ago and are similar to other African remains from this time in combining ancient and modern features. Omo 2 is the more archaic, with a lower skull and a much broader and more angled cranial rear, resembling those of Laetoli 18 from Tanzania. Its browridge, however, is smaller than Omo 1's, which generally appears more



JAW MORPHOLOGY distinguishes many Neandertal skeletons. In most living people and in fossils, the rim around the mandibular nerve canal opening is grooved (*left*), but in a number of Neandertals, it was surrounded by a bony bridge (*right*). Some later Europeans also had this Neandertal feature, although it was less common.

PATRICIA J. WYNNE, BASED ON WORK BY MARIA OSTENDORF SMITH

modern in its higher skull and more rounded cranial rear. An associated mandible has a definite chin. Like the Levant remains of similar age from Qafzeh and Skhūl, even this small Omo sample combines a mix of archaic- and modern-appearing individuals.

The best excavated remains are from Klasies River and are securely dated to between 80,000 and 100,000 years ago. Some of the skull fragments are small and delicate and are said to "prove" that modern humans were present. Yet a comparative analysis of the entire sample by Rachel Caspari of the University of Michigan at Ann Arbor showed that others are not modern-looking at all. Two of the four lower jaws do not have chins, so thorough proof of a modern jaw is lacking. The single cheekbone from the site is not only larger than those of living Africans but also larger and more robust than those of both the earlier transitional humans and the archaic humans found in Africa. The claim that this sample contains modern Africans is highly dubious and does not justify the proposal that the earliest modern humans arose in Africa.

DNA Reanalyzed

WITH THE DISPROOF of the unique African ancestry theory for the living people of most areas and the lack of evidence showing that modern people first appeared in Africa, we conclude that the predictions of the Eve theory cannot be substantiated. We must wonder why the analysis of mitochondrial DNA suggested a theory so contrary to the facts. Perhaps the mitochondrial DNA has been misinterpreted.

The basic difficulty with using mitochondrial DNA to interpret recent evolutionary history stems from the very source of its other advantages: in reproduction, the mitochondrial DNA clones itself instead of recombining. Because mitochondrial DNA is transmitted only through the maternal line, the potential for genetic drift—the accidental loss of lines—is great: some mitochondrial DNA disappears every time a generation has no daughters.

The problem is analogous to the way in which family surnames are lost whenever there is a generation without sons. Imagine an immigrant neighborhood in a large city where all the families share a surname. An observer might assume that all these families were descended from a single successful immigrant family that completely replaced its neighbors. An alternative explanation is that many families immigrated to the neighborhood and intermarried; over time, all the surnames but one were randomly eliminated through the occasional appearance of families that had no sons to carry on their names. The surviving family name would have come from a single immigrant, but all the immigrants would have contributed to the genes of the modern population. In the same way, generations without daughters could have extinguished some lines of mitochondrial

DNA from Eve's descendants and her contemporaries.

Any interpretation of the surviving mitochondrial DNA mutations in populations consequently depends on a knowledge of how the size of the populations has changed over time and how many maternal lines may have vanished. Random losses from genetic drift alter a reconstruction of the tree of human mitochondrial DNA branching by pruning off signs of past divergences. Each uncounted branch is a mutation never taken into account when determining how long ago Eve lived.

Changes in population sizes have been dramatic. In parts of the Northern Hemisphere, some human populations shrank because of climate fluctuations during the ice ages. Archaeological evidence from both Africa and Australia suggests that similar population reductions may have taken place there as well. These reductions could have exacerbated genetic drift and the loss of mitochondrial DNA types.

At the end of the ice ages, along with the first domestication of animals and plants, some populations expanded explosively throughout a wide band of territory from the Mediterranean to the Pacific coast of Asia. Although the number of people expanded, the number of surviving mitochondrial DNA lines could not—those lost were gone forever.

Human populations with dissimilar demographic histories can therefore be expected to preserve different numbers of mutations since their last common mitochondrial DNA ancestor. They cannot be used together in a model that assumes the lengths of mitochondrial lineages reflect the age of their divergence. One cannot assume that all the variation in a population's mitochondrial DNA stems solely from mutations: the history of the population is also important.

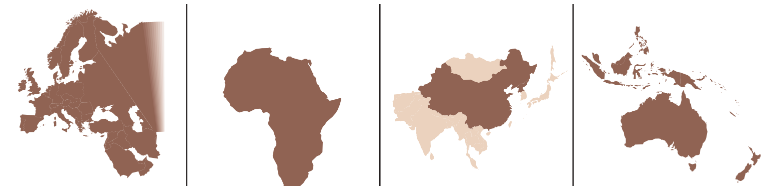
No Molecular Clock

A MAJOR PROBLEM with the Eve theory, therefore, is that it depends on an accurate molecular clock. Its accuracy must be based on mutation rates at many different loci, or gene positions. Yet genes in the mitochondrial DNA cannot recombine as genes in the nucleus do. All the mitochondrial DNA genes are the equivalent of a single locus. The molecular clock based on mitochondrial DNA is consequently unreliable.

Mitochondrial DNA may not be neutral enough to serve as the basis for a molecular clock, because some data suggest that it plays a role in several diseases. Because of random loss and natural selection, some vertebrate groups have rates of mitochondrial DNA evolution that are dramatically slower than Wilson and his colleagues have claimed for humans. A number of molecular geneticists disagree with Wilson's interpretation of the mitochondrial genetic data.

The molecular clock has, we believe, major problems: its rate of ticking has probably been overestimated in some cases and underestimated in others. Rebecca L. Cann of the University of Hawaii at Manoa and Mark Stoneking of Pennsylvania State University, two of Wilson's students, have acknowledged that their clock was able to date Eve to only between 50,000 and 500,000 years ago. Because of the uncertainty, we believe that for the past half a million years or more of human evolution, for all intents and purposes, there is no molecular clock.

Putting aside the idea of a clock, one can interpret the genetic data in a much more reasonable way: Eve carried the



		EUROPE AND LEVANT	AFRICA	EAST ASIA	AUSTRALASIA
UPPER PLEISTOCENE	LATE	Lagar Velho, Předmostí, Mladeč	Afalou, Lukenya	Shandingdong, Ziyang, Liujiang	Kow Swamp, Keilor, Willandra Lakes 50
	MIDDLE	Vindija, Kebara, La Ferrassie, La Chapelle	Dar es Soltan	Maba	Lake Mungo 1, 3
	EARLY	Qafzeh, Krapina	Klasies, Omo Kibish	Dingcun, Xujiayao	
MIDDLE PLEISTOCENE	LATE	Ehringsdorf, Biache, Zuttiyeh	Ngaloba, Florisbad	Dali, Jinniushan	Sambungmachan 1, 3, Ngandong
	MIDDLE	Sima de los Huesos, Petralona, Arago, Steinheim	Kabwe, Ndutu	Zhoukoudian H, Hexian, Nanjing	
	EARLY	Gran Dolina	Bodo, Ternifine, Olduvai 12	Zhoukoudian D, E, L, Chenjiawo, Yunxian	Sangiran 2, 10, 12, 17, Trinil
LOWER PLEISTOCENE	LATE		Buia, Bouri, Olduvai 9	Gongwangling, Yuanmou	
	MIDDLE		Konso Gardula, Lake Turkana (east) 992		Sangiran 4, 27, 31
	EARLY	Dmanisi	Lake Turkana (east) 730, 3883, 3733 (west) 15000		Mojokerto

WELL-DATED FOSSILS point to the continuous, linked evolution of modern humans at sites around the world. Modern human groups in different regions developed distinct anatomical identities. Nevertheless, gene flow between the groups through interbreeding spread important changes throughout and was sufficient to maintain humans as a single species.

LAURIE GRACE

most recent common ancestor of all existing human mitochondria, but she is not the most recent common ancestor of all living people. Mitochondrial history is not population history, just as the history of names mentioned earlier is not the same as the history of populations. Such an interpretation can fully reconcile the fossil record with the genetic data. We propose that future research might more productively focus on attempts to disprove this hypothesis than on attempts to recalibrate a clock that does not work.

The dramatic genetic similarities across the entire human race show the consequences of linkages between people that extend to when our ancestors first populated the Old World. They are the results of an ancient history of population connections and mate exchanges that has characterized the human race since its inception. Human evolution happened everywhere because every area was always part of the whole.

Neither anatomical nor genetic analyses provide a basis for the Eve theory. Instead the fossil record and the interpretation of mitochondrial DNA variation can be synthesized to form a view of human origins that does fit all the currently known data. This synthetic view combines the best sources of evidence about human evolution by making sense of the archaeological and fossil record and the information locked up in the genetic variation of living people all over the world. The richness of human diversity, which contrasts with the closeness of human genetic relationships, is a direct consequence of evolution. We are literally most alike where it matters—under the skin.

Epilogue

IN THE DECADE since this article originally appeared in *Scientific American,* significant discoveries and analyses have changed the nature of the debate about the pattern of human evolution. The finding of a 25,000-year-old Portuguese child from Lagar Velho who has a combination of Neandertal and "modern European" characteristics suggests that Neandertals mixed with other populations and therefore were the same species. A million-year-old Ethiopian skull found in Bouri that is similar to Asian *Homo erectus* remains, and is anatomically intermediate between earlier and later Africans, suggests that the evolving *Homo* lineage in the early and middle Pleistocene was a single species, not a mix of different species evolving in different places. Early specimens of "moderns" are also instructive. In the Australian case, significant ancestry in the Ngandong fossils from Indonesia could not be excluded. In the European case, a 50 percent contribution by Neandertals for the earliest moderns could not be excluded. These anatomical studies support the idea of multiregional evolution.

Meanwhile genetic research has become more definitive. The rate of change of mitochondrial DNA (mtDNA) was first estimated over millions of years from comparisons with chimpanzees, but with modern intergenerational studies the rates have been found to be many times as fast. The effects of accidental loss of mtDNA variation were greatly underestimated. Then came the realization that because mtDNA is a single molecule, it cannot recombine or have crossover, so selection on any part of it is selection on the whole. Natural selection has repeatedly reduced its variation; the same has been found in the nonrecombining parts of the nuclear chromosomes. If selection and not population history accounts for mtDNA variation, it does not address the Eve theory.

MtDNA has also been recovered from Neandertals and from ancient Australians, and some of it is unlike the modern form. This evidence addresses the issues of how, and how quickly, mtDNA changes, but it does not help resolve the pattern of evolution. Also less than helpful is the possibility that all the Neandertal mtDNA recovered so far may have been altered by contamination or DNA breakdown. This is suspected because the most recent Neandertal mtDNA is most like that of living humans, whereas the oldest is least alike—the opposite of what we would expect from unaltered Neandertal mtDNA evolving in a separate genetic line.

More recently, researchers have obtained sequences of nuclear DNA, and they provide a different picture. Most fundamentally, nuclear genes prove to be older than the mitochondrial gene, in some cases by millions of years. If the origin of today's mtDNA was also the origin of a new species, all the older nuclear variations should have been eliminated, and most genes should be the approximate age of the species or younger. This is the most significant disproof of the Eve theory. Nuclear genes are much older than Eve and preserve evidence of past migrations, mostly out of Africa but also from some other regions, followed by population mixtures that preserve past variation. This genetic evidence significantly supports multiregional evolution.

A greater focus on epistemology also has made it clear that the original debate over modern human origin was indeed a debate about the *pattern* of human evolution. The multiregional model is an intraspecific, network model, fundamentally different from the tree-based Eve theory. This was important because an assumption that tree (branching) attributes describe population histories underlies the acceptance of gene trees as population trees. The increasing molecular and anatomical evidence against recent speciation underscores the appropriateness of such a network model. Molecular and anatomical variation reflect something different than the time since the separation of populations. They include the complexities of gene flow between groups, different histories of selection, and different population structures across space and over time. SA

MORE TO EXPLORE

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the recent African Genesis of humans

Genetic studies reveal that an African woman from less than 200,000 years ago was our common ancestor

By Rebecca L. Cann and Allan C. Wilson

POINT-COUNTERPOINT: For an opposing view of how humankind arose around the globe, see "The Multiregional Evolution of Humans," on page 46.

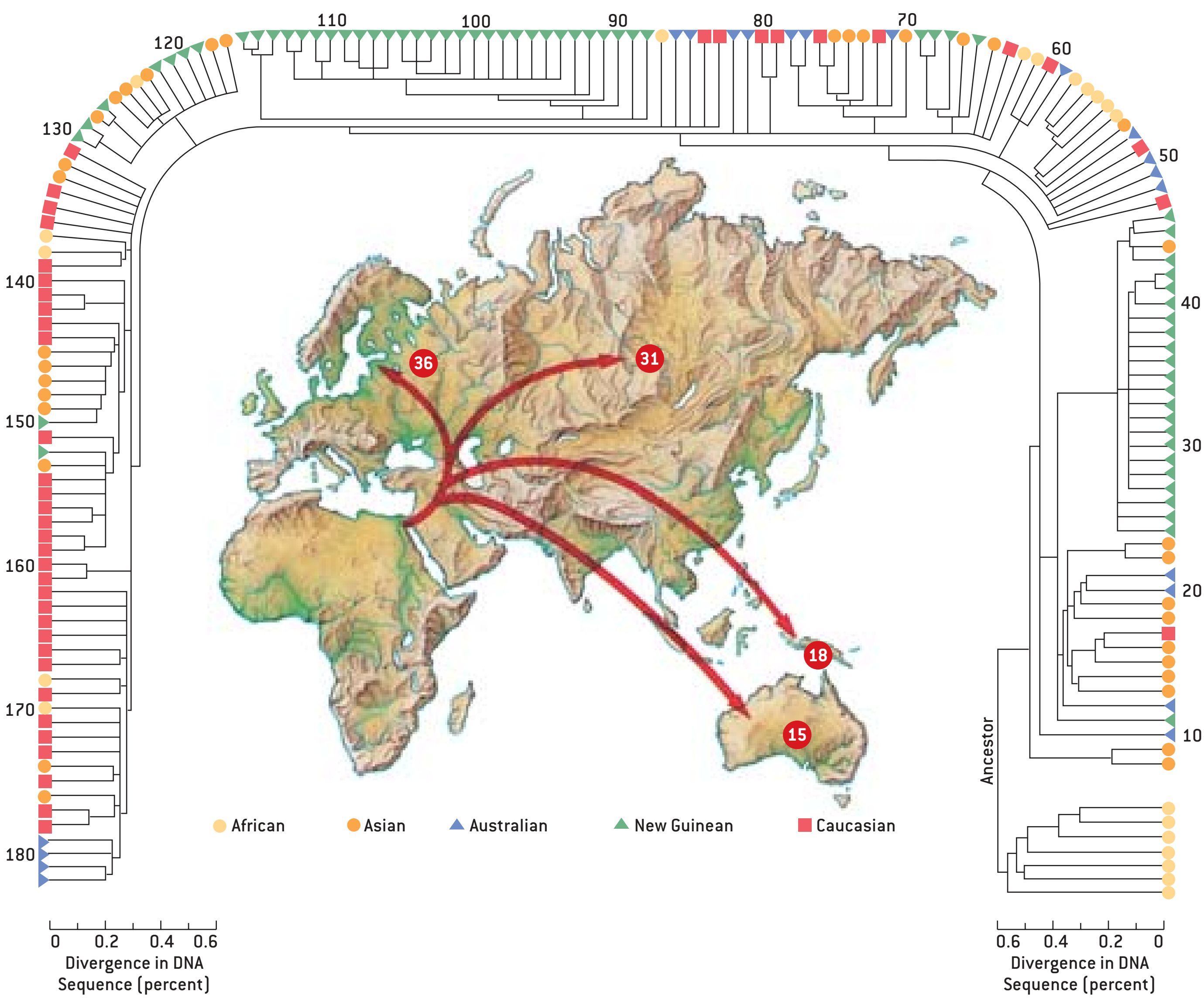
Updated from the April 1992 issue

In the quest for the facts about human evolution, we molecular geneticists have engaged in two major debates with the paleontologists. Arguing from their fossils, most paleontologists had claimed the evolutionary split between humans and the great apes occurred as long as 25 million years ago. We maintained human and ape genes were too similar for the schism to be more than a few million years old. After 15 years of disagreement, we won that argument when the paleontologists admitted we had been right and they had been wrong.

Once again we are engaged in a debate, this time over the latest phase of human evolution. The paleontologists say modern humans evolved from their archaic forebears around the world over the past million years. Conversely, our genetic comparisons convince us that all humans today can be traced along maternal lines of descent to a woman who lived about 200,000 years ago, probably in Africa. Modern humans arose in one place and spread elsewhere.

Neither the genetic information of living subjects nor the fossilized remains of dead ones can explain in isolation how, when and where populations originated. But the former evidence has a crucial advantage in determining the structure of family trees: living genes must have

AFRICAN ORIGIN for all modern humans is indicated by the genetic evidence. A genealogy based on 182 current mitochondrial DNA types (*outer edges*) points to the existence of a common female ancestor from Africa. The arrows on the map (*center*) indicate the route and the minimum number of unrelated females (*red circles*) who colonized various areas, as inferred from the branching pattern.



JOE LeMONNIER (*map*); LAURIE GRACE

ancestors, whereas dead fossils may not have descendants. Molecular biologists know the genes they are examining must have been passed through lineages that survived to the present; paleontologists cannot be sure that the fossils they examine do not lead down an evolutionary blind alley.

The molecular approach is free from several other limitations of paleontology. It does not require well-dated fossils or tools from each part of the family tree it hopes to describe. It is not vitiated by doubts about whether tools found near fossil remains were in fact made and used by the population those remains represent. And it concerns itself with a set of characteristics that is complete and objective.

A genome, or full set of genes, is complete because it holds all the inherited biological information of an individual. Moreover, all the variants on it that appear within a population—a group of individuals who breed only with one another—can be studied, so specific peculiarities need not distort the interpretation of the data. Genomes are objective because they present evidence that has not been defined, at the outset, by any particular evolutionary model. Gene sequences are empirically verifiable and not shaped by theoretical prejudices.

The fossil record, on the other hand, is infamously spotty because a handful of surviving bones may not represent the majority of organisms that left no trace of themselves. Fossils cannot, in principle, be interpreted objectively: the physical characteristics by which they are classified necessarily reflect the models the paleontologists wish to test. If one classifies, say, a pelvis as human because it supported an upright posture, then one is presupposing that bipedalism distinguished early hominids from apes. Such reasoning tends to circularity. The paleontologist's perspective therefore contains a built-in bias that limits its power of observation.

As such, biologists trained in modern evolutionary theory must reject the notion that the fossils provide the most direct evidence of how human evolution actually proceeded. Fossils help to fill in the knowledge of how biological processes worked in the past, but they should not blind us to new lines of evidence or new interpretations of poorly understood and provisionally dated archaeological materials.

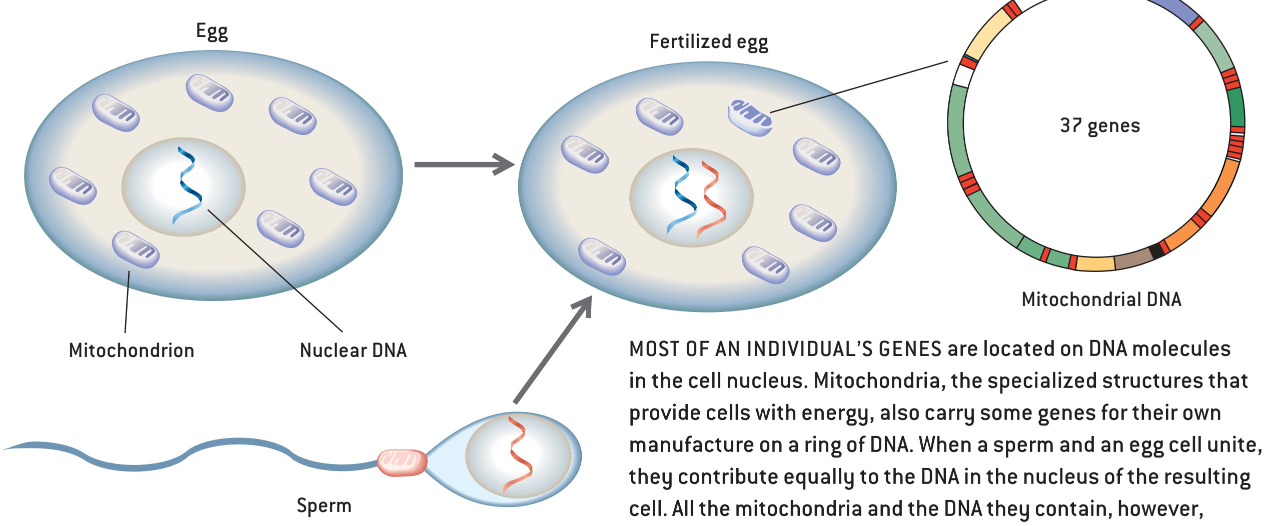
Molecular Clock

ALL THE ADVANTAGES of our field stood revealed in 1967, when Vincent M. Sarich, working in Wilson's laboratory at the University of California at Berkeley, challenged a fossil primate called *Ramapithecus*. Paleontologists had dated its fossils to about 25 million years ago. On the basis of the enamel thickness of the molars and other skeletal characteristics, they believed that *Ramapithecus* appeared after the divergence of the human and ape lineages and that it was directly ancestral to humans.

Sarich measured the evolutionary distance between humans and chimpanzees by studying their blood proteins, knowing the differences reflected mutations that have accumulated since the species diverged. (At the time, it was much easier to compare proteins for subtle differences than to compare the genetic sequences that encode the proteins.) To check that mutations had occurred equally fast in both lineages, he compared humans and chimpanzees against a reference species and found that all the genetic distances tallied.

Sarich now had a molecular clock; the next step was to calibrate it. He did so by calculating the mutation rate in other species whose divergences could be reliably dated from fossils. Finally, he applied the clock to the chimpanzee-human split, dating it to between five million and seven million years ago—far later than anyone had imagined.

The Inheritance of Mitochondrial DNA



MOST OF AN INDIVIDUAL'S GENES are located on DNA molecules in the cell nucleus. Mitochondria, the specialized structures that provide cells with energy, also carry some genes for their own manufacture on a ring of DNA. When a sperm and an egg cell unite, they contribute equally to the DNA in the nucleus of the resulting cell. All the mitochondria and the DNA they contain, however, derive from the egg. Studies of mitochondrial DNA can reveal an individual's maternal ancestry.

LAURIE GRACE

Mitochondrial DNA is inherited from the mother alone, so all of it today had one female ancestor.

At first, most paleontologists clung to the much earlier date. But new fossil finds undermined the human status of *Ramapithecus:* it is now clear that *Ramapithecus* is actually *Sivapithecus,* a creature ancestral to orangutans and not to any of the African apes at all. Moreover, the age of some sivapithecine fossils was downgraded to only about six million years. By the early 1980s almost all paleontologists came to accept Sarich's more recent date for the separation of the human and ape lines. Those who continue to reject his methods have been reduced to arguing that Sarich arrived at the right answer purely by chance.

Two novel concepts emerged from the early comparisons of proteins from different species. One was the concept of inconsequential, or neutral, mutations. Molecular evolution appears to be dominated by such mutations, and they accumulate at surprisingly steady rates in surviving lineages. In other words, evolution at the gene level results mainly from the relentless accumulation of mutations that seem to be neither harmful nor beneficial. The second concept, molecular clocks, stemmed from the observation that rates of genetic change from point mutations (changes in individual DNA base pairs) were so steady over long periods that one could use them to time divergences from a common stock.

Mitochondrial Clue

WE COULD BEGIN to apply these methods to the reconstruction of later stages in human evolution only after 1980, when DNA restriction analysis made it possible to explore genetic differences with high resolution. Workers at Berkeley, including Wes Brown, Mark Stoneking and us, applied the technique to trace the maternal lineages of people sampled from around the world.

The DNA we studied resides in the mitochondria, cellular organelles that convert food into a form of energy the rest of the cell can use. Unlike the DNA of the nucleus, which forms bundles of long fibers, each consisting of a protein-coated double helix, the mitochondrial DNA comes in small, two-stranded rings. Whereas nuclear DNA encodes an estimated 100,000 genes—most of the information needed to make a human being—mitochondrial DNA encodes only 37. In this handful of genes, every one is essential: a single adverse mutation in any of them is known to cause some severe neurological diseases.

