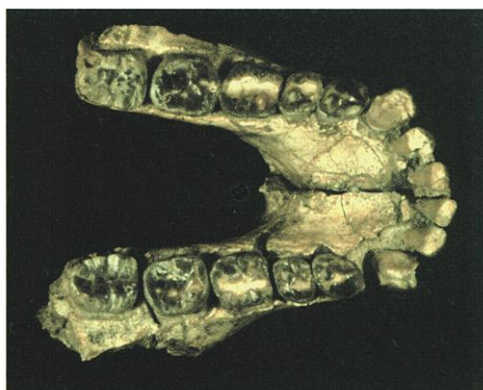


new species has doubled in the past decade, Walker cautions that they are spread over millions of years. "I think there's no strong evidence that there's anything more than one evolving hominid from 6 million years to 2.5 million years," he says. White and his collaborators share this linear view, even connecting the dots between species, saying that *Ardipithecus ramidus* gave rise to *A. anamensis*, then *A. afarensis* on down to *Homo*, with some diversity at about the time *Homo* emerges.

But the field is deeply divided over this issue. When researchers such as Leakey, Wood, Tattersall, Pickford, and Senut look at the new fossils, instead of a parade of hominids, they see a bushy tree with different hominids hanging off different branches at the same time, making it difficult to draw a clear line of descent. "We're seeing a radiation," says Wood. "If you look at other mammals, what's so unusual about that?" Indeed, says Tattersall, "the big lesson from each of these new finds is that diversity [in anatomy and



An ancestor's smile. The teeth, jaw, and other bones of *A. anamensis* suggest that it is Lucy's ancestor.

species] was present from the start."

Defining what is special about the human lineage gets harder as the fossils get older and older. "I just told my students, 'I'm sorry, but I don't know how to distinguish the earliest hominid from the earliest chimp ancestor anymore,'" says Wood. Others say there are a

few signs of hominid status—at least for now. "Right now the two key traits are bipedality and canine reduction and shape modification," says Arizona State's Kimbel. "As we go back further in time, it will be fascinating to see if one of these fades away, leaving the other as the seminal hominid modification."

Even the current favorite trait, bipedalism, may not be enough to qualify as a hominid if other ancient apes were bipedal too. In the late Miocene, "there was a whole proliferation of these apes, sometimes running around on two legs, sometimes not. Why do they have to be ancestral to us?" wonders paleo-anthropologist Peter Andrews of the Natural History Museum in London.

For casual visitors to that museum of human evolution, all the early figures may look similar—and very much like other apes. But in one ape-man's smile or stance, researchers hope to find the hint of things to come.

—ANN GIBBONS

BECOMING HUMAN

MODERN HUMANS

What Made Humans Modern?

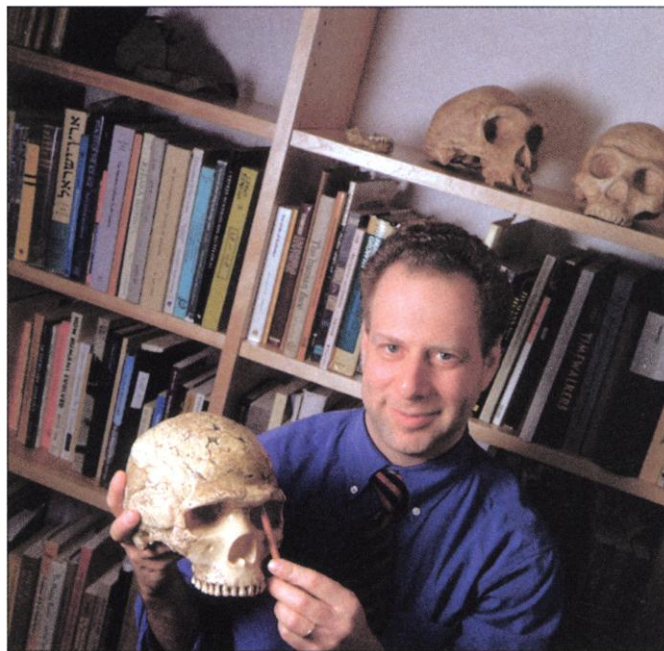
Could our species have been born in a rapid burst of change? Researchers from different disciplines are trying to find out

CAMBRIDGE, MASSACHUSETTS, AND CAMBRIDGE, U.K.—Three hominid skull casts sit in a row on Daniel Lieberman's desk, their empty eye sockets staring eerily ahead. If they could see, they might catch a glimpse of Harvard University's peaceful green quad, just outside the anthropologist's window. But these skulls bear witness, between them, to some of the most dramatic events in human prehistory, including the mysterious birth of our own species, *Homo sapiens*.

The first skull, perhaps 300,000 years old, was found in Zambia. It comes from a species that may have been ancestral to both modern humans and Neandertals. The second is a Neandertal from France dating back 70,000 years. And the last is a 100,000-year-old *H. sapiens* discovered in Israel.

Lieberman picks up each skull in turn and pokes a pencil up through the eye socket. "Look at the difference," he says. "When I do this with the modern human,

I touch the underside of the frontal lobe. But with the other two, my pencil ends up under the thick, bony brow ridge." In modern hu-



Poking into human origins. Daniel Lieberman thinks a few genetic changes might have produced the *Homo sapiens* skull.

mans, he explains, the face and eyes are tucked under the braincase, rather than thrust forward prognathously, as in all other now-extinct human species. And the modern human skull is globular like a volleyball, instead of oblong like a football.

In Lieberman's view, these two traits—rather than the long list of characters anthropologists usually rely on—are the key distinguishing features of modern human skulls. And, he says that this reshaping of the skull, which may have accommodated an expansion

in the key frontal or temporal lobes of the brain, was produced by small evolutionary adjustments in a few bones along the base of the skull, possibly due to only a handful of genetic changes. If he's right, the rise of modern humans may have been a relatively abrupt event rather than a gradual evolution.

"It shows that the speciation event doesn't have to be complicated, with a lot of steps," says Lieberman. "You may only need one change, not 15 or 20 changes."

Lieberman's bold proposal is the latest entry in a newly invigorated debate over the making of modern humans. A flurry of new evidence from three sources—fossils, art and artifacts, and genes—is forcing researchers to rethink just what traits mark the origin of our species and how and when these traits appeared.

Some of this new evidence challenges the notion that the de-

velopment of modern humans was a slow, gradual process. Whereas Lieberman zeroes in on a few key anatomic traits, for example, other studies raise the possibility that the birth of *H. sapiens* hinged on only a handful of genetic changes. Some geneticists are even hunting for a few mutations that might have helped launch hominid brains into cognitive hyperspace.

But other researchers are skeptical that the rise of our species can be explained by the throwing of just a few genetic switches. Indeed, archaeologists—some of whom have long argued for a rapid explosion of cognitive abilities—are now digesting new evidence implying a more gradual development of sophisticated behavior. “In Africa, where our species emerged, we don’t see any sudden leaps,” argues anthropologist Alison Brooks of George Washington University (GWU) in Washington, D.C. She and other scientists see the birth of our species as a gradual process of both physical and behavioral change, nurtured by climatic and environmental factors (see sidebar on p. 1225).

Which scenario is correct is still an open question. “Are we talking about 10 or 1000 or 10,000 significant genetic changes?” asks Oxford University molecular geneticist Chris Tyler-Smith. “We don’t know.” But the new wave of research, as well as heightened cross talk among disciplines, is boosting the chances that these different lines of evidence may