For the purpose of scientists studying when lineages diverged, mitochondrial DNA has two advantages over nuclear DNA. First, the sequences in mitochondrial DNA that interest us accumulate mutations rapidly and steadily, according to empirical observations. Because many mutations do not alter the mitochondrion's function, they are effectively neutral, and natural selection does not eliminate them.

This mitochondrial DNA therefore behaves like a fast-ticking clock, which is essential for identifying recent genetic changes. Any two humans chosen randomly from anywhere on the planet are so alike in most of their DNA sequences that we can measure evolution in our species only by concentrating on the genes that mutate fastest. Genes controlling skeletal characters do not fall within this group.

Second, unlike nuclear DNA, mitochondrial DNA is inherited from the mother alone, unchanged except for chance mutations. The father's contribution ends up on the cutting-room floor, as it were. The nuclear genes, to which the father does contribute, descend in what we may call ordinary lineages, which are of course important to the transmission of physical characteristics. For our studies of modern human origins, however, we focus on the mitochondrial, maternal lineages.

Maternal lineages are closest among siblings because their mitochondrial DNA has had only one generation in which to accumulate mutations. The degree of relatedness declines step by step as one moves along the pedigree, from first cousins descended from the maternal grandmother, to second cousins descended from a common maternal great-grandmother and so on. The farther back the genealogy goes, the larger the circle of maternal relatives becomes, until at last it embraces everyone alive.

Logically, then, all human mitochondrial DNA must have had an ultimate common female ancestor. But it is easy to show she did not necessarily live in a small population or constitute the only woman of her generation. Imagine a static population that always contains 15 mothers. Every new generation must contain 15 daughters, but some mothers will not produce a daughter, whereas others will produce two or more. Because maternal lineages die out whenev-

THE AUTHORS

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er there is no daughter to carry it on, it is only a matter of time before all but one lineage disappears. In a stable population, the time for this fixation of the maternal lineage to occur is the length of a generation multiplied by twice the population size.

Eve in Africa

ONE MIGHT REFER to the lucky woman whose lineage survives as Eve. Bear in mind, however, that other women were living in Eve's generation and that Eve did not occupy a specially favored place in the breeding pattern. She is purely the beneficiary of chance. Moreover, if we were to reconstruct the ordinary lineages for the population, they would trace back to many of the men and women who lived at the same time as Eve. Population geneticists Daniel L. Hartl, now at Harvard University, and Andrew G. Clark, now at Cornell University, estimate that as many as 10,000 people could have lived then. The name "Eve" can therefore be misleading—she is not the ultimate source of all the ordinary lineages, as the biblical Eve was.

From mitochondrial DNA data, it is possible to define the maternal lineages of living individuals all the way back to a common ancestor. In theory, a great number of different genealogical trees could give rise to any set of genetic data. To recognize the one that is most probably correct, one must apply the parsimony principle, which requires that subjects be connected in the simplest possible way. The most efficient hypothetical tree must be tested by comparison with other data to see whether it is consistent with them. If the tree holds up, it is analyzed for evidence of the geographic history inherent in elements.

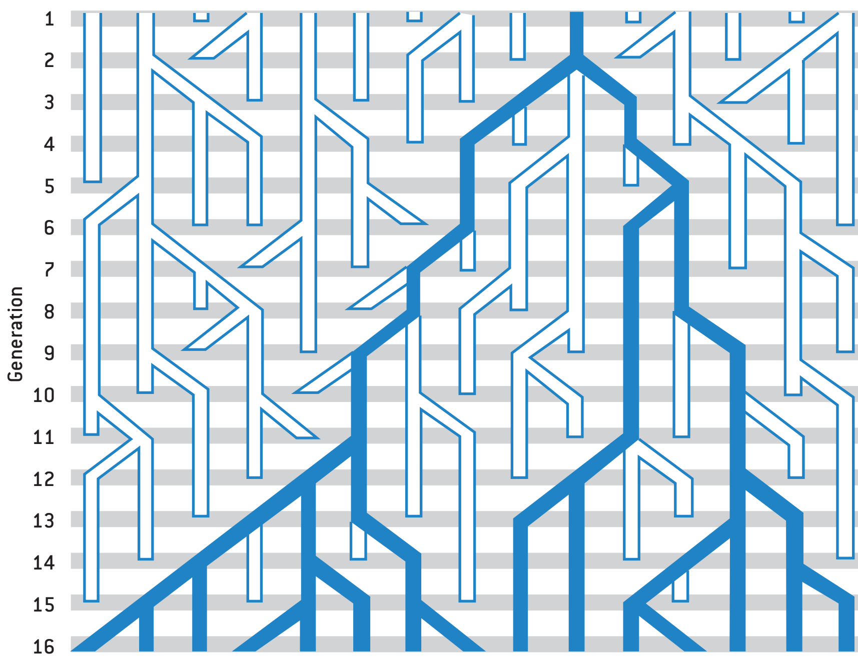
In 1988 Thomas D. Kocher of Berkeley (now at the University of New Hampshire) applied just such a parsimonious interpretation to the interrelatedness of the mitochondrial DNA of 14 humans from around the world. He determined that 13 branching points were the fewest that could account for the differences he found. Taking the geographic considerations into account, he then concluded that Africa was the ultimate human homeland: the global distribution of mitochondrial DNA types he saw could then be explained most easily as the result of no more than three migration events to other continents.

A crucial assumption in this analysis is that all the mitochondrial lineages evolve at the same rate. So when Kocher conducted his comparison of the human mitochondrial DNAs, he also included analogous sequences from four chimpanzees. If the human lineages had differed in the rate at which they accumulated mutations, then some of the 14 human sequences would be significantly closer or farther away from the chimpanzee sequences than others. In fact, all 14 human sequences are nearly equidistant from the chimpanzee sequences, which implies that the rates of change among humans are fairly uniform.

The chimpanzee data also illustrated how remarkably homogeneous humans are at the genetic level: chimpanzees commonly show as much as 10 times the genetic variation of humans. That fact alone suggests that all of modern humanity sprang from a relatively small stock of common ancestors.

Working at Berkeley with Stoneking, we expanded on Kocher's work by examining a larger genealogical tree made up of 182 distinct types of mitochondrial DNA from 241 individuals. The multiple occurrences of mitochondrial DNA types were always found among people from the same continent and usually in persons who lived within 100 miles of one another. Because the tree we constructed had two main branches, both of which led back to Africa, it, too, supported the hypothesis that Africa was the place of origin for modern humans.

One noteworthy point that jumps out of our study is that although geographic barriers do influence a population's mitochondrial DNA, people from a given continent do not generally all belong to the same maternal lineage. The New Guineans are typical in this respect. Their genetic diversity had been suspected from linguistic analyses of the remarkable variety of language families—usually classified as Papuan—spoken on this one island [see "The Austronesian Dispersal and the Origin of Languages," by Peter Bellwood; SCIENTIFIC AMERICAN, July 1991]. On our genealogical tree,



UNIVERSAL MATERNAL ANCESTOR can be found for all the members of any population. The example shown here traces the lineages of 15 females in a stable population. In each generation, some maternal lineages proliferate and others become extinct. Eventually, by chance, one maternal lineage (*dark blue*) replaces all the others.

LAURIE GRACE

Huge levels of gene flow between early continents—very unlikely—would have been needed for multiregionalism.

New Guineans showed up on several different branches, which proved that the common female ancestor of all New Guineans was not someone in New Guinea. The population of New Guinea must have been founded by many mothers whose maternal lineages were most closely related to those in Asia.

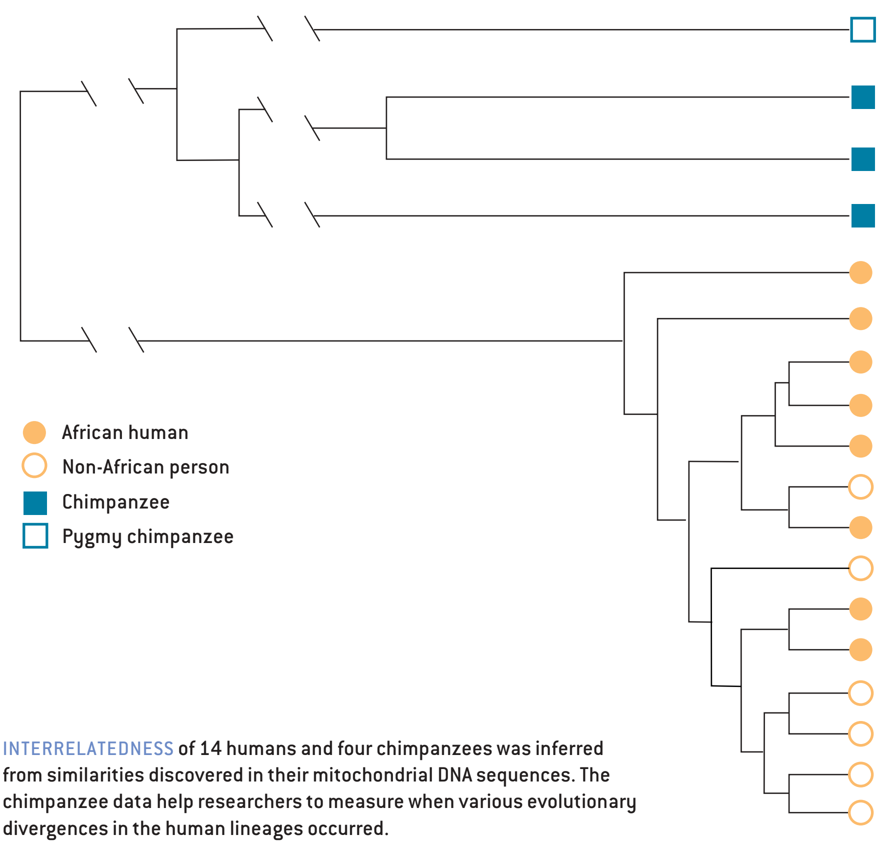
That finding is what one would expect if the African origin hypothesis were true: as people walked east out of Africa, they would have passed through Asia. Travel was probably slow, and during the time it took to reach New Guinea, mutations accumulated both in the lineages that stayed in Asia and in those that moved on.

Thus, people who are apparently related by membership in a common geographic race need not be very closely related in their mitochondrial DNA. Mitochondrially speaking, races are not like biological species. We propose that the anatomical characteristics uniting New Guineans were not inherited from the first settlers. They evolved after people colonized the island, chiefly as the result of mutations in nuclear genes spread by sex and recombination throughout New Guinea. Similarly, the light skin color of many whites is probably a late development that occurred in Europe after that continent was colonized by Africans.

During the early 1980s, when we were constructing our genealogical tree, we had to rely on black Americans as substitutes for Africans, whose mitochondrial DNA was difficult to obtain in the required quantities. Fortunately, the development of a technique called the polymerase chain reaction has eliminated that constraint. The reaction makes it possible to duplicate DNA sequences easily, ad infinitum; a small starting sample of DNA can expand into an endless supply.

The polymerase chain reaction enabled Linda Vigilant of Pennsylvania State University to redo our study using mitochondrial DNA data from 120 Africans, representing six diverse parts of the sub-Saharan region. Vigilant traced a genealogical tree whose 14 deepest branches lead exclusively to Africans and whose 15th branch leads to both Africans and non-Africans. The non-Africans lie on shallow secondary branches stemming from the 15th branch. Considering the number of African and non-African mitochondrial DNAs surveyed, the probability that the 14 deepest branches would be exclusively African is one in 10,000 for a tree with this branching order.

Satoshi Horai and Kenji Hayasaka of the National Institute of Genetics in Mishima, Japan, analogously surveyed population samples that included many more Asians and individuals from fewer parts of Africa; they, too, found that the mitochondrial lineages led back to Africa. We estimate the odds of their arriving at that conclusion accidentally were only four in 100. Although these statistical evaluations are not strong or rigorous tests, they do make it seem likely that the theory of an African origin for human mitochondrial DNA is now fairly secure.



INTERRELATEDNESS of 14 humans and four chimpanzees was inferred from similarities discovered in their mitochondrial DNA sequences. The chimpanzee data help researchers to measure when various evolutionary divergences in the human lineages occurred.

LAURIE GRACE

200,000 Years or Less

BECAUSE OUR COMPARISONS with the chimpanzee data showed that the human mitochondrial DNA clock has ticked steadily for millions of years, we knew it should be possible to calculate when the common mother of humanity lived. We assumed that the human and chimpanzee lineages diverged five million years ago, as Sarich's work had shown. We then calculated how much humans had diverged from one another relative to how much they had diverged from chimpanzees—that is, we found the ratio of mitochondrial DNA divergence among humans to that between humans and chimpanzees.

Using two different sets of data, we determined that the ratio was less than 1:25. Human maternal lineages therefore grew apart in a period less than $1/25$ as long as five million years, or less than 200,000 years. With a third set of data on changes in a section of the mitochondrial DNA called the control region, we arrived at a more ancient date for the common mother. That date is less certain, however, because questions remain about how to correct for multiple mutations that occur within the control region.

One might object that a molecular clock known to be accurate over five million years could still be unreliable for shorter periods. It is conceivable, for example, that intervals of genetic stagnation might be interrupted by short bursts of change when, say, a new mutagen enters the environment, or a virus infects the germ-line cells, or intense natural selection affects all segments of the DNA. To rule out the possibility that the clock might run by fits and starts, we ran a test to measure how much mitochondrial DNA has evolved in populations founded at a known time.

The aboriginal populations of New Guinea and Australia are estimated to have been founded less than 50,000 to 60,000 years ago. The amount of evolution that has since occurred in each of those places seems about one third of that shown by the whole human species. Accordingly, we can infer that Eve lived three times 50,000 to 60,000 years ago, or roughly 150,000 to 180,000 years ago. All our estimates thus agree that the split happened not far from 200,000 years ago.

Those estimates fit with at least one line of fossil evidence. The remains of anatomically modern people appear first in Africa, then in the Middle East, and later in Europe and east Asia. Anthropologists have speculated that in east Africa the transition from anatomically archaic to modern people took place as recently as 130,000 years ago [see "The Emergence of Modern Humans," by Christopher B. Stringer; SCIENTIFIC AMERICAN, December 1990].

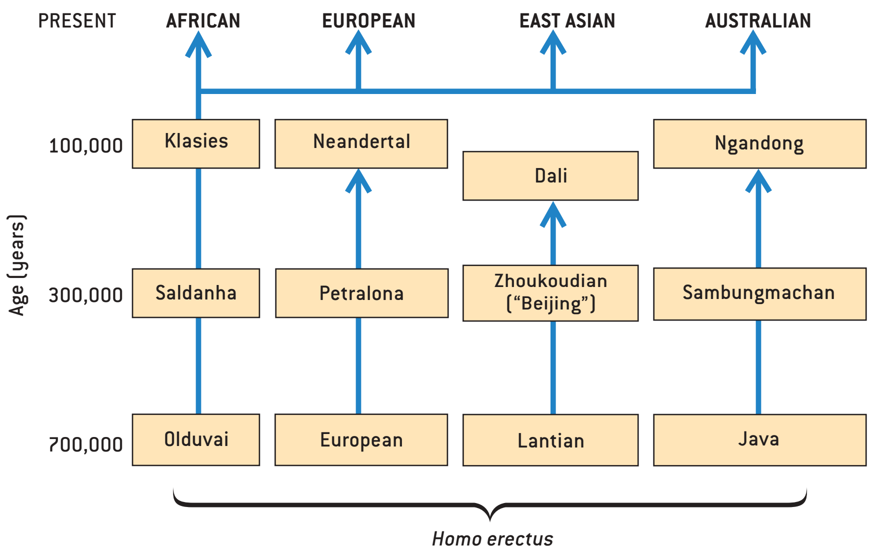
On the other hand, a second line of evidence appears to conflict with this view. The fossil record shows clearly that the southern parts of Eurasia were occupied by archaic people who had migrated from Africa to Asia nearly a million years ago. Such famous fossils as Java Man and Beijing Man are of this type. This finding and the hypothesis that the archaic Eurasian population underwent anatomical changes that made them resemble more modern people led to the multiregional evolution model: similar evolutionary changes in separate geographic regions converted the inhabitants from archaic small-brained types to modern big-brained types.

Huge levels of gene flow between continents, however, would be necessary to maintain human populations as one biological species. The multiregional evolution model also predicts that at least some genes in the modern east Asian population would be linked more closely to those of their archaic Asian predecessors than to those of modern Africans. We would expect to find deep lineages in Eurasia, especially in the Far East. Yet surveys in our laboratories and in others, involving more than 1,000 people from Eurasia and its mitochondrial DNA satellites (Australia, Oceania and the Americas), have given no hint of that result.

It therefore seems very unlikely that any truly ancient lineages survive undetected in Eurasia. We simply do not see the result predicted by the regional model. Moreover, geneticists such as Masatoshi Nei of Pennsylvania State University, Kenneth K. Kidd of Yale University, James Wainscoat of the University of Oxford and Luigi L. Cavalli-Sforza of Stanford University have found support for an African origin model in their studies of nuclear genes.

Multiregional Mystery

PROPONENTS OF the multiregional evolution model typically emphasize that they have documented a continuity of anatomical morphologies between the archaic and modern residents of different regions; they insist that these morphologies would be unlikely to evolve independently in any invading people. For that argument to hold true, however, it must also be shown that the cranial features in question are truly indepen-



ARCHAIC HUMAN GROUPS were gradually replaced throughout the Old World by modern humans who arose in Africa. Archaic females do not seem to have contributed mitochondrial genes to the modern people of Europe, east Asia and Australia.

LAURIE GRACE

dent of one another—that is, that natural selection would not tend to favor certain constellations of functionally related features anyway. Yet we know that powerful jaw muscles may impose changes on the mandible, the browridge and other points on the skull; circumstances that promoted the evolution of these features in one population might do so again in a related population.

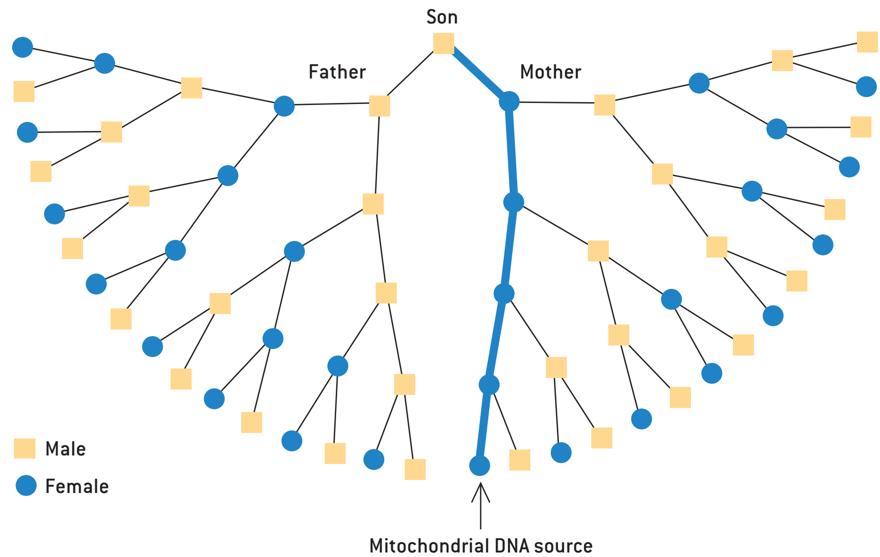
Other paleontologists also dispute the evidence for continuity. They argue that modern populations are not linked to past ones by morphological characteristics that evolved uniquely in the fossil record. Instead fossils and modern populations are united by their shared retention of still older ancestral characteristics. The continuity seen by believers in multiregional evolution may be an illusion.

The idea that modern humans could cohabit a region with archaic ones and replace them completely without any mixture may sound unlikely. Nevertheless, some fossil finds do support the idea. Discoveries in the caves at Qafzeh in Israel suggest that Neandertals and modern humans lived side by side for 40,000 years, yet they left little evidence of interbreeding.

How one human population might have replaced archaic humans without any detectable genetic mixing is still a compelling mystery. One of us (Cann) suspects that infectious diseases could have contributed to the process by helping to eliminate one group. Cavalli-Sforza has speculated that the ancestors of modern humans may have developed some modern trait, such as advanced language skills, that effectively cut them off from breeding with other hominids. This and related questions may yield as molecular biologists learn how to link specific genetic sequences to the physical and behavioral traits that those sequences ultimately influence.

Even before then, further studies of both nuclear and mitochondrial DNA will render more informative genetic trees. Particularly enticing are the sequences on the Y chromosome that determine maleness and that are therefore inherited from the father alone. Gerard Lucotte, while at the College of France, and his colleagues have indirectly compared such sequences in an effort to trace paternal lineages to a single progenitor—"Adam," if you will. Those preliminary results also point to an African homeland, and with further refinements this work on paternal lineages may be able to provide an invaluable check on our results for maternal lineages. Unfortunately, base changes accumulate slowly on useful regions of the Y chromosome, making it technically difficult to conduct a detailed genealogical analysis.

More progress can be expected soon, as molecular biologists learn to apply their techniques to materials uncovered by our friendly rivals, the paleontologists. Preliminary molecular studies have already been conducted on DNA from mummified tissues found in a Florida bog and dated to 7,500 years ago. Improved methods of extracting DNA from still older fossilized bone now appear close at hand. With them, we may begin building the family tree from a root that was alive when the human family was young.



PEDIGREE of one individual illustrates the difference between the patterns of nuclear and mitochondrial inheritance. All 32 ancestors from five generations ago contributed equally to his nuclear DNA. His mitochondrial lineage (*blue line*) leads back to only one person in every generation.

Epilogue

SINCE THIS ARTICLE was first published, further genetic work on the mitochondrial DNA sequences of three Neandertal specimens upholds our conclusions about the lack of a mixture between ancient and modern *Homo sapiens*. Furthermore, whole mitochondrial genome sequencing—all 16,569 base pairs from more than 50 donors—gives more precise resolution to the timescale of our emergence. It now seems that the earliest migration out of Africa is closer to 120,000 years ago than 200,000 years ago—more recent, yet still within the range we had originally estimated. SA

MORE TO EXPLORE

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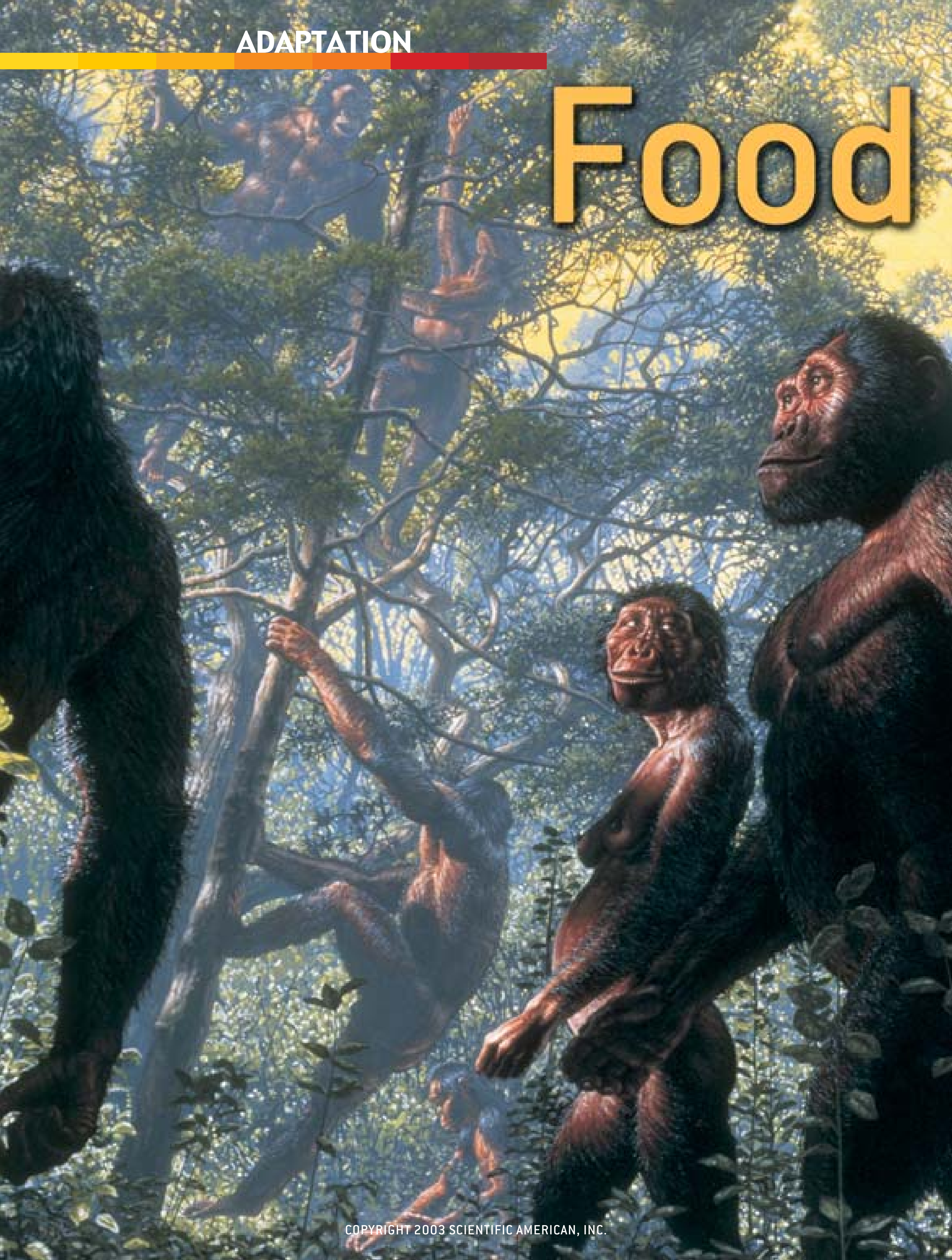
LAURIE GRACE

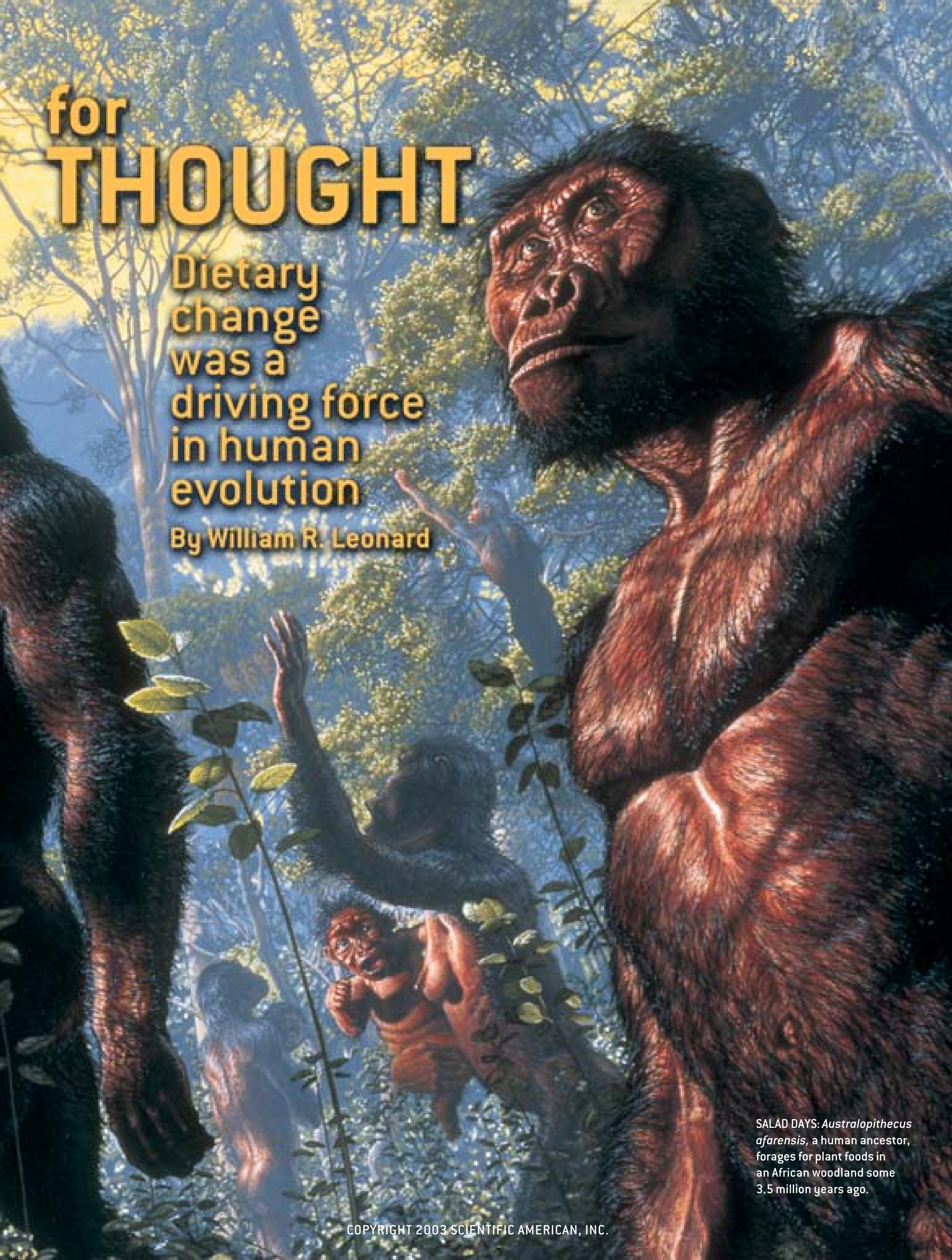
Food



for THOUGHT

Dietary change was a driving force in human evolution

By William R. Leonard



SALAD DAYS: *Australopithecus afarensis,* a human ancestor, forages for plant foods in an African woodland some 3.5 million years ago.

SKELETAL REMAINS indicate that our ancient forebears the australopithecines were bipedal by four million years ago. In the case of *A. afarensis* (*right*), one of the earliest hominids, telltale features include the arch in the foot, the nonopposable big toe, and certain characteristics of the knee and pelvis. But these hominids retained some apelike traits—short legs, long arms and curved toes, among others—suggesting both that they probably did not walk exactly like we do and that they spent some time in the trees. It wasn't until the emergence of our own genus, *Homo* (*a contemporary representative of which appears on the left*), that the hind limb features required for upright walking evolved. These include the fully modern limb and foot proportions and pelvis morphology.

JOHN GURCHE (*preceding pages and above*)

We humans are strange primates.

We walk on two legs, carry around enormous brains and have colonized every corner of the globe. Anthropologists and biologists have long sought to understand how our lineage came to differ so profoundly from the primate norm in these ways, and over the years all manner of hypotheses aimed at explaining each of these oddities have been put forth. But a growing body of evidence indicates that these miscellaneous quirks of humanity in fact have a common thread: they are largely the result of natural selection acting to maximize dietary quality and foraging efficiency. Changes in food availability over time, it seems, strongly influenced our hominid ancestors. Thus, in an evolutionary sense, we are very much what we ate.

Accordingly, what we eat is yet another way in which we differ from our primate kin. Contemporary human populations the world over have diets richer in calories and nutrients than those of our cousins, the great apes. So when and how did our ancestors' eating habits diverge from those of other primates? Further, to what extent have modern humans departed from the ancestral dietary pattern?

Scientific interest in the evolution of human nutritional requirements has a long history. But relevant investigations started gaining momentum after 1985, when S. Boyd Eaton and Melvin J. Konner of Emory University published a seminal paper in the *New England Journal of Medicine* entitled "Paleolithic Nutrition." They argued that the prevalence in modern societies of many chronic diseases—

obesity, hypertension, coronary heart disease and diabetes, among them—is the consequence of a mismatch between modern dietary patterns and the type of diet that our species evolved to eat as prehistoric hunter-gatherers. Since then, however, understanding of the evolution of human nutritional needs has advanced considerably—thanks in large part to new comparative analyses of traditionally living human populations and other primates—and a more nuanced picture has emerged. We now know that humans have evolved not to subsist on a single, Paleolithic diet but to be flexible eaters, an insight that has important implications for the current debate over what people today should eat in order to be healthy.

To appreciate the role of diet in human evolution, we must remember that the search for food, its consumption and, ultimately, how it is used for biological processes are all critical aspects of an organism's ecology. The energy dynamic between organisms and their environments—that is, energy expended in relation to energy acquired—has important adaptive consequences for survival and reproduction. These two components of Darwinian fitness are reflected in the way we divide up an animal's energy budget. Maintenance energy is what keeps an animal alive on a day-to-day basis. Productive energy, on the other hand, is associated with producing and raising offspring for the next generation. For mammals, this must cover the increased costs that mothers incur during pregnancy and lactation.

The type of environment a creature inhabits will influence the distribution of energy between these components, with harsher conditions creating higher maintenance demands. Nevertheless, the goal of all organisms is the same: to devote sufficient funds to reproduction, which ensures the long-term success of the species. Thus, by looking at the way animals go about obtaining and then allocating food energy, we can better discern how natural selection produces evolutionary change.

Becoming Bipeds

WHEN THEY ARE on the ground, living nonhuman primates typically move around on all fours, or quadrupedally. Scientists generally assume therefore that the last common ancestor of humans and chimpanzees (our closest living relative) was also a quadruped. Exactly when the last common ancestor lived is unknown, but clear indications of bipedalism—the trait that distinguished ancient humans from other apes—are evident in the oldest known species of *Australopithecus,* which lived in Africa roughly four million years ago. Ideas about why bipedalism evolved abound in the paleoanthropological literature. C. Owen Lovejoy of Kent State University proposed in 1981 that two-legged locomotion freed the arms to carry children and foraged goods. More recently, Kevin D. Hunt of Indiana University has posited that bipedalism emerged as a feeding posture that enabled access to foods that had previously been out of reach. Peter Wheeler of Liverpool John Moores University submits that moving upright allowed early humans to better regulate their body temperature by exposing less surface area to the blazing African sun.

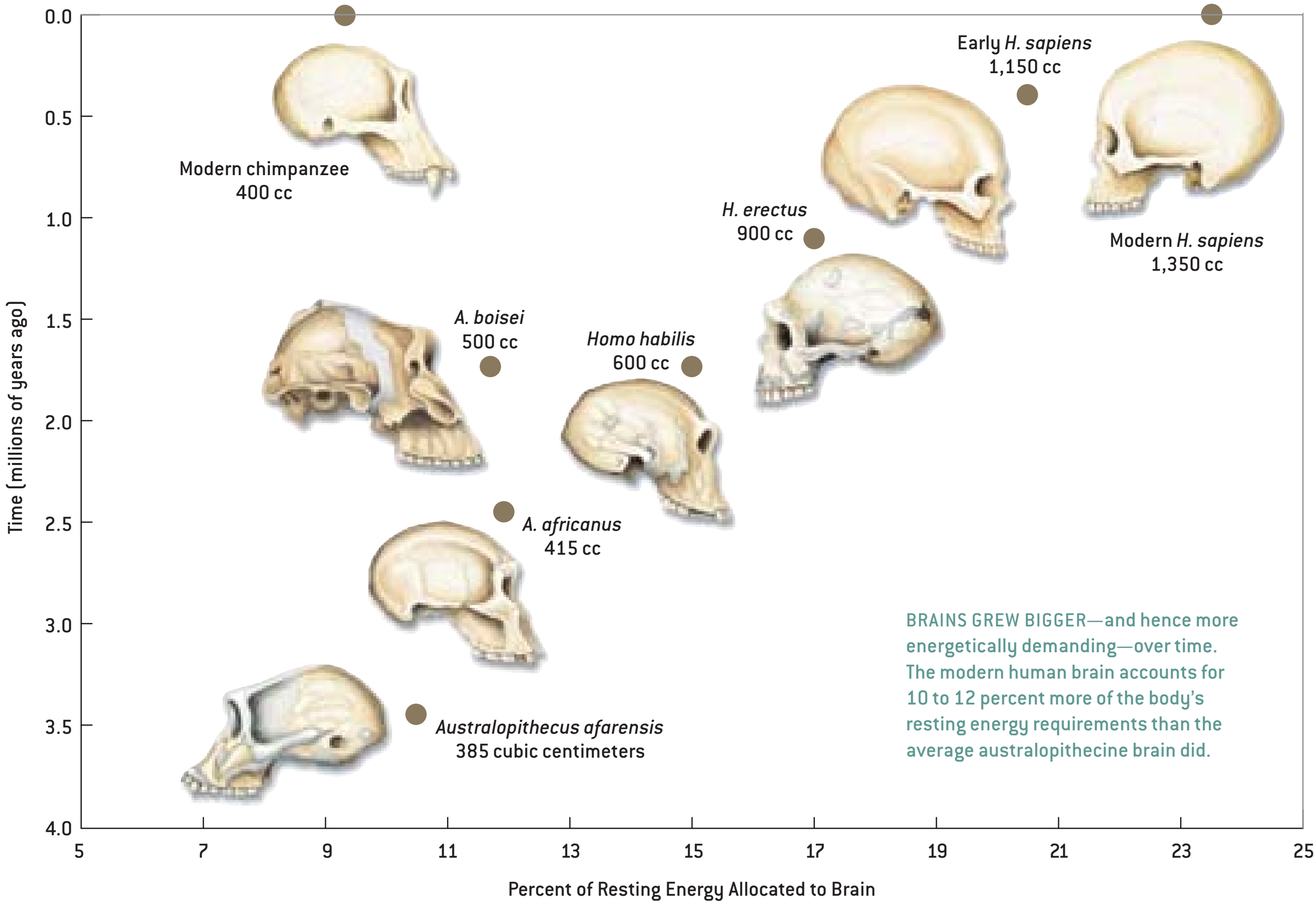
The list goes on. In reality, a number of factors probably selected for this type of locomotion. My own research, conducted in collaboration with my wife, Marcia L. Robertson, suggests that bipedalism evolved in our ancestors at least in part because it is less energetically expensive than quadrupedalism. Our analyses of the energy costs of movement in living animals of all sizes have shown that, in general, the strongest predictors of cost are the weight of the animal and the speed at which it travels. What is striking about human bipedal movement is that it is notably more economical than quadrupedal locomotion at walking rates.

Apes, in contrast, are not economical when moving on the ground. For instance, chimpanzees, which employ a peculiar form of quadrupedalism known as knuckle walking, spend some 35 percent more calories during locomotion than does a typical mammalian quadruped of the same size—a large dog, for example. Differences in the settings in which humans and apes evolved may help explain the variation in costs of movement. Chimps, gorillas and orangutans evolved in and continue to occupy dense forests where only a mile or so of trekking over the course of the day is all that is needed to find enough to eat. Much of early hominid evolution, on the other hand, took place in more open woodland and grassland, where sustenance is harder to come by. Indeed, modern human hunter-gatherers living in these environments, who provide us with the best available model of early human subsistence patterns, often travel six to eight miles daily in search of food.

These differences in day range have important locomotor implications. Because apes travel only short distances each day, the potential energetic benefits of moving more efficiently are very small. For far-ranging foragers, however, cost-effective walking saves many calories in maintenance energy needs—calories that can instead go toward reproduction. Se-

Overview/*Diet and Human Evolution*

- The characteristics that most distinguish humans from other primates are largely the results of natural selection acting to improve the quality of the human diet and the efficiency with which our ancestors obtained food. Some scientists have proposed that many of the health problems modern societies face are consequences of a discrepancy between what we eat and what our Paleolithic forebears ate.
- Yet studies of traditionally living populations show that modern humans are able to meet their nutritional needs using a wide variety of dietary strategies. We have evolved to be flexible eaters. The health concerns of the industrial world, where calorie-packed foods are readily available, stem not from deviations from a specific diet but from an imbalance between the energy we consume and the energy we expend.



BRAINS GREW BIGGER—and hence more energetically demanding—over time. The modern human brain accounts for 10 to 12 percent more of the body's resting energy requirements than the average australopithecine brain did.

CORNELIA BLIK

lection for energetically efficient locomotion is therefore likely to be more intense among far-ranging animals because they have the most to gain.

For hominids living between five million and 1.8 million years ago, during the Pliocene epoch, climate change spurred this morphological revolution. As the African continent grew drier, forests gave way to grasslands, leaving food resources patchily distributed. In this context, bipedalism can be viewed as one of the first strategies in human nutritional evolution, a pattern of movement that would have substantially reduced the number of calories spent in collecting increasingly dispersed food resources.

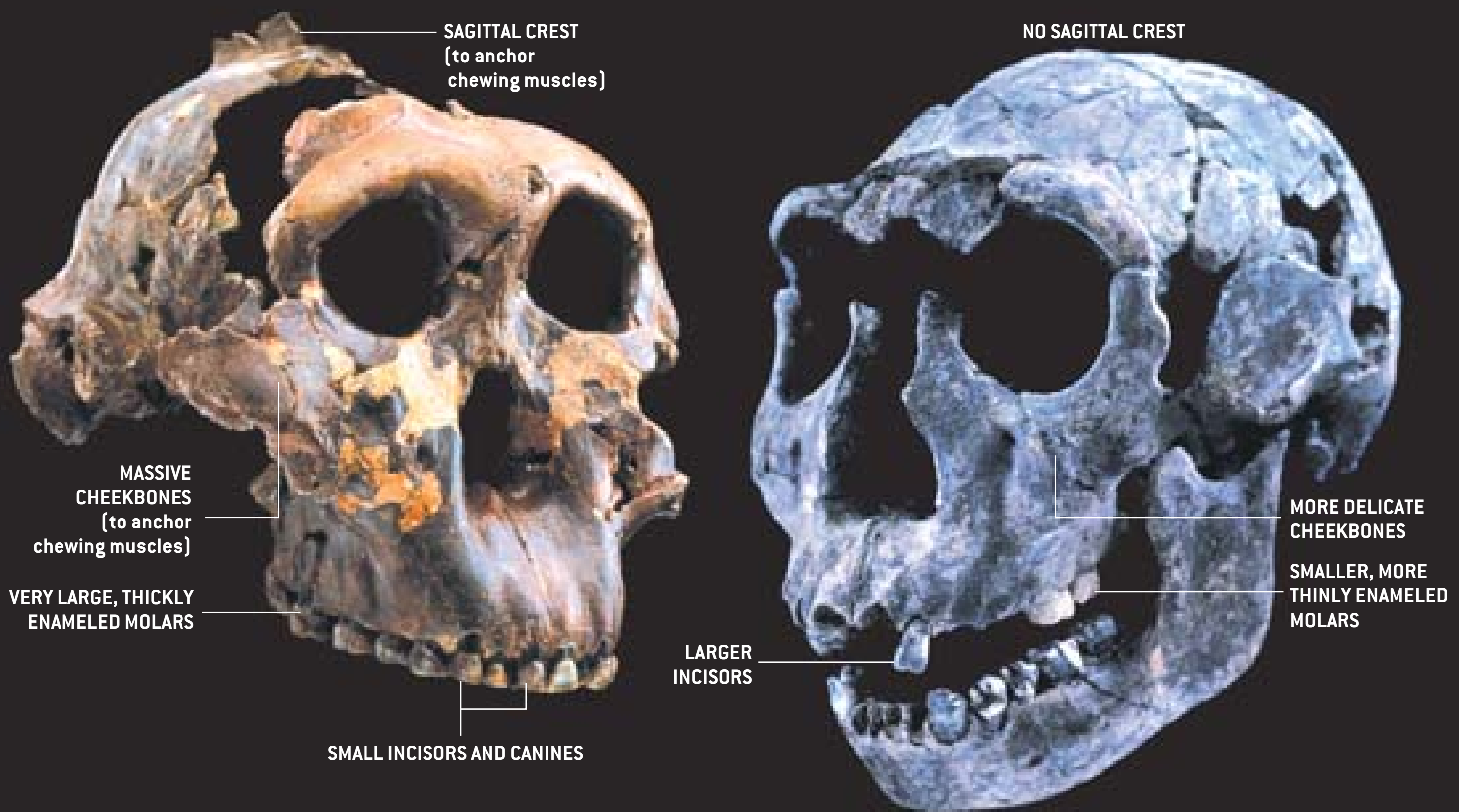
Big Brains and Hungry Hominids

NO SOONER HAD humans perfected their stride than the next pivotal event in human evolution—the dramatic enlargement of the brain—began. According to the fossil record, the australopithecines never became much brainier than living apes, showing only a modest increase in brain size, from around 400 cubic centimeters four million years ago to 500 cubic centimeters two million years later. *Homo* brain sizes, in contrast, ballooned from 600 cubic centimeters in *H. habilis* some two million years ago up to 900 cubic centimeters in early *H. erectus* just 300,000 years later. The *H. erectus* brain did not attain modern human proportions (1,350 cubic centimeters on average), but it exceeded that of living nonhuman primates.

From a nutritional perspective, what is extraordinary about our large brain is how much energy it consumes—roughly 16 times as much as muscle tissue per unit weight. Yet although humans have much bigger brains relative to body weight than do other primates (three times larger than expected), the total resting energy requirements of the human body are no greater than those of any other mammal of the same size. We therefore use a much greater share of our daily energy budget to feed our voracious brains. In fact, at-rest brain metabolism accounts for a whopping 20 to 25 percent of an adult human's energy needs—far more than the 8 to 10 percent observed in nonhuman primates, and more still than the 3 to 5 percent allotted to the brain by other mammals.

By using estimates of hominid body size compiled by Henry M. McHenry of the University of California at Davis, Robertson and I have reconstructed the proportion of resting energy needs that would have been required to support the brains of our ancient ancestors. Our calculations suggest that a typical, 80- to 85-pound australopithecine with a brain size of 450 cubic centimeters would have devoted about 11 percent of its resting energy to the brain. For its part, *H. erectus*, which weighed in at 125 to 130 pounds and had a brain size of some 900 cubic centimeters, would have earmarked about 17 percent of its resting energy—that is, about 260 out of 1,500 kilocalories a day—for the organ.

How did such an energetically costly



ROBUST AUSTRALOPITHECINES like *A. boisei* (*left*) had pronounced adaptations to eating tough, fibrous plant foods. *H. erectus* (*right*), in contrast, evolved to eat a softer, higher-quality diet—one that most likely featured meat regularly.

DAVID BRILL

brain evolve? One theory, developed by Dean Falk of Florida State University, holds that bipedalism enabled hominids to cool their cranial blood, thereby freeing the heat-sensitive brain of the temperature constraints that had kept its size in check. I suspect that, as with bipedalism, a number of selective factors were probably at work. But brain expansion almost certainly could not have occurred until hominids adopted a diet sufficiently rich in calories and nutrients to meet the associated costs.

Comparative studies of living animals support that assertion. Across all primates, species with bigger brains dine on richer foods, and humans are the extreme example of this correlation, boasting the largest relative brain size and the choicest diet [see "Diet and Primate Evolution," by Katharine Milton; Scientific American, August 1993]. According to recent analyses by Loren Cordain of Colorado State University, contemporary hunter-gatherers derive, on average, 40 to 60 percent of their dietary energy from animal foods (meat, milk and other products). Modern chimps, in comparison, obtain only 5 to 7 percent of their calories from these comestibles. Animal foods are far denser in calories and nutrients than most plant foods. For example, 3.5 ounces of meat provides upward of 200 kilocalories. But the same amount of fruit provides only 50 to 100 kilocalories. And a comparable serving of foliage yields just 10 to 20 kilocalories. It stands to reason, then, that for early *Homo,* acquiring more gray matter meant seeking out more of the energy-dense fare.

Fossils, too, indicate that improvements to dietary quality accompanied evolutionary brain growth. All australopithecines had cranial and dental features built for processing tough, low-quality plant foods. The later, robust australopithecines—a dead-end branch of the human family tree that lived alongside members of our own genus—had especially pronounced adaptations for grinding up fibrous plant foods, including massive, dish-shaped faces; heavily built mandibles; ridges, or sagittal crests, atop the skull for the attachment of powerful chewing muscles; and huge, thickly enameled molar teeth. (This is not to say that australopithecines never ate meat. They almost certainly did on occasion, just as chimps do today.) In contrast, early members of the genus *Homo,* which descended from the gracile australopithecines, had much smaller faces, more delicate jaws, smaller molars and no sagittal crests—despite being far larger in terms of overall body size than their predecessors. Together these features suggest that early *Homo* was consuming less

THE AUTHOR

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INTO THE FIRE

EATING MORE ANIMAL FOODS is one way of boosting the caloric and nutrient density of the diet, a shift that appears to have been critical in the evolution of the human lineage. But might our ancient forebears have improved dietary quality another way? Richard Wrangham of Harvard University and his colleagues recently examined the importance of cooking in human evolution. They showed that cooking not only makes plant foods softer and easier to chew, it substantially increases their available energy content, particularly for starchy tubers such as potatoes and manioc. In their raw form, starches are not readily broken down by the enzymes in the human body. When heated, however, these complex carbohydrates become more digestible, thereby yielding more calories.

The researchers propose that *Homo erectus* was probably the first hominid to apply fire to food, starting perhaps 1.8 million years ago. They argue that early cooking of plant foods (especially tubers) enabled this species to evolve smaller teeth and bigger brains than those of their predecessors. Additionally, the extra calories allowed *H. erectus* to start hunting—an energetically costly activity—more frequently.

From an energetics perspective, this is a logical enough line of reasoning. What makes the hypothesis difficult to swallow is the archaeological evidence Wrangham's team uses to make its case. The authors cite the East African sites of Koobi Fora and Chesowanja, which date to around 1.6 million and 1.4 million years ago, respectively, to indicate control of fire by *H. erectus*. These localities do indeed exhibit evidence of fires, but whether hominids were responsible for creating or harnessing the flames is a matter of some debate. The earliest unequivocal manifestations of fire use—stone hearths and burned animal bones from sites in Europe—are only some 200,000 years old.

Cooking was clearly an innovation that considerably improved the quality of the human diet. But it remains unclear when in our past this practice arose. *—W.R.L.*

EARLY COOKING of plant foods, especially tubers, enabled brain expansion, argue Richard Wrangham of Harvard University and his colleagues.

I. DEVORE *Anthro-Photo File*

plant material and more animal foods.

As to what prompted *Homo*'s initial shift toward the higher-quality diet necessary for brain growth, environmental change appears to have once more set the stage for evolutionary change. The continued desiccation of the African landscape limited the amount and variety of edible plant foods available to hominids. Those on the line leading to the robust australopithecines coped with this problem morphologically, evolving anatomical specializations that enabled them to subsist on more widely available, difficult-to-chew foods. *Homo* took a different path. As it turns out, the spread of grasslands also led to an increase in the relative abundance of grazing mammals such as antelope and gazelle, creating opportunities for hominids capable of exploiting them. *H. erectus* did just that, developing the first hunting-and-gathering economy in which game animals became a significant part of the diet and resources were shared among members of the foraging groups. Signs of this behavioral revolution are visible in the archaeological record, which shows an increase in animal bones at hominid sites during this period, along with evidence that the beasts were butchered using stone tools.

These changes in diet and foraging behavior did not turn our ancestors into strict carnivores; however, the addition of modest amounts of animal foods to the menu, combined with the sharing of resources that is typical of hunter-gatherer groups, would have significantly increased the quality and stability of hominid diets. Improved dietary quality alone cannot explain *why* hominid brains grew, but it appears to have played a critical role in enabling that change. After the initial spurt in brain growth, diet and brain expansion probably interacted synergistically: bigger brains produced more complex social behavior, which led to further shifts in foraging tactics and improved diet, which in turn fostered additional brain evolution.

A Movable Feast

THE EVOLUTION of *H. erectus* in Africa 1.8 million years ago also marked a third turning point in human evolution: the initial movement of hominids out of Africa. Until recently, the locations and ages of known fossil sites suggested that early *Homo* stayed put for a few hundred thousand years before venturing out of the motherland and slowly fanning out into the rest of the Old World. Earlier work hinted that improvements in tool technology around 1.4 million years ago—namely, the advent of the Acheulean hand ax—allowed hominids to leave Africa. But new discoveries indicate that *H. erectus* hit the ground running, so to speak. Rutgers University geochronologist Carl Swisher III and his colleagues have shown that the earliest *H. erectus* sites outside of Africa, which are in Indonesia and the Republic of Georgia, date to between 1.8 million and 1.7 million years ago. It seems that the first appearance of *H. erectus* and its initial spread from Africa were almost simultaneous.

The impetus behind this newfound wanderlust again appears to be food. What an animal eats dictates to a large extent how much territory it needs to survive. Carnivorous animals generally require far bigger home ranges than do herbivores of comparable size because they have fewer total calories available to them per unit area.

Large-bodied and increasingly dependent on animal foods, *H. erectus* most likely needed much more turf than the smaller, more vegetarian australopithecines did. Using data on contemporary primates and human hunter-gatherers as a guide, Robertson, Susan C. Antón of Rutgers University and I have estimated that the larger body size of *H. erectus,* combined with a moderate increase in meat consumption, would have necessitated an eightfold to 10-fold increase in home range size compared with that of the late australopithecines—enough, in fact, to account for the abrupt expansion of the species out of Africa. Exactly how far beyond the continent that shift would have taken *H. erectus* remains unclear, but migrating animal herds may have helped lead it to these distant lands.

As humans moved into more northern latitudes, they encountered new dietary challenges. The Neandertals, who lived during the last ice ages of Europe, were among the first humans to inhabit arctic environments, and they almost certainly would have needed ample calories to endure under those circumstances. Hints at what their energy requirements might have been come from data on traditional human populations that live in northern settings today. The Siberian reindeer-herding populations known as the Evenki, which I have studied with Peter Katzmarzyk of Queen's University in Ontario and Victoria A. Galloway of the University of Toronto, and the Inuit (Eskimo) populations of the Canadian Arctic have resting metabolic rates that are about 15 percent higher than those of people of similar size living in temperate environments. The energetically expensive activities associated with living in a northern climate ratchet their caloric cost of living up further still. Indeed, whereas a 160-pound American male with a typical urban way of life requires about 2,600 kilocalories a day, a diminutive, 125-pound Evenki man needs more than 3,000 kilocalories a day to sustain himself. Using these modern northern populations as benchmarks, Mark Sorensen of Northwestern University and I have estimated that Neandertals most likely would have required as many as 4,000 kilocalories a day to survive. That they were able to meet these de-

NEANDERTAL HUNTERS

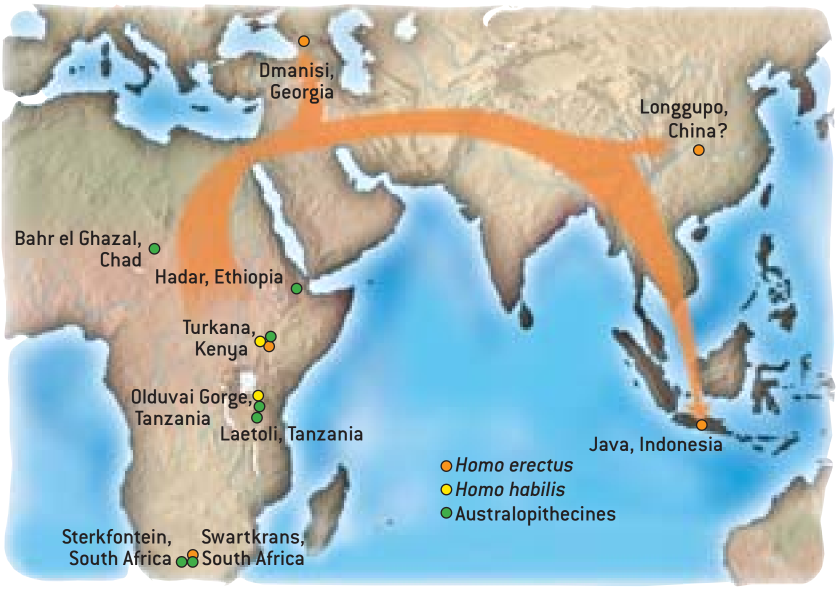
TO RECONSTRUCT what early humans ate, researchers have traditionally studied features on their fossilized teeth and skulls, archaeological remains of food-related activities, and the diets of living humans and apes. Increasingly, however, investigators have been tapping another source of data: the chemical composition of fossil bones. This approach has yielded some especially intriguing findings with regard to the Neandertals.

Michael Richards, now at the University of Bradford in England, and his colleagues recently examined isotopes of carbon (^{13}C) and nitrogen (^{15}N) in 29,000-year-old Neandertal bones from Vindija cave in Croatia. The relative proportions of these isotopes in the protein part of human bone, known as collagen, directly reflect their proportions in the protein of the individual's diet. Thus, by comparing the isotopic "signatures" of the Neandertal bones to those of other animals living in the same environments, the authors were able to determine whether the Neandertals were deriving the bulk of their protein from plants or from animals.

The analyses show that the Vindija Neandertals had ^{15}N levels comparable to those seen in northern carnivores such as foxes and wolves, indicating that they obtained almost all their dietary protein from animal foods. Earlier work hinted that inefficient foraging might have been a factor in the subsequent demise of the Neandertals. But Richards and his collaborators argue that in order to consume as much animal food as they apparently did, the Neandertals had to have been skilled hunters. These findings are part of a growing body of literature that suggests Neandertal subsistence behavior was more complex than previously thought [see "Who Were the Neandertals?" on page 28]. *—W.R.L.*

NEANDERTAL MEALS consisted mostly of meat (from, for example, reindeer), according to analyses of carbon and nitrogen isotopes in fossilized bone.

HELLIO & VAN INGEN *Photo Researchers, Inc.*



AFRICAN EXODUS began as soon as *H. erectus* evolved, around 1.8 million years ago, probably in part because it needed a larger home range than that of its smaller-bodied predecessors.

mands for as long as they did speaks to their skills as foragers [*see box on preceding page*].

Modern Quandaries

JUST AS PRESSURES to improve dietary quality influenced early human evolution, so, too, have these factors played a crucial role in the more recent increases in population size. Innovations such as cooking, agriculture and even aspects of modern food technology can all be considered tactics for boosting the quality of the human diet. Cooking, for one, augmented the energy available in wild plant foods [*see box on page 68*]. With the advent of agriculture, humans began to manipulate marginal plant species to increase their productivity, digestibility and nutritional content—essentially making plants more like animal foods. This kind of tinkering continues today, with genetic modification of crop species to make "better" fruits, vegetables and grains. Similarly, the development of liquid nutritional supplements and meal replacement bars is a continuation of the trend that our ancient ancestors started: gaining as much nutritional return from our food in as little volume and with as little physical effort as possible.

Overall, that strategy has evidently worked: humans are here today and in record numbers to boot. But perhaps the strongest testament to the importance of energy- and nutrient-rich foods in human evolution lies in the observation that so many health concerns facing societies around the globe stem from deviations from the energy dynamic that our ancestors established. For children in rural populations of the developing world, low-quality diets lead to poor physical growth and high rates of mortality during early life. In these cases, the foods fed to youngsters during and after weaning are often not sufficiently dense in energy and nutrients to meet the high nutritional needs associated with this period of rapid growth and development. Although these children are typically similar in length and weight to their U.S. counterparts at birth, they are much shorter and lighter by the age of three, often resembling the smallest 2 to 3 percent of American children of the same age and sex.

In the industrial world, we are facing the opposite problem: rates of childhood and adult obesity are rising because the energy-rich foods we crave—notably those packed with fat and sugar—have become widely available and relatively in-

VARIOUS DIETS can satisfy human nutritional requirements. Some populations subsist almost entirely on plant foods; others eat mostly animal foods. Although Americans consume less meat than do a number of the traditionally living people described here, they have on average higher cholesterol levels and higher levels of obesity (as indicated by body mass index) because they consume more energy than they expend and eat meat that is higher in fat.

Population	Energy Intake (kilocalories/day)	Energy from Animal Foods (percent)	Energy from Plant Foods (percent)	Total Blood Cholesterol (milligrams/deciliter)	Body Mass Index (weight/height squared)
HUNTER-GATHERERS					
!Kung (Botswana)	2,100	33	67	121	19
Inuit (North America)	2,350	96	4	141	24
PASTORALISTS					
Turkana (Kenya)	1,411	80	20	186	18
Evenki (Russia)	2,820	41	59	142	22
AGRICULTURALISTS					
Quechua (Highland Peru)	2,002	5	95	150	21
INDUSTRIAL SOCIETIES					
U.S.	2,250	23	77	204	26

Note: Energy intake figures reflect the adult average (males and females); blood cholesterol and body mass index (BMI) figures are given for males. Healthy BMI = 18.5–24.9; overweight = 25.0–29.9; obese = 30 and higher. BMI is weight (kilograms)/height (meters) squared.

LAURIE GRACE (*map*)

expensive. According to recent estimates, more than half of adult Americans are overweight or obese. Obesity has also appeared in parts of the developing world where it was virtually unknown less than a generation ago. This seeming paradox has emerged as people who grew up malnourished move from rural areas to urban settings where food is more readily available. In some sense, obesity and other common diseases of the modern world are continuations of a tenor that started millions of years ago. We are victims of our own evolutionary success, having developed a calorie-packed diet while minimizing the amount of maintenance energy expended on physical activity.

The magnitude of this imbalance becomes clear when we look at traditionally living human populations. Studies of the Evenki reindeer herders that I have conducted in collaboration with Michael Crawford of the University of Kansas and Ludmila Osipova of the Russian Academy of Sciences in Novosibirsk indicate that the Evenki derive almost half their daily calories from meat, more than 2.5 times the amount consumed by the average American. Yet when we compare Evenki men with their U.S. peers, they are 20 percent leaner and have cholesterol levels that are 30 percent lower.

These differences partly reflect the compositions of the diets. Although the Evenki diet is high in meat, it is relatively low in fat (about 20 percent of their dietary energy comes from fat, compared with 35 percent in the average U.S. diet), because free-ranging animals such as reindeer have less body fat than cattle and other feedlot animals do. The composition of the fat is also different in free-ranging animals, tending to be lower in saturated fats and higher in the polyunsaturated fatty acids that protect against heart disease. More important, however, the Evenki way of life necessitates a much higher level of energy expenditure.

Thus, it is not just changes in diet that have created many of our pervasive health problems but the interaction of shifting diets and changing lifestyles. Too often modern health problems are portrayed as the result of eating "bad" foods that are departures from *the* natural human diet—an oversimplification embodied by the current debate over the relative merits of a high-protein, high-fat Atkins-type diet or a low-fat one that emphasizes complex carbohydrates. This is a fundamentally flawed approach to assessing human nutritional needs. Our species was not designed to subsist on a single, optimal diet. What is remarkable about human beings is the extraordinary variety of what we eat. We have been able to thrive in almost every ecosystem on the earth, consuming diets ranging from almost all animal foods among populations of the Arctic to primarily tubers and cereal grains among populations in the high Andes. Indeed, the hallmarks of human evolution have been the diversity of strategies that we have developed to create diets that meet our distinctive metabolic requirements and the ever increasing efficiency with which we extract energy and nutrients from the environment. The challenge our modern societies now face is balancing the calories we consume with the calories we burn. SA

A DIVERSITY OF DIETS

THE VARIETY OF SUCCESSFUL dietary strategies employed by traditionally living populations provides an important perspective on the ongoing debate about how high-protein, low-carbohydrate regimens such as the Atkins diet compare with those that underscore complex carbohydrates and fat restriction. The fact that both these schemes produce weight loss is not surprising, because both help people shed pounds through the same basic mechanism: limiting major sources of calories. When you create an energy deficit—that is, when you consume fewer calories than you expend—your body begins burning its fat stores and you lose weight.

The larger question about healthy weight-loss or weight-maintenance diets is whether they create eating patterns that are sustainable over time. On this point it appears that diets that severely limit large categories of foods (carbohydrates, for example) are much more difficult to sustain than are moderately restrictive diets. In the case of the Atkins-type regimen, there are also concerns about the potential long-term consequences of eating foods derived largely from feedlot animals, which tend to contain more fat in general and considerably more saturated fats than do their free-ranging counterparts.

In September 2002 the National Academy of Sciences's Institute of Medicine put forth new diet and exercise guidelines that mesh well with the ideas presented in this article. Not only did the institute set broader target ranges for the amounts of carbohydrates, fat and protein that belong in a healthy diet—in essence, acknowledging that there are various ways to meet our nutritional needs—the organization also doubled the recommended amount of moderately intense physical activity to an hour a day. By following these guidelines and balancing what we eat with exercise, we can live more like the Evenki of Siberia and other traditional societies—and more like our hominid ancestors. —W.R.L.

MORE TO EXPLORE

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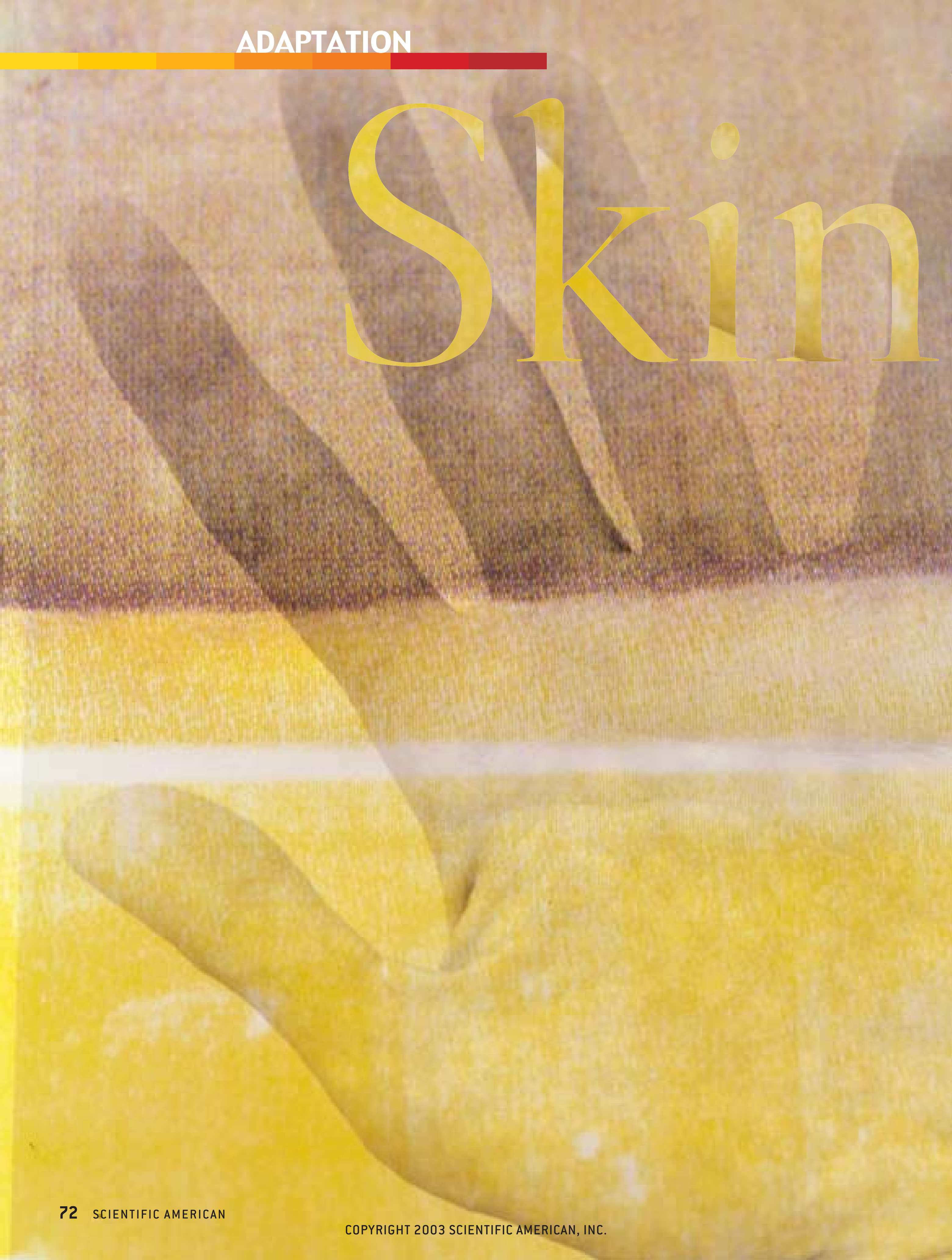
Skin



Throughout the world, human skin color has evolved to be dark enough to prevent sunlight from destroying the nutrient folate but light enough to foster the production of vitamin D

By Nina G. Jablonski and George Chaplin

Among primates, only humans have

a mostly naked skin that comes in different colors. Geographers and anthropologists have long recognized that the distribution of skin colors among indigenous populations is not random: darker peoples tend to be found nearer the equator, lighter ones closer to the poles. For years, the prevailing theory has been that darker skins evolved to protect against skin cancer. But a series of discoveries has led us to construct a new framework for understanding the evolutionary basis of variations in human skin color. Recent epidemiological and physiological evidence suggests to us that the worldwide pattern of human skin color is the product of natural selection acting to regulate the effects of the sun's ultraviolet (UV) radiation on key nutrients crucial to reproductive success.

The evolution of skin pigmentation is linked with that of hairlessness, and to comprehend both these stories, we need to page back in human history. Human beings have been evolving as an independent lineage of apes since at least seven million years ago, when our immediate ancestors diverged from those of our closest relatives, chimpanzees. Because chimpanzees have changed less over time than humans have, they can provide an idea of what human anatomy and physiology must have been like. Chimpanzees' skin is light in color and is covered by hair over most of their bodies. Young animals have pink faces, hands, and feet and become freckled or dark in these areas

Deep

only as they are exposed to sun with age. The earliest humans almost certainly had a light skin covered with hair. Presumably hair loss occurred first, then skin color changed. But that leads to the question, When did we lose our hair?

The skeletons of ancient humans—such as the well-known skeleton of Lucy, which dates to about 3.2 million years ago—give us a good idea of the build and the way of life of our ancestors. The daily activities of Lucy and other hominids that lived before about three million years ago appear to have been similar to those of primates living on the open savannas of Africa today. They probably spent much of their day foraging for food over three to four miles before retiring to the safety of trees to sleep.

By 1.6 million years ago, however, we see evidence that this pattern had begun to change dramatically. The famous skeleton of Turkana Boy—which belonged to the species *Homo ergaster*—is that of a long-legged, striding biped that probably walked long distances. These more active early humans faced the problem of staying cool and protecting their brains from overheating. Peter Wheeler of Liverpool John Moores University has shown that this was accomplished through an increase in the number of sweat glands on the surface of the body and a reduction in the covering of body hair. Once rid of most of their hair, early members of the genus *Homo* then encountered the challenge of protecting their skin from the damaging effects of sunlight, especially UV rays.

Built-in Sunscreen

IN CHIMPANZEES, the skin on the hairless parts of the body contains cells called melanocytes that are capable of synthesizing the dark-brown pigment melanin in response to exposure to UV radiation. When humans became mostly hairless, the ability of the skin to produce melanin assumed new importance. Melanin is nature's sunscreen: it is a large organic molecule that serves the dual purpose of physically and chemically filtering the harmful effects of UV radiation; it absorbs UV rays, causing them to lose energy, and it neutralizes harmful chemicals called free radicals that form in the skin after damage by UV radiation.

Anthropologists and biologists have generally reasoned that high concentrations of melanin arose in the skin of peoples in tropical areas because it protected them against skin cancer. James E. Cleaver of the University of California at San Francisco, for instance, has shown that people with the disease xeroderma pigmentosum, in which melanocytes are destroyed by exposure to the sun, suffer from significantly higher than normal rates of squamous and basal cell carcinomas, which are usually easily treated. Malignant melanomas are more frequently fatal, but they are rare (representing 4 percent of skin cancer diagnoses) and tend to strike only light-skinned people. But all skin cancers typically arise later in life, in most cases after the first reproductive years, so they could not have exerted enough evolutionary pressure for skin protection alone to account for darker skin colors. Accordingly, we began to ask what role melanin might play in human evolution.

Overview/*Skin Color Evolution*

- After losing their hair as an adaptation for keeping cool, early hominids gained pigmented skins. Scientists initially thought that such pigmentation arose to protect against skin-cancer-causing ultraviolet (UV) radiation.
- Skin cancers tend to arise after reproductive age, however. An alternative theory suggests that dark skin might have evolved primarily to protect against the breakdown of folate (folic acid), a nutrient essential for fertility and for fetal development.
- Skin that is too dark blocks the sunlight necessary for catalyzing the production of vitamin D, which is crucial for maternal and fetal bones. Accordingly, humans have evolved to be light enough to make sufficient vitamin D yet dark enough to protect their stores of folate.
- As a result of recent human migrations, many people now live in areas that receive more (or less) UV radiation than is appropriate for their skin color.

The Folate Connection

IN 1991 ONE OF US (Jablonski) ran across what turned out to be a critical paper published in 1978 by Richard F. Branda and John W. Eaton, now at the University of Vermont and the University of Louisville, respectively. These investigators showed that light-skinned people who had been exposed to simulated strong sunlight had abnormally low levels of the essential B vitamin folate in their blood. The scientists also observed that subjecting human blood serum to the same conditions resulted in a 50 percent loss of folate content within one hour.

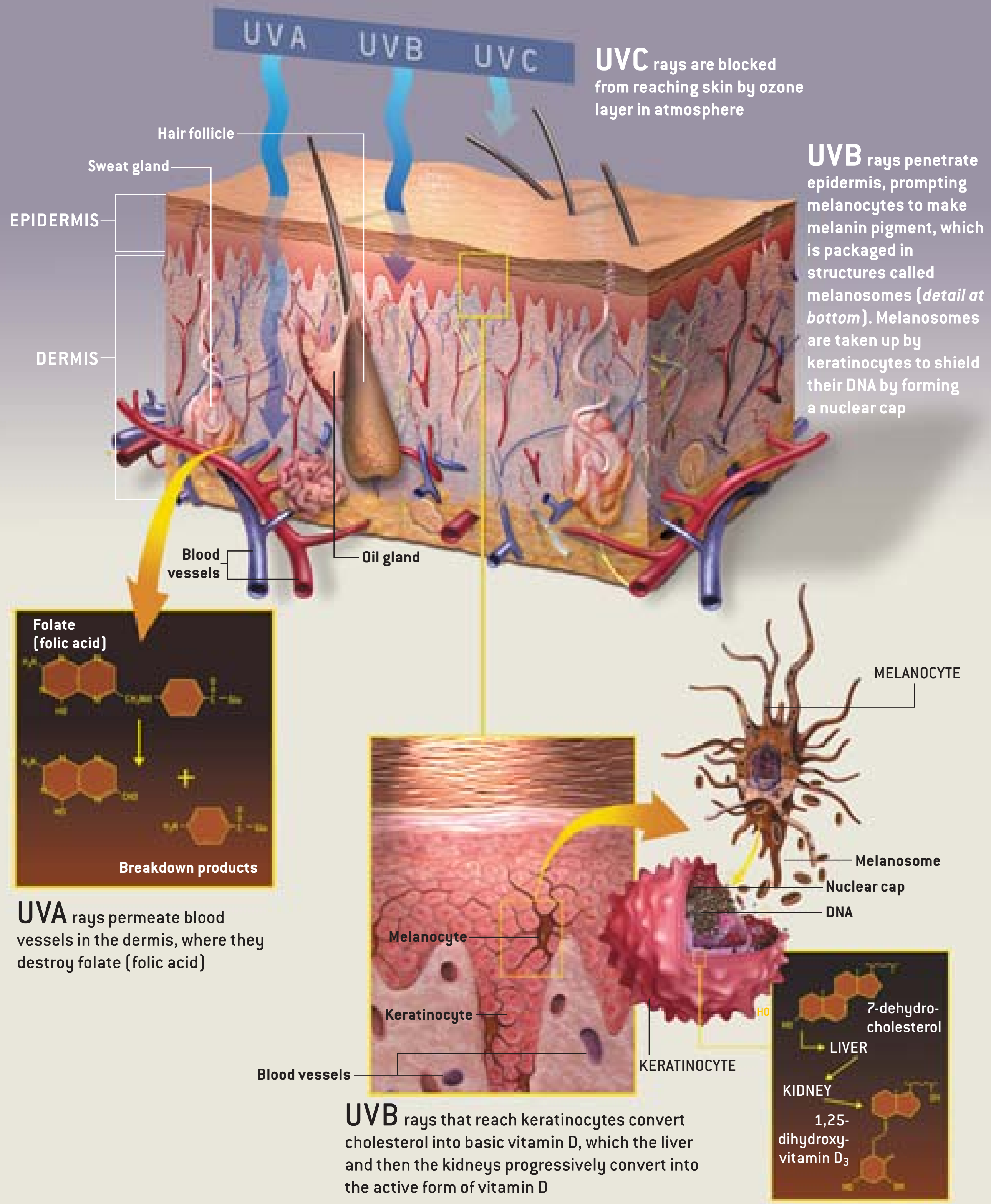
The significance of these findings to reproduction—and hence evolution—became clear when we learned of research being conducted on a major class of birth defects by our colleagues at the University of Western Australia. There Fiona J. Stanley and Carol Bower had established by the late 1980s that folate deficiency in pregnant women is related to an increased risk of neural tube defects such as spina bifida, in which the arches of the spinal vertebrae fail to close around the spinal cord. Many research groups throughout the world have since confirmed this correlation, and efforts to supplement foods with folate (folic acid) and to educate women about the importance of the nutrient have become widespread.

We discovered soon afterward that folate is important not only in preventing neural tube defects but also in a host of other processes. Because folate is essential for the synthesis of DNA in dividing cells, anything that involves rapid cell proliferation, such as spermatogenesis (the production of sperm cells), requires folate. Male rats and mice with chemically induced folate deficiency have impaired spermatogenesis and are infertile. Although no comparable studies of humans have been conducted, Wai Yee Wong and his colleagues at the University Medical Center of Nijmegen in the Netherlands have recently reported that folic acid treatment can boost the sperm counts of men with fertility problems.

IRAIDA ICAZA (*preceding pages*)

SKIN IN THE SUN

THE ULTRAVIOLET (UV) RAYS of the sun are a mixed blessing: they spur the production of vitamin D but destroy folate and can cause cancer by damaging DNA. Melanin pigment produced by melanocytes protects against DNA damage and folate breakdown. But keratinocytes must get enough UV rays to make vitamin D. —*N.G.J. and G.C.*



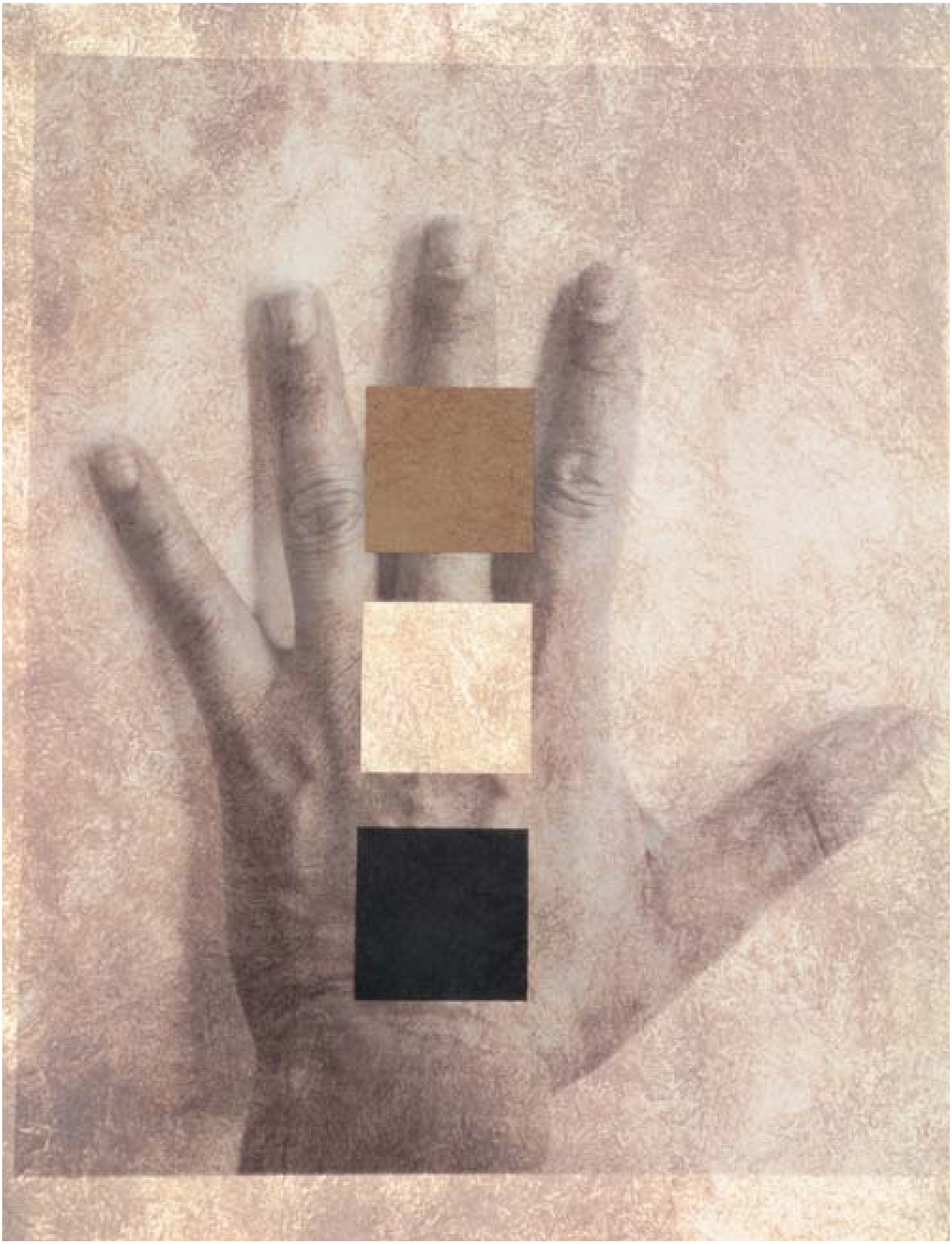
UVC rays are blocked from reaching skin by ozone layer in atmosphere

UVB rays penetrate epidermis, prompting melanocytes to make melanin pigment, which is packaged in structures called melanosomes (*detail at bottom*). Melanosomes are taken up by keratinocytes to shield their DNA by forming a nuclear cap

UVA rays permeate blood vessels in the dermis, where they destroy folate (folic acid)

UVB rays that reach keratinocytes convert cholesterol into basic vitamin D, which the liver and then the kidneys progressively convert into the active form of vitamin D

KEITH KASNOT



IRAIDA ICAZA

Such observations led us to hypothesize that dark skin evolved to protect the body's folate stores from destruction. Our idea was supported by a report published in 1996 by Argentine pediatrician Pablo Lapunzina, who found that three young and otherwise healthy women whom he had attended gave birth to infants with neural tube defects after using sun beds to tan themselves in the early weeks of pregnancy. Our evidence about the breakdown of folate by UV radiation thus supplements what is already known about the harmful (skin-cancer-causing) effects of UV radiation on DNA.

Human Skin on the Move

THE EARLIEST MEMBERS of *Homo sapiens*, or modern humans, evolved in Africa between 120,000 and 100,000 years ago and had darkly pigmented skin adapted to the conditions of UV radiation and heat that existed near the equator. As modern humans began to venture out of the tropics, however, they encountered environments in which they received significantly less UV radiation during the year. Under these conditions their high concentrations of natural sunscreen probably proved detrimental. Dark skin contains so much melanin that very little UV radiation, and specifically very little of the shorter-wavelength UVB radiation, can penetrate the skin. Although most of the effects of UVB are harmful, the rays perform one indispensable function: initiating the formation of vitamin D in the skin. Dark-skinned people living in the tropics generally receive sufficient UV radiation during the year for UVB to penetrate the skin and allow them to make vitamin D. Outside the tropics this is not the case. The solution, across evolutionary time, has been for migrants to northern latitudes to lose skin pigmentation.

The connection between the evolution of lightly pigmented skin and vitamin D synthesis was elaborated in 1967 by W. Farnsworth Loomis of Brandeis University. He established the importance of vitamin D to reproductive success because of its role in enabling calcium absorption by the intestines, which in turn makes possible the normal development of the skeleton and the maintenance of a healthy immune system. Research led by Michael Holick of the Boston University School of Medicine has, over the past 20 years, further cemented the significance of vitamin D in development and immunity. His team also showed that not all sunlight contains enough UVB to stimulate vitamin D production. In Boston, for instance, which is located at about 42 degrees north latitude, human skin cells begin to produce vitamin D only after mid-March. In the wintertime there isn't enough UVB to do the job. We realized that this was another piece of evidence essential to the skin color story.

During the course of our research in the early 1990s, we sought in vain to find sources of data on actual UV radiation levels at the earth's surface. We were rewarded in 1996, when we contacted Elizabeth Weatherhead of the Cooperative Institute for Research in Environmental Sciences at the University of Colorado at Boulder. She shared with us a database of measurements of UV radiation at the earth's surface taken by NASA's Total Ozone Mapping Spectrophotometer satellite between 1978 and 1993. We were then able to model the distribution of UV radiation on the earth and relate the satellite data to the amount of UVB necessary to produce vitamin D.

We found that the earth's surface could be divided into three vitamin D zones: one comprising the tropics, one the subtropics and temperate regions, and the last the circumpolar regions north and south of about 45 degrees latitude. In the first, the dosage of UVB throughout the year is high enough that humans have ample opportunity to synthesize vitamin D all year. In the second, at least one month during the year has insufficient UVB radiation, and in the third area not enough UVB arrives on average during the entire year to prompt vitamin D synthesis. This distribution could explain why indigenous peoples in the tropics generally have dark skin, whereas people in the subtropics and temperate regions are lighter-skinned but have the ability to tan, and those who live in regions near the poles tend to be very light skinned and burn easily.

One of the most interesting aspects of this investigation was the examination of groups that did not precisely fit the predicted skin color pattern. An example is the Inuit people of Alaska and northern Canada. The Inuit exhibit skin color that is somewhat darker than would be predicted given the UV levels at their latitude. This is probably caused by two factors. The first is that they are relatively recent inhabitants of these climes, having migrated to North America only roughly 5,000 years ago. The second is that the traditional diet of the Inuit is extremely high in foods containing vitamin D, especially fish and marine mammals. This vitamin D–rich diet offsets the problem that they would otherwise have with vitamin D synthesis in their skin at northern latitudes and permits them to remain more darkly pigmented.

Our analysis of the potential to synthesize vitamin D allowed us to understand another trait related to human skin color: women in all populations are generally lighter-skinned than men. (Our data show that women tend to be between 3 and 4 percent lighter than men.) Scientists have often speculated on the reasons, and most have argued that the phenomenon stems from sexual selection—the preference of men for women of lighter color. We contend that although this is probably part of the story, it is not the original reason for the sexual difference. Females have significantly greater needs for calcium throughout their reproductive lives, especially during pregnancy and lactation, and must be able to make the most of the calcium contained in food.

THE AUTHORS

NINA G. JABLONSKI and *GEORGE CHAPLIN* work at the California Academy of Sciences in San Francisco, where Jablonski is Irvine Chair and curator of anthropology and Chaplin is a research associate in the department of anthropology. Jablonski's research centers on the evolutionary adaptations of monkeys, apes and humans. She is particularly interested in how primates have responded to changes over time in the global environment. Chaplin is a private geographic information systems consultant who specializes in describing and analyzing geographic trends in biodiversity. In 2001 he was awarded the Student of the Year prize by the Association of Geographic Information in London for his master's thesis on the environmental correlates of skin color.

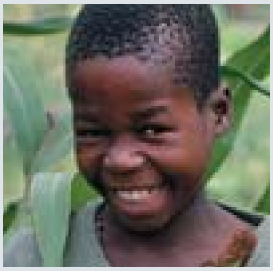
SKIN AND MIGRATION

THE SKIN OF PEOPLES who have inhabited particular areas for millennia has adapted to allow vitamin D production while protecting folate stores. The skin tones of more recent immigrants will take thousands of years to catch up, putting light-skinned individuals at risk for skin cancer and dark-skinned people in danger of vitamin D deficiency. *—N.G.J. and G.C.*

LONG-TERM RESIDENT | **RECENT IMMIGRANT**

SOUTHERN AFRICA: LATITUDE ~20–30° S

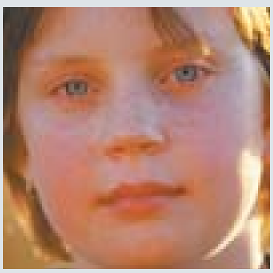
Khoisan (Hottentot)



Zulu: arrived about 1,000 years ago

AUSTRALIA: LATITUDE ~10–35° S

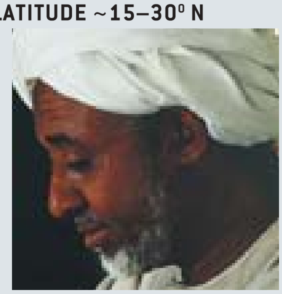
Aborigine



European: ~300 years ago

BANKS OF RED SEA: LATITUDE ~15–30° N

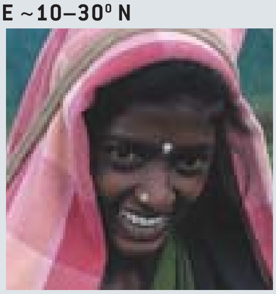
Sudanese



Arab: ~2,000 years ago

INDIA: LATITUDE ~10–30° N

Bengali



Tamil: ~100 years ago

We propose, therefore, that women tend to be lighter-skinned than men to allow slightly more UVB rays to penetrate their skin and thereby increase their ability to produce vitamin D. In areas of the world that receive a large amount of UV radiation, women are indeed at the knife's edge of natural selection, needing to maximize the photoprotective function of their skin on the one hand and the ability to synthesize vitamin D on the other.

Where Culture and Biology Meet

AS MODERN HUMANS MOVED throughout the Old World about 100,000 years ago, their skin adapted to the environmental conditions that prevailed in different regions. The skin color of the indigenous people of Africa has had the longest time to adapt because anatomically modern humans first evolved there. The skin color changes that modern humans underwent as they moved from one continent to another—first Asia, then Austro-Melanesia, then Europe and, finally, the Americas—can be reconstructed to some extent. It is important to remember, however, that those humans had clothing and shelter to help protect them from the elements. In some places, they also had the ability to harvest foods that were extraordinarily rich in vitamin D, as in the case of the Inuit. These two factors had profound effects on the tempo and degree of skin color evolution in human populations.

Africa is an environmentally heterogeneous continent. A number of the earliest movements of contemporary humans outside equatorial Africa were into southern Africa. The descendants of some of these early colonizers, the Khoisan (previously known as Hottentots), are still found in southern Africa and have significantly lighter skin than indigenous equatorial Africans do—a clear adaptation to the lower levels of UV radiation that prevail at the southern extremity of the continent.

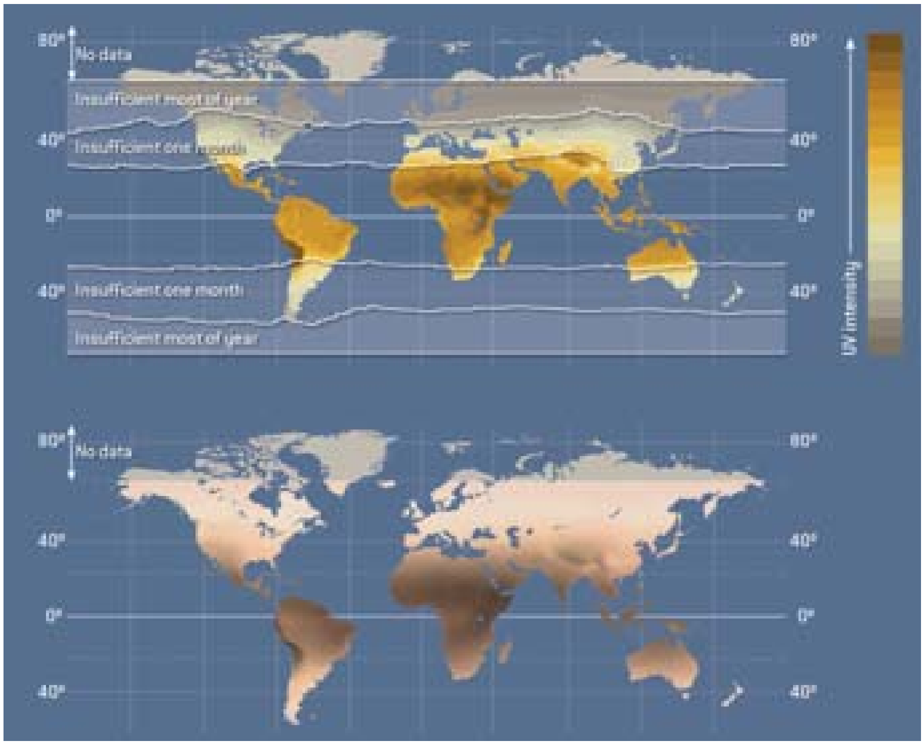
Interestingly, however, human skin color in southern Africa is not uniform. Populations of Bantu-language speakers who live in southern Africa today are far darker than the Khoisan. We know from the history of this region that Bantu speakers migrated into this region recently—probably within the past 1,000 years—from parts of West Africa near the equator. The skin color difference between the Khoisan and Bantu speakers such as the Zulu indicates that the length of time that a group has inhabited a particular region is important in understanding why they have the color they do.

Cultural behaviors have probably also strongly influenced the evolution of skin color in recent human history. This effect can be seen in the indigenous peoples who live on the eastern and western banks of the Red Sea. The tribes on the western side, which speak so-called Nilo-Hamitic languages, are thought to have inhabited this region for as long as 6,000 years. These individuals are distinguished by very darkly pigmented skin and long, thin bodies with long limbs, which are excellent biological adaptations for dissipating heat and intense UV radiation. In contrast, modern agricultural and pastoral groups on the eastern bank of the Red Sea, on the Arabian Peninsula, have lived there for only about 2,000 years. These earliest Arab people, of European origin, have adapted to very similar envi-

PETER JOHNSON *Corbis* (*Khoisan*); BARBARA BANNISTER *Gallo Images/Corbis* (*Zulu*); PENNY TWEEDIE *Corbis* (*Aborigine*); DAVID McLAIN *Aurora* (*European*); ERIC WHEATER *Lonely Planet Images* (*Sudanese*); WAYNE EASTEP *Getty Images* (*Arab*); ROGER WOOD *Corbis* (*Bengali*); JEREMY HORNER *Corbis* (*Tamil*)

WHO MAKES ENOUGH VITAMIN D?

POPULATIONS THAT LIVE in the tropics receive enough ultraviolet light from the sun (*top map, brown and orange*) to synthesize vitamin D all year long. But those that live at northern or southern latitudes do not. In the temperate zones (*light-shaded band*), people lack sufficient UV light to make vitamin D one month of the year; those nearer the poles (*dark-shaded band*) do not get enough UV light most months for vitamin D synthesis. The bottom map shows predicted skin colors for humans based on UV light levels. In the Old World, the skin color of indigenous peoples closely matches predictions. In the New World, however, the skin color of long-term residents is generally lighter than expected—probably because of their recent migration and factors such as diet. *—N.G.J. and G.C.*



ronmental conditions by almost exclusively cultural means—wearing heavy protective clothing and devising portable shade in the form of tents. (Without such clothing, one would have expected their skin to have begun to darken.) Generally speaking, the more recently a group has migrated into an area, the more extensive its cultural, as opposed to biological, adaptations to the area will be.

Perils of Recent Migrations

DESPITE GREAT IMPROVEMENTS in overall human health in the past century, some diseases have appeared or reemerged in populations that had previously been little affected by them. One of these is skin cancer, especially basal and squamous cell carcinomas, among light-skinned peoples. Another is rickets, brought about by severe vitamin D deficiency, in dark-skinned peoples. Why are we seeing these conditions?

As people move from an area with one pattern of UV radiation to another region, biological and cultural adaptations have not been able to keep pace. The light-skinned people of northern European origin who bask in the sun of Florida or northern Australia increasingly pay the price in the form of premature aging of the skin and skin cancers, not to mention the unknown cost in human life of folate depletion. Conversely, a number of dark-skinned people of southern Asian and African origin now living in the northern U.K., northern Europe or the northeastern U.S. suffer from a lack of UV radiation and vitamin D, an insidious problem that manifests itself in high rates of rickets and other diseases related to vitamin D deficiency.

The ability of skin color to adapt over long periods to the various environments to which humans have moved reflects the importance of skin color to our survival. But its unstable nature also makes it one of the least useful characteristics in determining the evolutionary relations between human groups. Early Western scientists used skin color improperly to delineate human races, but the beauty of science is that it can and does correct itself. Our current knowledge of the evolution of human skin indicates that variations in skin color, like most of our physical attributes, can be explained by adaptation to the environment through natural selection. We look ahead to the day when the vestiges of old scientific mistakes will be erased and replaced by a better understanding of human origins and diversity. Our variation in skin color should be celebrated as one of the most visible manifestations of our evolution as a species. SA

SARA CHEN

MORE TO EXPLORE

The Evolution of Human Skin Coloration. Nina G. Jablonski and George Chaplin in *Journal of Human Evolution,* Vol. 39, No. 1, pages 57–106; July 1, 2000.

Why Skin Comes in Colors. Blake Edgar in *California Wild,* Vol. 53, No. 1, pages 6–7; Winter 2000. The article is also available at **www.calacademy.org/calwild/winter2000/html/horizons.html**

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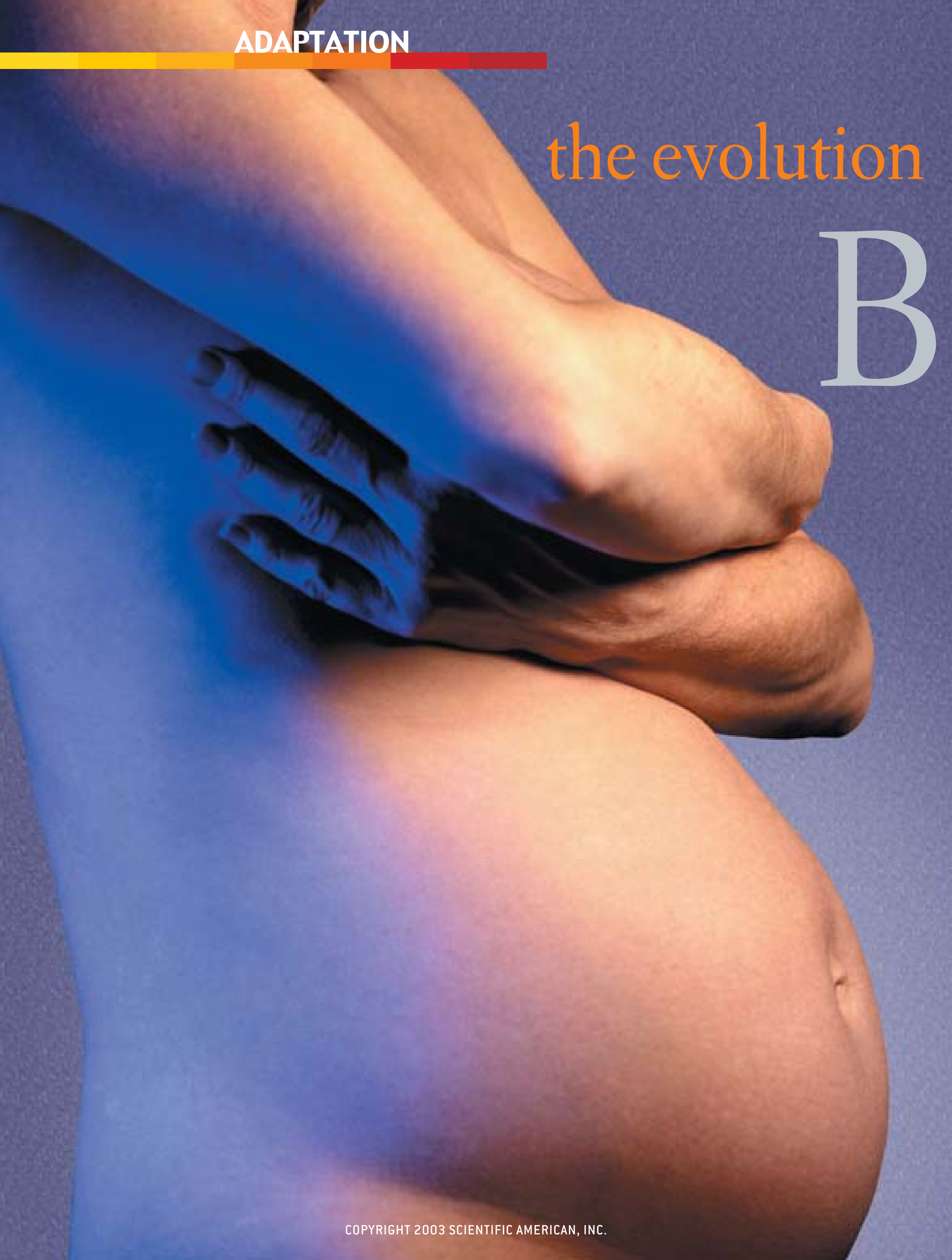


# of Human irth

By Karen R. Rosenberg and Wenda R. Trevathan

The difficulties of childbirth have probably challenged humans and their ancestors for millions of years—which means that the modern custom of seeking assistance during delivery may have similarly ancient roots

GIVING BIRTH IN THE TREETOPS is not the normal human way of doing things, but that is exactly what Sophia Pedro was forced to do during the height of the floods that ravaged southern Mozambique in March 2000. Pedro had survived for four days perched high above the raging floodwaters that killed more than 700 people in the region. The day after her delivery, television broadcasts and newspapers all over the world featured images of Pedro and her newborn child being plucked from the tree during a dramatic helicopter rescue.

Treetop delivery rooms are unusual for humans but not for other primate species. For millions of years, primates have secluded themselves in treetops or bushes to give birth. Human beings are the only primate species that regularly seeks assistance during labor and delivery. So when and why did our female ancestors abandon their unassisted and solitary habit? The answers lie in the difficult and risky nature of human birth.

Many women know from experience that pushing a baby through the birth canal is no easy task. It's the price we pay for our large brains and intelligence: humans have exceptionally big heads relative to the size of their bodies. Those who have delved deeper into the subject know that the opening in the human pelvis through which the baby must pass is limited in size by our upright posture. But only recently have anthropologists begun to realize that the complex twists and turns that human babies make as they travel through the birth canal have troubled humans and their ancestors for at least 100,000 years. Fossil clues also indicate that anatomy, not just our social nature, has led human mothers—in contrast to our closest primate relatives and almost all other mammals—to ask for help during childbirth. Indeed, this practice of seeking assistance may have been in place when the earliest members of our genus, *Homo,* emerged and may possibly date back to five million years ago, when our ancestors first began to walk upright on a regular basis.

Tight Squeeze

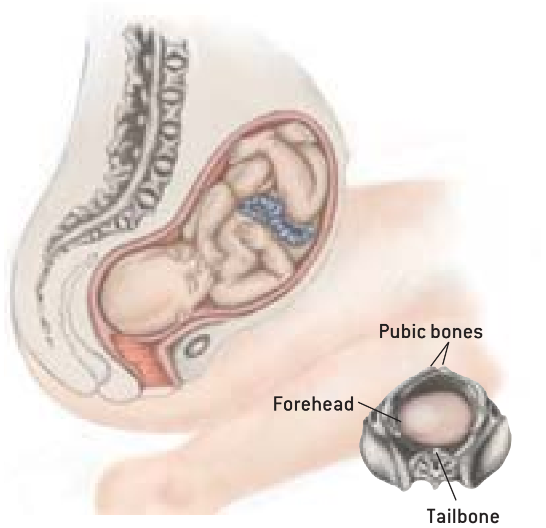
TO TEST OUR THEORY that the practice of assisted birth may have been around for millennia, we considered first what scientists know about the way a primate baby fits through the mother's birth canal. Viewed from above, the infant's head is basically an oval, longest from the forehead to the back of the head and narrowest from ear to ear. Conveniently, the birth canal—the bony opening in the pelvis through which the baby must travel to get from the uterus to the outside world—is also an oval shape. The challenge of birth for many primates is that the size of the infant's head is close to the size of that opening.

For humans, this tight squeeze is complicated by the birth canal's not being a constant shape in cross section. The entrance of the birth canal, where the baby begins its journey, is widest from side to side relative to the mother's body. Midway through, however, this orientation shifts 90 degrees, and the long axis of the oval extends from the front of the mother's body to her back. This means that the human infant must negotiate a series of turns as it works its way through the birth canal so that the two parts of its body with the largest dimensions—the head and the shoulders—are always aligned with the largest dimension of the birth canal [*see illustration at right*].

To understand the birth process from the mother's point of view, imagine you are about to give birth. The baby is most likely upside down, facing your side, when its head enters the birth canal. Midway through the canal, however, it must turn to face your back, and the back of its head is pressed against your pubic bones. At that time, its shoulders are oriented side to side. When the baby exits your body, it is still facing backward, but it will turn its head slightly to the side. This rotation helps to turn the baby's shoulders so that they can also fit between your pubic bones and tailbone. To appreciate the close correspondence of the maternal and fetal dimensions, consider that the average pelvic opening in human females is 13 centimeters at its largest diameter and 10 centimeters at its smallest. The average infant head is 10 centimeters from front to back, and the shoulders are 12 centimeters across. This journey through a passageway of changing cross-sectional shape makes human birth difficult and risky for the vast majority of mothers and babies.

If we retreat far enough back along the family tree of human ancestors, we would eventually reach a point where birth was not so difficult. Although humans are more closely related to apes genetically, monkeys may present a better model for birth in prehuman primates. One line of reasoning to support this assertion is as follows: Of the primate fossils discovered from the time before the first known hominids, one possible remote ancestor is *Proconsul,* a primate fossil dated to about 25 million years ago. This tailless creature probably looked like an ape, but its skeleton suggests that it moved more like a monkey. Its pelvis, too, was more monkeylike. The heads of modern monkey infants are typically about 98 percent the diameter of the mother's birth canal—a situation more comparable with that of humans than that of chimps, whose birth canals are relatively spacious.

Despite the monkey infant's tight squeeze, its entrance into the world is less challenging than that of a human baby. In contrast to the twisted birth canal of modern humans, monkeys' birth canals maintain the same cross-sectional shape from entrance to exit. The longest diameter of this oval shape is oriented front to back, and the broadest part of the oval is against the mother's

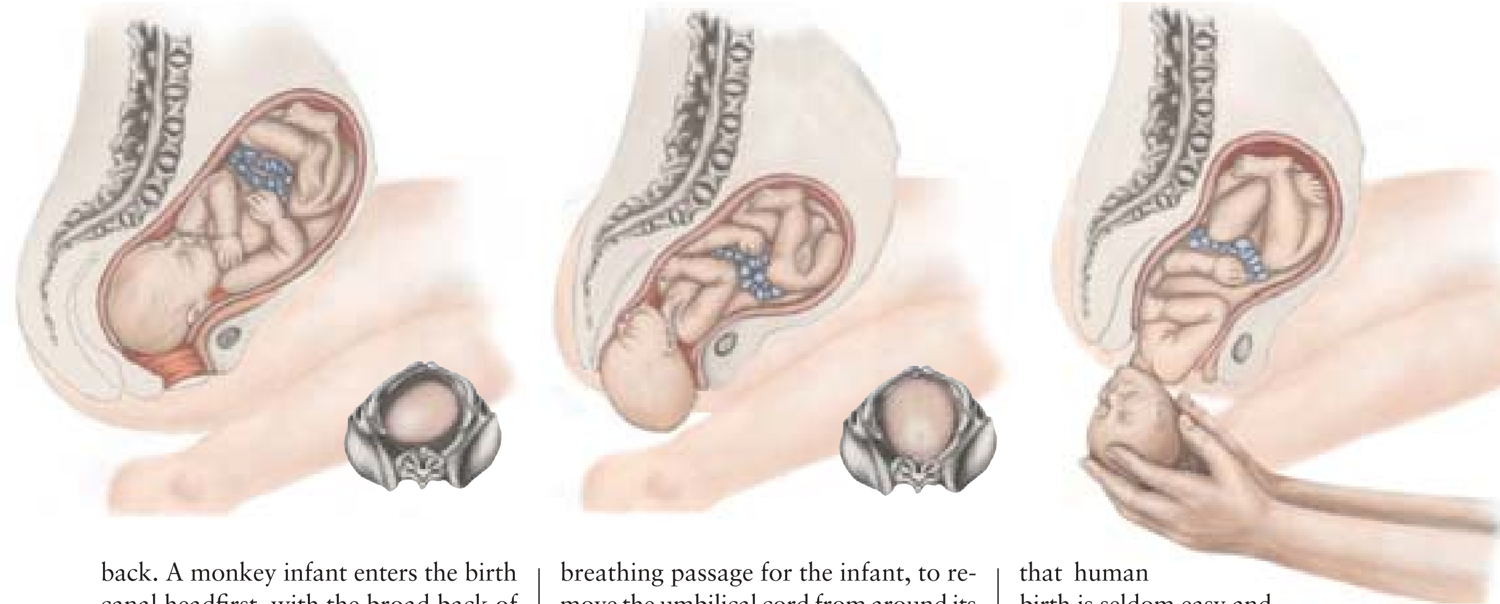


BABY BORN FACING BACKWARD, with the back of its head against the mother's pubic bones, makes it difficult for a human female to guide the infant from the birth canal—the opening in the mother's pelvis (*insets*)—without assistance.

NINA FINKEL

THE AUTHORS

KAREN R. ROSENBERG and *WENDA R. TREVATHAN* bring different perspectives to the study of human birth. Rosenberg, a paleoanthropologist at the University of Delaware, specializes in pelvic morphology and has studied hominid fossils from Europe, Israel, China and South Africa. About 15 years ago she began studying the pelvis as a way to reconstruct the evolution of the birth process. That's when she met Trevathan, a biological anthropologist at New Mexico State University, whose particular interests include childbirth, maternal behavior, sexuality, menopause and evolutionary medicine. Both authors have experienced birth firsthand: Rosenberg has two daughters, and Trevathan is trained as a midwife.



back. A monkey infant enters the birth canal headfirst, with the broad back of its skull against the roomy back of the mother's pelvis and tailbone. That means the baby monkey emerges from the birth canal face forward—in other words, facing the same direction as the mother.

Firsthand observations of monkey deliveries have revealed a great advantage in babies' being born facing forward. Monkeys give birth squatting on their hind legs or crouching on all fours. As the infant is born, the mother reaches down to guide it out of the birth canal and toward her nipples. In many cases, she also wipes mucus from the baby's mouth and nose to aid its breathing. Infants are strong enough at birth to take part in their own deliveries. Once their hands are free, they can grab their mother's body and pull themselves out.

If human babies were also born face forward, their mothers would have a much easier time. Instead the evolutionary modifications of the human pelvis that enabled hominids to walk upright necessitate that most infants exit the birth canal with the back of their heads against the pubic bones, facing in the opposite direction as the mother (in a position obstetricians call "occiput anterior"). For this reason, it is difficult for the laboring human mother—whether squatting, sitting, or lying on her back—to reach down and guide the baby as it emerges. This configuration also greatly inhibits the mother's ability to clear a breathing passage for the infant, to remove the umbilical cord from around its neck or even to lift the baby up to her breast. If she tries to accelerate the delivery by grabbing the baby and guiding it from the birth canal, she risks bending its back awkwardly against the natural curve of its spine. Pulling on a newborn at this angle risks injury to its spinal cord, nerves and muscles.

For contemporary humans, the response to these challenges is to seek assistance during labor and delivery. Whether a technology-oriented professional, a lay midwife or a family member who is familiar with the birth process, the assistant can help the human mother do all the things the monkey mother does by herself. The assistant can also compensate for the limited motor abilities of the relatively helpless human infant. The advantages of even simple forms of assistance have reduced maternal and infant mortality throughout history.

Assisted Birth

OF COURSE, OUR ANCESTORS and even women today can and do give birth alone successfully. Many fictional accounts portray stalwart peasant women giving birth alone in the fields, perhaps most famously in the novel *The Good Earth,* by Pearl S. Buck. Such images give the impression that delivering babies is easy. But anthropologists who have studied childbirth in cultures around the world report that these perceptions are highly romanticized and that human birth is seldom easy and rarely unattended. Today virtually all women in all societies seek assistance at delivery. Even among the !Kung of southern Africa's Kalahari Desert—who are well known for viewing solitary birth as a cultural ideal—women do not usually manage to give birth alone until they have delivered several babies at which mothers, sisters or other women are present. So, though rare exceptions do exist, assisted birth comes close to being a universal custom in human cultures [*see box on next page*].

Knowing this—and believing that this practice is driven by the difficulty and risk that accompany human birth—we began to think that midwifery is not unique to contemporary humans but instead has its roots deep in our ancestry. Our analysis of the birth process throughout human evolution has led us to suggest that the practice of midwifery might have appeared as early as five million years ago, when bipedalism constricted the size and shape of the pelvis and birth canal.

A behavior pattern as complex as midwifery obviously does not fossilize, but pelvic bones do. The tight fit between the infant's head and the mother's birth canal in humans means that the mechanism of birth can be reconstructed if we know the relative sizes of each. Pelvic anatomy is now fairly well known from most time periods in the human fossil record, and we can estimate infant brain and skull size based on our extensive knowledge of adult skull sizes. (The delicate skulls of infants are not commonly found preserved until the point when humans began to bury their dead about 100,000 years ago.) Knowing the size and shape of the skulls and pelvises has also helped us and other researchers to understand whether infants were born facing forward or backward relative to their mothers—in turn revealing how challenging the birth might have been.

Walking on Two Legs

IN MODERN HUMANS, both bipedalism and enlarged brains constrain birth in important ways, but the first fundamental shift away from a nonhuman primate way of birth came about because of bipedalism alone. This unique way of walking appeared in early human ancestors of the genus *Australopithecus* at least four million years ago [see "Evolution of Human Walking," by C. Owen Lovejoy; SCIENTIFIC AMERICAN, November 1988]. Despite their upright posture, australopithecines typically stood no more than four feet tall, and their brains were not much bigger than those of living chimpanzees. Recent evidence has called into question which of the several australopithecine species were part of the lineage that led to *Homo*. Understanding the way any of them gave birth is still important, however, because walking on two legs would have constricted the maximum size of the pelvis and birth canal in similar ways among related species.

The anatomy of the female pelvis from this time period is well known from two complete fossils. Anthropologists unearthed the first (known as Sts 14 and presumed to be 2.5 million years old) in Sterkfontein, a site in the Transvaal region of South Africa. The second is best known as Lucy, a fossil discovered in the Hadar region of Ethiopia and dated at just over three million years old. Based on these specimens and on estimates of newborns' head size, C. Owen Lovejoy of Kent State University and Robert G. Tague of Louisiana State University concluded in the mid-1980s that birth in early hominids was unlike that known for any living species of primate.

The shape of the australopithecine birth canal is a flattened oval with the greatest dimension from side to side at both the entrance and exit. This shape appears to require a birth pattern different from that of monkeys, apes or modern humans. The head would not have rotated within the birth canal, but we think that in order for the shoulders to fit through, the baby might have had to turn its head once it emerged. In other words, if the baby's head entered the birth canal facing the side of the mother's body, its shoulders would have been oriented in a line from the mother's belly to her back. This starting position would have meant that the shoulders probably also had to turn sideways to squeeze through the birth canal.

This simple rotation could have introduced a kind of difficulty in australopithecine deliveries that no other known primate species had ever experienced. Depending on which way the baby's shoulders turned, its head could have exited the birth canal facing either forward or backward relative to the mother. Because the australopithecine birth canal is a symmetrical opening of unchanging shape, the baby could have just as easily turned its shoulders toward the front or back of its body, giving it about a 50–50 chance of emerging in the easier, face-forward position. If the infant were born facing backward, the australopithecine mother—like modern human mothers—may well have benefited from some kind of assistance.

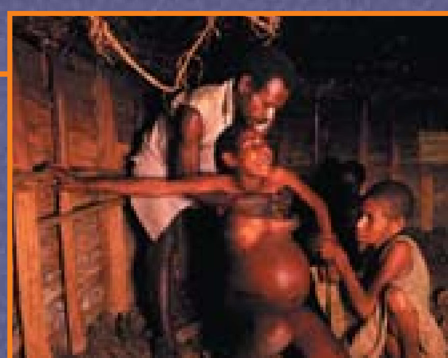
Growing Bigger Brains

IF BIPEDALISM ALONE did not introduce into the process of childbirth enough difficulty for mothers to benefit from assistance, then the expanding size of the hominid brain certainly did. The most significant expansion in adult and infant brain size evolved subsequent to the australopithecines, particularly in the genus *Homo*. Fossil remains of the

Childbirth across Cultures

THE COMPLICATED CONFIGURATION of the human birth canal is such that laboring women and their babies benefit—by lower rates of mortality, injury and anxiety—from the assistance of others. This evolutionary reality helps to explain why attended birth is a near universal feature of human cultures. Individual women throughout history have given birth alone in certain circumstances, of course. But much more common is the attendance of familiar friends and relatives, most of whom are women. (Men may be variously forbidden, tolerated, welcomed or even required at birth.) In Western societies, where women usually give birth in the presence of strangers, recent research on birth practices has also shown that a doula—a person who provides social and emotional support to a woman in labor—reduces the rate of complications.

In many societies, a woman may not be recognized as an adult until she has had a baby. The preferred location of the delivery is often specified, as are the positions that the laboring women assume. The typical expectation in Western culture is that women should give birth lying flat on their backs on a bed, but in the rest of the world the most prevalent position for the delivery is upright—sitting, squatting or, in some cases, standing. *—K.R.R. and W.R.T.*



SQUATTING is one of the most typical positions for women to give birth in non-Western cultures.

DANNY LEHMAN *Corbis*

pelvis of early *Homo* are quite rare, and the best-preserved specimen, the 1.6-million-year-old Nariokotome fossil from Kenya, is an adolescent often referred to as Turkana Boy. Researchers have estimated that the boy's adult relatives probably had brains about twice as large as those of australopithecines but still only two thirds the size of modern human brains.

By reconstructing the shape of the boy's pelvis from fragments, Christopher B. Ruff of Johns Hopkins University and Alan Walker of Pennsylvania State University have estimated what he would have looked like had he reached adulthood. Using predictable differences between male and female pelvises in more recent hominid species, they could also infer what a female of that species would have looked like and could estimate the shape of the birth canal. That shape turns out to be a flattened oval similar to that of the australopithecines. Based on these reconstructions, the researchers determined that Turkana Boy's kin probably had a birth mechanism like that seen in australopithecines.

In recent years, scientists have been testing an important hypothesis that follows from Ruff and Walker's assertion: the pelvic anatomy of early *Homo* may have limited the growth of the human brain until the evolutionary point at which the birth canal expanded enough to allow a larger infant head to pass. This assertion implies that bigger brains and roomier pelvises were linked from an evolutionary perspective. Individuals who displayed both characteristics were more successful at giving birth to offspring who survived to pass on the traits. These changes in pelvic anatomy, accompanied by assisted birth, may have allowed the dramatic increase in human brain size that took place from two million to 100,000 years ago.

Fossils that span the past 300,000 years of human evolution support the connection between the expansion of brain size and changes in pelvic anatomy. In the past 20 years, scientists have uncovered three pelvic fossils of archaic *Homo sapiens:* a male from Sima de los Huesos in Sierra Atapuerca, Spain (more than 200,000 years old); a female from Jinniushan, China (280,000 years old); and the male Kebara Neandertal—which is also an archaic *H. sapiens*—from Israel (about 60,000 years old). These specimens all have the twisted pelvic openings characteristic of modern humans, which suggests that their large-brained babies would most likely have had to rotate the head and shoulders within the birth canal and would thus have emerged facing away from the mother—a major challenge that human mothers face in delivering their babies safely.

The triple challenge of big-brained infants, a pelvis designed for walking upright, and a rotational delivery in which the baby emerges facing backward is not merely a contemporary circumstance. For this reason, we suggest that natural selection long ago favored the behavior of seeking assistance during birth because such help compensated for these difficulties. Mothers probably did not seek assistance solely because they predicted the risk that childbirth poses, however. Pain, fear and anxiety more likely drove their desire for companionship and security.

BABY BORN FACING FORWARD makes it possible for a monkey mother to reach down and carefully guide the infant out of the birth canal. She can also wipe mucus from the baby's face to assist its breathing.

Psychiatrists have argued that natural selection might have favored such emotions—also common during illness and injury—because they led individuals who experienced them to seek the protection of companions, which would have given them a better chance of surviving [see "Evolution and the Origins of Disease," by Randolph M. Nesse and George C. Williams; Scientific American, November 1998]. The offspring of the survivors would then also have an enhanced tendency to experience such emotions during times of pain or disease. Taking into consideration the evolutionary advantage that fear and anxiety impart, it is no surprise that women commonly experience these emotions during labor and delivery.

Modern women giving birth have a dual evolutionary legacy: the need for physical as well as emotional support. When Sophia Pedro gave birth in a tree surrounded by raging floodwaters, she may have had both kinds of assistance. In an interview several months after her helicopter rescue, she told reporters that her mother-in-law, who was also in the tree, helped her during delivery. Desire for this kind of support, it appears, may well be as ancient as humanity itself. SA

MORE TO EXPLORE

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NINA FINKEL

Once Were CAN

Clear evidence of cannibalism in the human fossil record has been rare, but it is now becoming apparent that the practice is deeply rooted in our history

BY TIM D. WHITE

NEANDERTAL CRANIUM from the Krapina rock-shelter in Croatia. Physical anthropologists and archaeologists have recently determined that this specimen and hundreds of other skeletal remains at this site attest to cannibalism. This cranium was smashed so the brain could be removed and consumed.

NIBALS

It can shock, disgust and fascinate in equal measure,

whether through tales of starved pioneers or airplane crash survivors eating the deceased among them or accounts of rituals in Papua New Guinea. It is the stuff of headlines and horror films, drawing people in and mesmerizing them despite their aversion. Cannibalism represents the ultimate taboo for many in Western societies—something to relegate to other cultures, other times, other places. Yet the understanding of cannibalism derived from the past few centuries of anthropological investigation has been too unclear and incomplete to allow either a categorical rejection of the practice or a fuller appreciation of when, where and why it might have taken place.

New scientific evidence is now bringing to light the truth about cannibalism. It has become obvious that long before the invention of metals, before Egypt's pyramids were built, before the origins of agriculture, before the explosion of Upper Paleolithic cave art, cannibalism could be found among many different peoples—as well as among many of our ancestors. Broken and scattered human bones, in some cases thousands of them, have been discovered from the prehistoric pueblos of the American Southwest to the islands of the Pacific. The osteologists and archaeologists studying these ancient occurrences are using increasingly sophisticated analytical tools and methods. In the past several years, the results of their studies have finally provided convincing evidence of prehistoric cannibalism.

Human cannibalism has long intrigued anthropologists, and they have worked for decades to classify the phenomenon. Some divide the behavior according to the affiliation of the consumed. Thus, endocannibalism refers to the consumption of individuals within a group, exocannibalism indicates the consumption of outsiders, and autocannibalism covers everything from nail biting to torture-induced self-consumption. In addition, anthropologists have come up with classifications to describe perceived or known motivations. Survival cannibalism is driven by starvation. Historically documented cases include the Donner Party—whose members were trapped during the harsh winter of 1846–47 in the Sierra Nevada—and people marooned in the Andes or the Arctic with no other food. In contrast, ritual cannibalism occurs when members of a family or community consume their dead during funerary rites in order to inherit their qualities or honor their memory. And pathological cannibalism is generally reserved for criminals who consume their victims or, more often, for fictional characters such as Hannibal Lecter in *The Silence of the Lambs*.

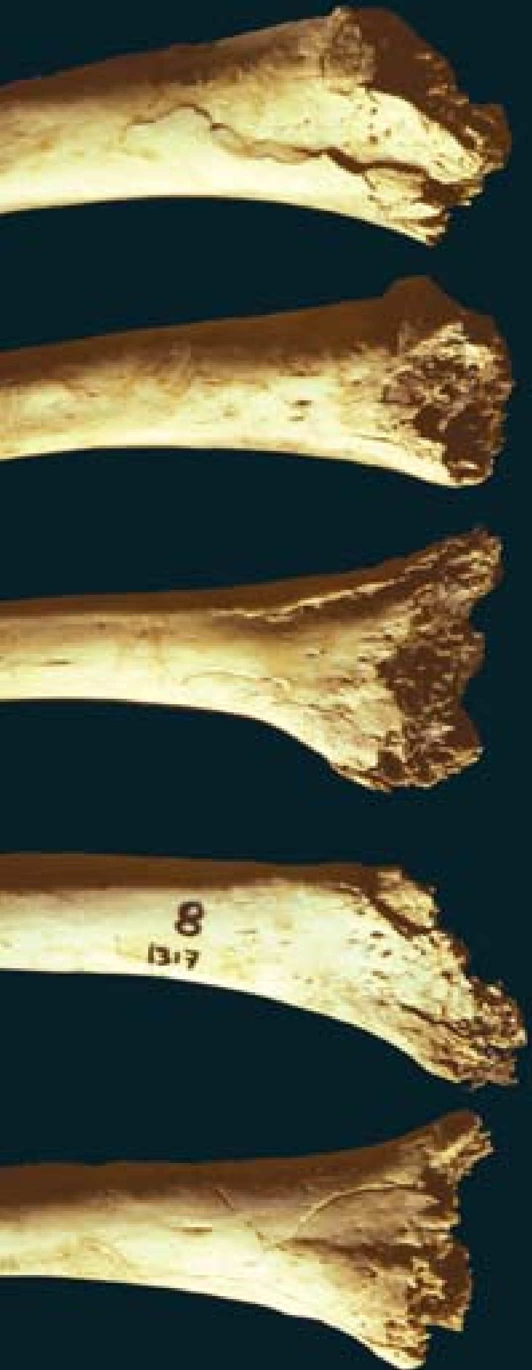
Despite these distinctions, however, most anthropologists simply equate the term "cannibalism" with the regular, culturally encouraged consumption of human flesh. In the age of ethnographic exploration—which lasted from the time of Greek historian Herodotus in about 400 B.C. to the early 20th century—the non-Western world and its inhabitants were scrutinized by travelers, missionaries, military personnel and anthropologists. These observers told tales of human cannibalism in different places, from Mesoamerica to the Pacific islands to central Africa.

Controversy has often accompanied these claims. Anthropologists participated in only the last few waves of these cultural contacts—those that began in the late 1800s. As a result, many of the historical accounts of cannibalism have come to be viewed skeptically.

THE AUTHOR

TIM D. WHITE is co-director of the Laboratory for Human Evolutionary Studies of the Museum of Vertebrate Zoology at the University of California, Berkeley. He is also a professor in Berkeley's department of integrative biology and a member of the National Academy of Sciences. White co-directs the Middle Awash research project in Ethiopia. His research interests are human paleontology, Paleolithic archaeology, and the interpretation of bone modification in contexts ranging from prehistoric archaeology to contemporary forensic situations.

DAVID BRILL (*preceding pages*); TIM D. WHITE (*opposite page*)



CRUSHING

Many different types of damage can be seen on bones left by human cannibals. When this damage is identical to that seen on animal bones at the same sites, archaeologists infer that the human remains were processed in the same manner and for the same reason: for consumption. In these metatarsal (foot) bones from Mancos Canyon in Colorado, the spongy tissues at the ends were crushed so that fat could be removed. (All the bones on the following pages are from the same Anasazi site in Mancos.)

In 1979 anthropologist William Arens of the State University of New York at Stony Brook extended this theme by reviewing the ethnographic record of cannibalism in his book *The Man-Eating Myth*. Arens concluded that accounts of cannibalism among people from the Aztec to the Maori to the Zulu were either false or inadequately documented. His skeptical assertion has subsequently been seriously questioned, yet he nonetheless succeeded in identifying a significant gulf between these stories and evidence of cannibalism: "Anthropology has not maintained the usual standards of documentation and intellectual rigor expected when other topics are being considered. Instead, it has chosen uncritically to lend its support to the collective representations and thinly disguised prejudices of western culture about others."

The anthropologists whom Arens was criticizing had not limited themselves to contemporary peoples. Some had projected their prejudices even more deeply—into the archaeological record. Interpretations of cannibalism inevitably followed many discoveries of prehistoric remains. In 1871 American author Mark Twain weighed in on the subject in an essay later published in *Life as I Find It:* "Here is a pile of bones of primeval man and beast all mixed together, with no more damning evidence that the man ate the bears than that the bears ate the man—yet paleontology holds a coroner's inquest in the fifth geologic period on an 'unpleasantness' which transpired in the quaternary, and calmly lays it on the MAN, and then adds to it what purports to be evidence of CANNIBALISM. I ask the candid reader, Does not this look like taking advantage of a gentleman who has been dead two million years...."

In the century after Twain's remarks, archaeologists and physical anthropologists described the hominids *Australopithecus africanus, Homo erectus* and *H. neanderthalensis* as cannibalistic. According to some views, human prehistory from about three million years ago until very recently was rife with cannibalism.

But in the early 1980s an important critical assessment of these conclusions appeared. Archaeologist Lewis Binford's book *Bones: Ancient Men and Modern Myths* argued that claims for early hominid cannibalism were unsound. He built on the work of other prehistorians concerned with the composition, context and modifications of Paleolithic bone assemblages. Binford emphasized the need to draw accurate inferences about past behaviors by grounding knowledge of the past on experiment and observation in the present. His influential work coupled skepticism with a plea for methodological rigor in studies of prehistoric cannibalism.

Standards of Evidence

IT WOULD BE HELPFUL if we could turn to modern-day cannibals with our questions, but such opportunities have largely disappeared. So today's study of this intriguing behavior must be accomplished through a historical science. Archaeology has therefore become the primary means of investigating the existence and extent of human cannibalism.

One of the challenges facing archaeologists, however, is the amazing variety of ways in which people dispose of their dead. Bodies may be buried, burned, placed on scaffolding, set adrift, put in tree trunks or fed to scavengers. Bones may be disinterred, washed, painted, buried in bundles or scattered on stones. In parts of Tibet, future archaeologists will have difficulty recognizing any mortuary practice at all. There most corpses are dismembered and fed to vultures and other carnivores. The bones are then collected, ground into powder, mixed with barley and flour and again fed to vultures. Given the various fates of bones and bodies, distinguishing cannibalism from other mortuary practices can be quite tricky.

Scientists have thus set the standard for recognizing ancient cannibalism very high. They confirm the activity when the processing patterns seen on human remains match those seen on the bones of other animals consumed for food. Archaeologists have long argued for such a comparison between human and faunal remains at a site. They reason that damage to *animal* bones and their arrangement can clearly show that the animals had been slaughtered and eaten for food. And when *human* remains are unearthed in similar cultural contexts, with similar patterns of damage, discard and preservation, they may reasonably be interpreted as evidence of cannibalism.

When one mammal eats another, it usually leaves a record of its activities in the form of modifications to the consumed animal's skeleton. During life, varying amounts of soft tissue, much of it with nutritive value, cover mammalian bones. When the tissue is removed and prepared, the bones often retain a record of this processing in the form of gnawing marks and fractures. When humans eat other animals, however, they mark bones with more than just their teeth. They process carcasses with tools of stone or metal. In so doing, they leave imprints of their presence and actions in the form of scars on the bones. These same imprints can be seen on butchered human skeletal remains.

The key to recognizing human cannibalism is to identify the patterns of processing—that is, the cut marks, hammering damage, fractures or burns seen on the remains—as well as the survival of different bones and parts of bones. Nutritionally valuable tissues, such as brains and marrow, reside within the bones and can be removed only with forceful hammering—and such forced entry leaves revealing patterns of bone damage. When human bones from archaeological sites show patterns of damage uniquely linked to butchery by other humans, the inference of cannibalism is strengthened. Judging which patterns are consistent with dietary butchery can be based on the associated archaeological record—particularly the nonhuman food-animal remains discovered in sites formed by the same culture—and checked against predictions embedded in ethnohistorical accounts.

This comparative system of determining cannibalism emphasizes multiple lines of osteological damage and contextual evidence. And, as noted earlier, it sets the standard for recognizing cannibalism very high. With this approach, for instance, the presence of cut marks on bones would not by themselves be considered evidence of cannibalism. For example, an American Civil War cemetery would contain skeletal remains with cut marks made by swords and bayonets. Medical school cadavers are dissected and their bones cut-marked.

With the threshold set so conservatively, most instances of past cannibalism will necessarily go unrecognized. A practice from Papua New Guinea, where cannibalism was recorded ethnographically, illustrates this point. There skulls of the deceased were carefully cleaned and the brains removed. The dry, mostly intact skulls were then handled extensively, often creating a polish on their projecting parts. They were sometimes painted and even mounted on poles for display and worship. Soft tissue, including brain matter, was eaten at the beginning of this process; thus, the practice would be identified as ritual cannibalism. If such skulls were encountered in an archaeological context without modern informants describing the cannibalism, they would not constitute direct evidence for cannibalism under the stringent criteria that my colleagues and I advocate.

Nevertheless, adoption of these standards of evidence has led us to some clear determinations in other, older situations. The best indication of prehistoric cannibalism now comes from the archaeological record of the American Southwest, where archaeologists have interpreted dozens of assemblages of human remains. Compelling evidence has also been found in Neolithic and Bronze

> One of the challenges facing archaeologists is the amazing variety of ways in which people dispose of their dead.

CHOPPING
Hack marks visible on the left side of this fragment of a human tibia are testament to the removal of muscle and tendon. Tools were also used to make finer slices, to remove tissue or to sever heads from bodies. Archaeologists have to be careful in their interpretations, however, because humans process their dead in many ways; not all slice or hack marks indicate cannibalism.

Age Europe. Even Europe's earliest hominid site has yielded convincing evidence of cannibalism.

Early European Cannibals

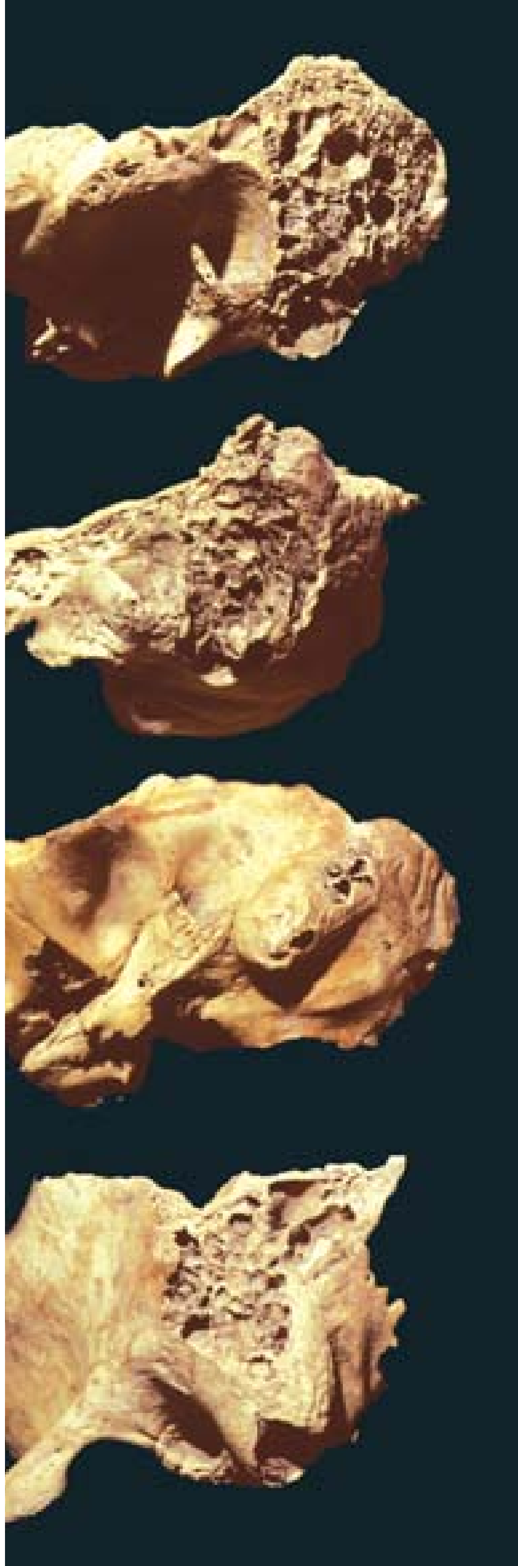
THE MOST IMPORTANT paleoanthropological site in Europe lies in northern Spain, in the foothills of the Sierra de Atapuerca. The oldest known section so far is the Gran Dolina, currently under excavation. The team working there has recovered evidence of occupation some 800,000 years ago by what may prove to be a new species of human ancestor, *H. antecessor*. The hominid bones were discovered in one horizon of the cave's sediment, intermingled with stone tools and the remains of prehistoric game animals such as deer, bison and rhinoceros. The hominid remains consist of 92 fragments from six individuals. They bear unmistakable traces of butchery with stone tools, including the skinning and removal of flesh and the processing of the braincase and the long bones for marrow. This pattern of butchery matches that seen on the nearby animal bones, providing the earliest evidence of hominid cannibalism.

Cannibalism among Europe's much younger Neandertals—who lived between 35,000 and 150,000 years ago—has been debated since the late 1800s, when the great Croatian paleoanthropologist Dragutin Gorjanovič-Kramberger found the broken, cut-marked and scattered remains of more than 20 Neandertals entombed in the sands of the Krapina rock-shelter. Unfortunately, these soft fossil bones were roughly extracted (by today's standards) and then covered with thick layers of preservative, which obscured evidence of processing and made interpretation exceedingly difficult. Some workers believe that the Krapina bones show clear signs of cannibalism; others have attributed the patterns of damage to rocks falling from the cave's ceiling, to carnivore chewing or to some form of burial. But recent analysis of the bones from Krapina and from another Croatian cave, Vindija—which has younger Neandertal and animal remains—indicates that cannibalism was practiced at both sites.

In the past few years, yet another site has offered evidence. On the banks of the Rhône River in southeastern France, Alban Defleur of the University of the Mediterranean at Marseilles has been excavating the cave of Moula-Guercy for more than a decade. Neandertals occupied this small cave 100,000 years ago. In one layer the team unearthed the remains of at least six Neandertals, ranging in age from six years to adult. Defleur's meticulous excavation and recovery standards have yielded data every bit the equivalent of a modern forensic crime scene investigation. Each fragment of fauna and Neandertal bone, each macrobotanical clue, each stone tool has been precisely plotted three-dimensionally. This care has allowed an understanding of how the bones were spread around a hearth that has been cold for 1,000 centuries.

Microscopic analysis of the Neandertal bone fragments and the faunal remains has led to the same conclusion that Spanish workers at the Gran Dolina site have drawn: cannibalism was practiced by some Paleolithic Europeans. Determining how often it was practiced and under what conditions represents a far more difficult challenge. Nevertheless, the frequency is striking. We know of just one very early European site with hominid remains, and those were cannibalized. The two Croatian Neandertal sites are separated by hundreds of generations, yet analyses suggest that cannibalism was practiced at both. And recently a Neandertal site in France was shown to support the same interpretation. These findings are built on exacting standards of evidence. Because of this, most paleoanthropologists these days are asking, "Why cannibalism?" rather than "Was this cannibalism?"

Similarly, discoveries at much younger sites in the American Southwest have altered the way anthropologists think of Anasazi culture in this area. Corn agriculturists have inhabited the Four Corners region for centuries, building their pueblos and spectacular cliff dwellings and leaving one of the richest and most fine-grained archaeological records on earth. Christy G. Turner II of



BURNING

The dark and damaged areas on these four mastoid regions—that is, the hard bump behind each ear—indicate that these human skulls were roasted. Because the mastoid region is not covered by much muscle or other tissue, damage from burning was often more intense in this area than on other parts of cranial bone. Burning patterns therefore provide clues about culinary practices.

TIM D. WHITE (*this and opposite page*)

Historical Accounts

ETHNOHISTORICAL REPORTS of cannibalism have been recorded for centuries in many corners of the globe. Although some involve well-documented accounts by eyewitnesses—such as the Donner Party expedition—other accounts by explorers, missionaries, travelers and soldiers often lack credibility. For example, these two artists' portraits depict cannibalism catalyzed by starvation in China in the late 1800s and a European view of cannibalism in the New World (based on a woodcut from 1497). Such ethnohistorical accounts do not carry the weight of archaeological and forensic evidence. They may, however, serve as rich sources of testable hypotheses, guiding future archaeological excavations.

HULTON-DEUTSCH COLLECTION *Corbis* (*top*); LEONARD DE SELVA *Corbis* (*bottom*)

Arizona State University conducted pioneering work on unusual sets of broken and burned human skeletal remains from Anasazi sites in Arizona, New Mexico and Colorado in the 1960s and 1970s. He saw a pattern suggestive of cannibalism: site after site containing human remains with the telltale signs. Yet little in the history of the area's more recent Puebloan peoples suggested that cannibalism was a widespread practice, and some modern tribes who claim descent from the Anasazi have found the idea disturbing.

The vast majority of Anasazi burials involve whole, articulated skeletons frequently accompanied by decorated ceramic vessels that have become a favorite target of pot hunters in this area. But, as Turner recorded, several dozen sites had fragmented, often burned human remains, and a larger pattern began to emerge. Over the past three decades the total number of human bone specimens from these sites has grown to tens of thousands, representing dozens of individuals spread across 800 years of prehistory and tens of thousands of square kilometers of the American Southwest. The assemblage that I analyzed in 1992 from an Anasazi site in the Mancos Canyon of southwestern Colorado, for instance, contained 2,106 pieces of bone from at least 29 Native American men, women and children.

These assemblages have been found in settlements ranging from small pueblos to large towns and were often contemporaneous with the abandonment of the dwellings. The bones frequently show evidence of roasting before the flesh was removed. They invariably indicate that people extracted the brain and cracked the limb bones for marrow after removing the muscle tissue. And some of the long bone splinters even show end polishing, a phenomenon associated with cooking in ceramic vessels. The bone fragments from Mancos revealed modifications that matched the marks left by Anasazi processing of game animals such as deer and bighorn sheep. The osteological evidence clearly demonstrated that humans were skinned and roasted, their muscles cut away, their joints severed, their long bones broken on anvils with hammerstones, their spongy bones crushed and the fragments circulated in ceramic vessels. But articles outlining the results have proved controversial. Opposition has sometimes seemed motivated more by politics than by science. Many practicing anthropologists believe that scientific findings should defer to social sensitivities. For such anthropologists, cannibalism is so culturally delicate, so politically incorrect, that they find any evidence for it impossible to swallow.

The most compelling evidence in support of human cannibalism at the various Anasazi sites was published in 2000 by Richard A. Marlar of the University of Colorado School of Medicine and his colleagues. The workers excavated three Anasazi pit dwellings dating to approximately A.D. 1150 at a site called Cowboy Wash near Mesa Verde in southwestern Colorado. The same pattern of findings that had been documented at other sites, such as Mancos, was present: disarticulated, broken, scattered human bones in nonburial contexts. Excellent preservation, careful excavation and thoughtful sampling provided a chemical dimension to the analysis and, finally, direct evidence of human cannibalism.

HAMMERING
It is clear from the archaeological record that meat—fat or muscle or other tissue—on the bone was not the only part of the body that was consumed. Braincases were broken open, and marrow was often removed from long bones. In these two examples, stone hammers split the upper arm bones lengthwise, exposing the marrow.

TIM D. WHITE

It remains much more difficult to establish why cannibalism took place than to establish that it did.

Marlar and his colleagues discovered residues of human myoglobin—a protein present in heart and skeletal muscle—on a ceramic vessel, suggesting that human flesh had been cooked in the pot. An unburned human coprolite, or ancient feces, found in the fireplace of one of the abandoned dwellings also tested positive for human myoglobin. Thus, osteological, archaeological and biochemical data indicate that prehistoric cannibalism occurred at Cowboy Wash. The biochemical data for processing and consumption of human tissue offer strong additional support for numerous osteological and archaeological findings across the Southwest.

Understanding Cannibalism

IT REMAINS MUCH more challenging to establish why cannibalism took place than to establish that it did. People usually eat because they are hungry, and most prehistoric cannibals were therefore probably hungry. But discerning more than that—such as whether the taste of human flesh was pleasing or whether cannibalism presented a way to get through the lean times or a satisfying way to get rid of outsiders—requires knowledge not yet available to archaeologists. Even in the case of the Anasazi, who have been well studied, it is impossible to determine whether cannibalism resulted from starvation or was rooted in religious beliefs, or was some combination of these and other things. What is becoming clear through the refinement of the science of archaeology, however, is that cannibalism is part of our collective past. SA

MORE TO EXPLORE

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if humans were BUILT TO LAST

By S. Jay Olshansky, Bruce A. Carnes and Robert N. Butler
Illustrations by Patricia J. Wynne

PERSON DESIGNED FOR A HEALTHY OLD AGE might possess the features highlighted here, along with countless other external and internal adjustments.

Bulging disks, fragile bones, fractured hips, torn ligaments, varicose veins, cataracts, hearing loss, hernias and hemorrhoids: the list of bodily malfunctions that plague us as we age is long and all too familiar. Why do we fall apart just as we reach what should be the prime of life?

The living machines we call our bodies deteriorate because they were not designed for extended operation and because we now push them to function long past their warranty period. The human body is artistically beautiful and worthy of all the wonder and amazement it evokes. But from an engineer's perspective, it is a complex network of bones, muscles, tendons, valves and joints that are directly analogous to the fallible pulleys, pumps, levers and hinges in machines. As we plunge further into our postreproductive years, our joints and other anatomical features that serve us well or cause no problems at younger ages reveal their imperfections. They wear out or otherwise contribute to the health problems that become common in the later years.

We would look a lot different if evolution had designed the human body to function smoothly for a century or more

In evolutionary terms, we harbor flaws because natural selection, the force that molds our genetically controlled traits, does not aim for perfection or endless good health. If a body plan allows individuals to survive long enough to reproduce (and, in humans and various other organisms, to raise their young), then that plan will be selected. That is, individuals robust enough to reproduce will pass their genes—and therefore their body design—to the next generation. Designs that seriously hamper survival in youth will be weeded out (selected against) because most affected individuals will die before having a chance to produce offspring. More important, anatomical and physiological quirks that become disabling only after someone has reproduced will spread. For example, if a body plan leads to total collapse at age 50 but does not interfere with earlier reproduction, the arrangement will get passed along despite the harmful consequences late in life.

Had we been crafted for extended operation, we would have fewer flaws capable of making us miserable in our later days. Evolution does not work that way, however. Instead it cobbles together new features by tinkering with existing ones in a way that would have made Rube Goldberg proud.

The upright posture of humans is a case in point. It was adapted from a body plan that had mammals walking on all fours. This tinkering undoubtedly aided our early hominid ancestors: standing on our own two feet is thought to have promoted everything from food gathering and tool use to enhanced intelligence. Our backbone has since adapted somewhat to the awkward change: the lower vertebrae have grown bigger to cope with the increased vertical pressure, and our spine has curved a bit to keep us from toppling over. Yet these fixes do not ward off an array of problems that arise from our bipedal stance.

What If?

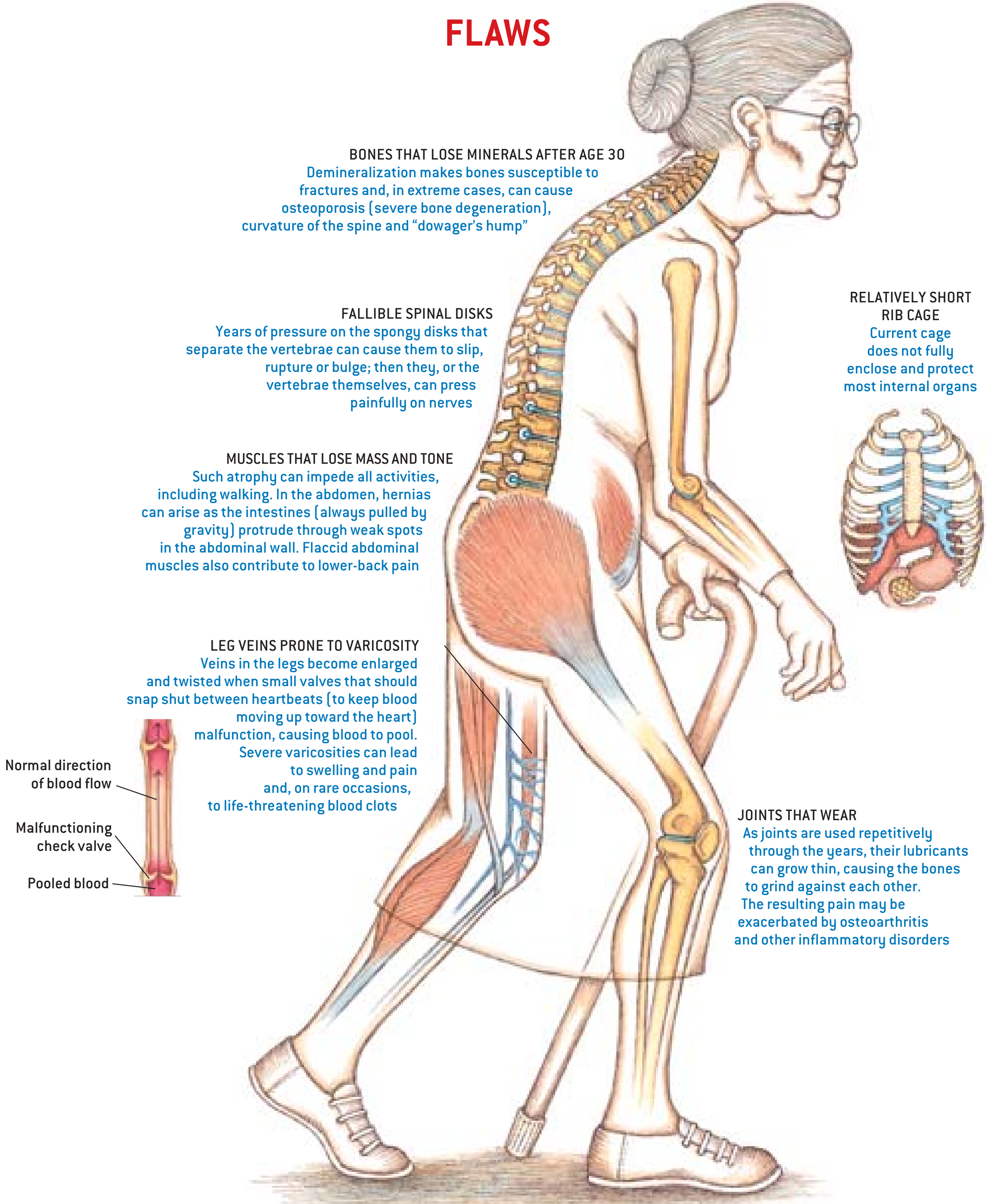
RECENTLY the three of us began pondering what the human body would look like had it been constructed specifically for a healthy long life. The anatomical revisions depicted on the following pages are fanciful and incomplete. Nevertheless, we present them to draw attention to a serious point. Aging is frequently described as a disease that can be reversed or eliminated. Indeed, many purveyors of youth-in-a-bottle would have us believe that the medical problems associated with aging are our own fault, arising primarily from our decadent lifestyles. Certainly any fool can shorten his or her life. But it is grossly unfair to blame people for the health consequences of inheriting a body that lacks perfect maintenance and repair systems and was not built for extended use or perpetual health. Our bodies would still wear out over time even if some mythical, ideal lifestyle could be identified and adopted.

This reality means that aging and many of its accom-

Continued on page 99

A NUMBER OF the debilitating and even some of the fatal disorders of aging stem in part from bipedal locomotion and an upright posture—ironically, the same features that have enabled the human species to flourish. Every step we take places extraordinary pressure on our feet, ankles, knees and back—structures that support the weight of the whole body above them. Over the course of just a single day, disks in the lower back are subjected to pressures equivalent to several tons per square inch. Over a lifetime, all this pressure takes its toll, as does repetitive use of our joints and the

FLAWS



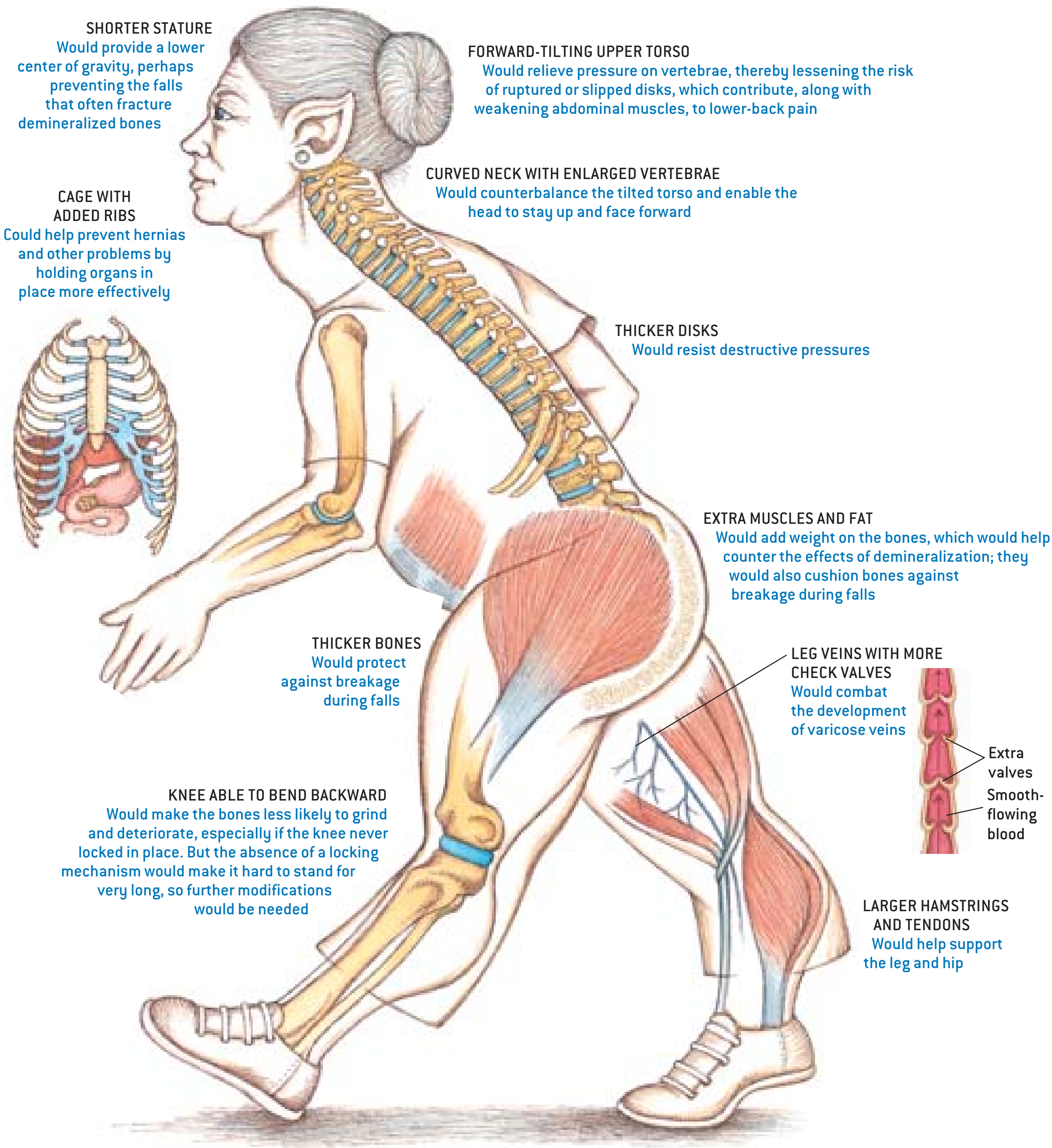
Updated from the March 2001 issue

constant tugging of gravity on our tissues.

Although gravity tends to bring us down in the end, we do possess some features that combat its ever present pull. For instance, an intricate network of tendons helps to tether our organs to the spine, keeping them from slumping down and crushing one another.

But these anatomical fixes—like the body in general—were never meant to work forever. Had longevity and persistent good health been the overarching aim of evolution, arrangements such as those depicted below might have become commonplace.

FIXES



PLAN A HEAD

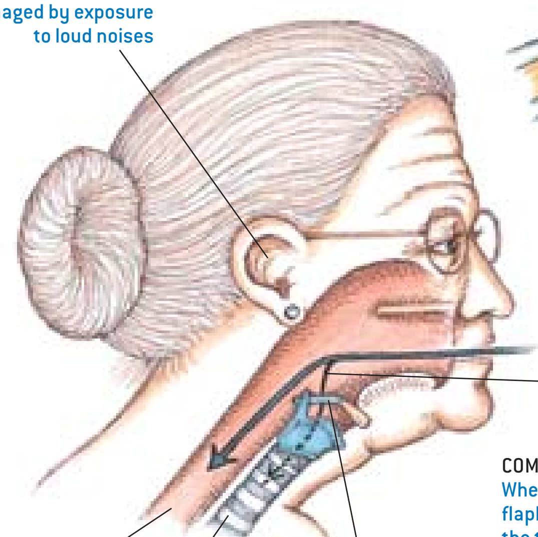
VARIOUS PARTS of the head and neck become problematic with disturbing regularity as people age. Consider the eye: the human version is an evolutionary marvel, but its complexity provides many opportunities for things to go wrong over a long lifetime.

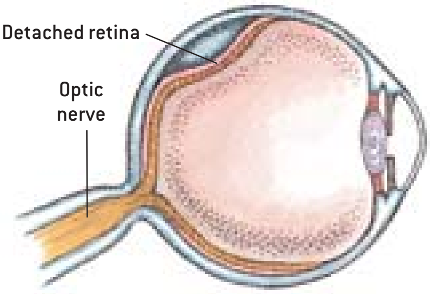
Our vision diminishes as the protective fluid of the cornea becomes less transparent over time. The muscles that control the opening of the iris and the focusing of the lens atrophy and lose responsiveness, and the lens thickens and yellows, impairing visual acuity and color perception. Further, the retina—responsible for transmitting images to the brain—can detach fairly easily from the back of the eye, leading to blindness.

Many of those problems would be difficult to design away, but the squid eye suggests an arrangement that could have reduced the likelihood of retinal detachment. A few anatomical tweaks could also have preserved hearing in the elderly.

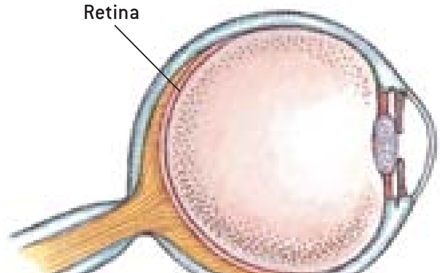
Suboptimal design of the upper respiratory and digestive systems makes choking another risk for older people. A simple rearrangement would have fixed that problem, albeit at the cost of severe trade-offs.

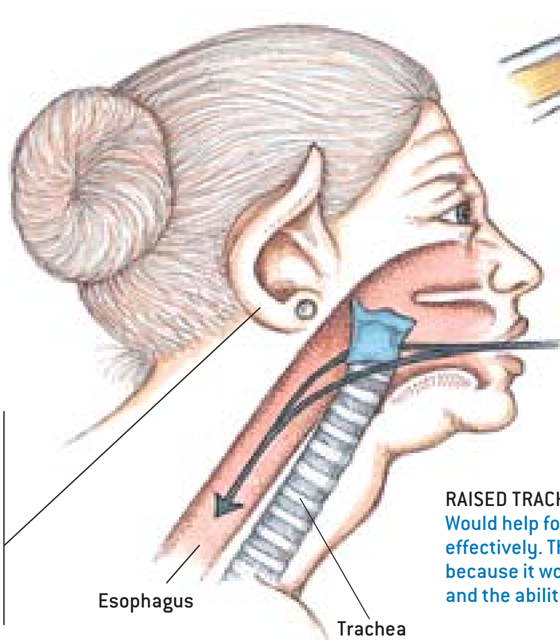
FLAWS





FIXES





Continued from page 95
panying disorders are neither unnatural nor avoidable. No simple interventions can make up for the countless imperfections that permeate our anatomy and are revealed by the passage of time. We are confident, however, that researchers in the various biomedical sciences will be able to ease certain of the maladies that result from our extended life spans. Investigators are rapidly identifying (and discerning the function of) our myriad genes, developing pharmaceuticals to control them, and learning how to harness and enhance the extraordinary repair capabilities that already exist inside our bodies. These profound advances will eventually help compensate for many of the design flaws contained within us all.

Health and Longevity

OUR RESEARCH interest in redesigning the *Homo sapiens* body is a reaction to the health and mortality consequences of growing old. We focus on anatomical "oddities" and "design flaws" not only because they would be familiar to most readers, but because they represent a small sample of lethal and disabling conditions that threaten the length and quality of life. It is important to recognize that we live in a world in which human ingenuity has made it possible for an unprecedented number of people to grow old. Our redesign goal is thus to draw attention to the health consequences associated with the aging of individuals and populations.

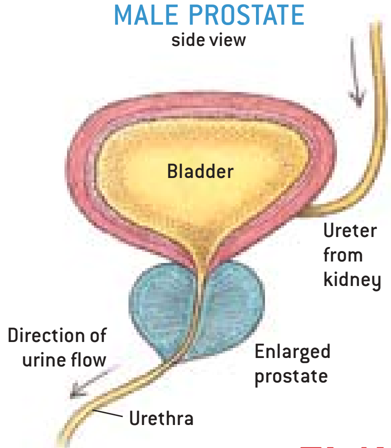
One critical message we wish to convey is that people were

CALL A PLUMBER

AN EXPERIENCED PLUMBER looking at the anatomy of a man's prostate might suspect the work of a young apprentice, because the urethra, the tube leading from the bladder, passes straight through the inside of the gland. This configuration may have as yet unknown benefits, but it eventually causes urinary problems in many men, including weak flow and a frequent need to urinate.

Women also cope with plumbing problems as they age, particularly incontinence. Both sexes could have been spared much discomfort if evolution had made some simple modifications in anatomical design.

MALE PROSTATE
side view



FLAW

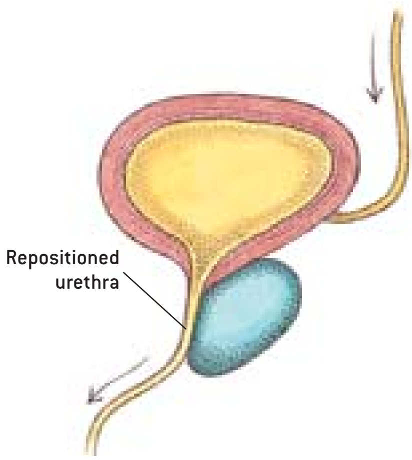
URETHRA PRONE TO CONSTRICTION

The prostate becomes enlarged in one of every two males at some point in life. As it grows, it squeezes the urethra, potentially obstructing the flow of urine. Total obstruction can be fatal

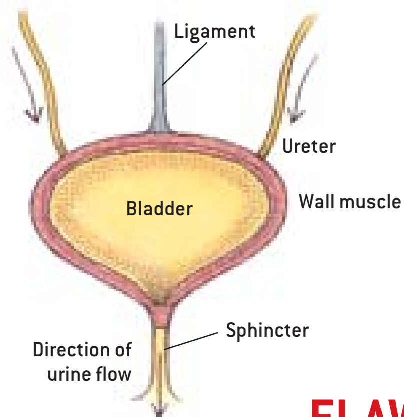
FIX

URETHRA HUGGING OUTSIDE OF PROSTATE

Would not be squeezed if the prostate became enlarged



FEMALE BLADDER
front view



FLAW

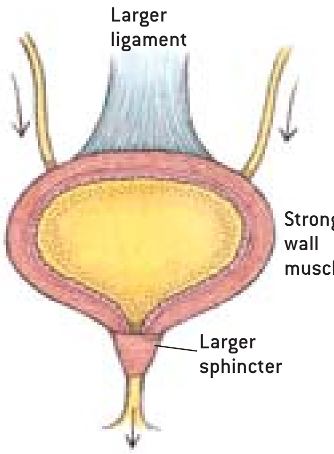
MUSCLES AND LIGAMENTS THAT WEAKEN WITH TIME

Particularly after multiple pregnancies, the muscles of the pelvic floor and the bladder, and the ligaments that support the bladder, can sag, leading to incontinence

FIX

STRONGER SPHINCTER MUSCLES IN BLADDER AND MORE DURABLE LIGAMENTS

Would increase control over bladder function



We need to EXPLOIT OUR KNOWLEDGE of evolution to enhance our quality of life as we grow older.

not designed by evolution for extended survival, so it is not their fault that they ultimately suffer age-related ailments. Most of what goes wrong with us as we grow older is a product of operating our living machines beyond their biological warranty period. Although we have considerable control over the quality of our lives at any age, there is little we can do about the length of our lives other than shorten them.

Even the term "flaw" requires clarification. Living things, and everything they make, eventually fail. The cause of failure is a flaw only when the failure is premature. A race car that fails beyond the end of the race has no engineering flaws. In the same way, bodies that fail in the postreproductive span of life may contain numerous design oddities, but they have no design flaws as far as evolution goes. Aging, disease and death are natural by-products of bodies that were optimized for reproduction.

There are countless other aspects of human biology that would merit modification if health and longevity were nature's primary objective. For example, gerontologists theorize that aging is caused, in part, by a combination of the molecular damage that inevitably arises from operating the machinery of life within cells and the imperfect mechanisms for molecular surveillance, maintenance and repair that permit damage to accumulate over time. If this view of the aging process is correct, then modifying these molecular processes to lessen the severity or accumulation of damage, or to enhance the maintenance and repair processes, should have a beneficial impact on health and longevity. These wondrous modifications, however, would have little effect unless the common sense that is needed to avoid destructive lifestyles becomes more widespread among people.

Living things are exceedingly complex, and experience teaches us that undesirable consequences invariably arise whenever humans have taken over the reins of evolution in order to modify organisms (microbes, plants and animals) to suit their purposes. The most worrisome trade-off for genetic manipulation directed toward living longer would be an extension of frailty and disability rather than an extension of youthful health and vitality.

Though cobbled together by the blind eye of evolution, humans have proved to be a remarkably successful species. We have outcompeted almost every organism that we have encountered, with the notable exception of microbes. We have blanketed the earth and even walked on the moon. We are also one of the only species that has figured out how to escape premature death and survive to old age.

At this point in history, we need to exploit our expanding knowledge of evolution to enhance the quality of our lives as we grow older, because the single-minded pursuit of life extension without considering health extension could be disastrous.

Our fanciful designs of anatomically "fixed" humans are not intended as a realistic exercise in biomechanical engineering. Given what is known today about human aging, if the task of designing a healthy long-lived human from scratch were given to a team comprising the father of evolution, Charles Darwin, the great painter Michelangelo, and the master engineer and scientist Leonardo da Vinci, they most certainly would have fashioned a living machine that differs from the one we now occupy. Indeed, anyone who tries his hand at redesign would probably construct a human body that would look unlike the ones we've created on these pages. Yet we invoke this approach as an instructive way of communicating the important message from evolutionary theory that, to a significant degree, the potential length of our lives and, to a lesser degree, the duration of health and vitality are genetic legacies from our ancestors, who needed to mature quickly to produce children before they were killed by the hostile forces of nature. SA

THE AUTHORS

S. JAY OLSHANSKY, BRUCE A. CARNES and *ROBERT N. BUTLER* all have an enduring interest in the processes that underlie human aging. Olshansky is professor in the School of Public Health at the University of Illinois at Chicago. He and Carnes, both senior research scientists at the National Opinion Research Center/Center on Aging at the University of Chicago, collaborate on studies—funded by the National Institute on Aging (NIA) and NASA—of the biodemography of aging (examining the biological reasons for age-related patterns of disease and death in populations). They are co-authors of *The Quest for Immortality: Science at the Frontiers of Aging* (W. W. Norton, 2001). Butler is president of the International Longevity Center in New York City and was founding director of the NIA.

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The Olshansky and Carnes Web site is **www.thequestforimmortality.com**

The International Longevity Center Web site is **www.ilcusa.org**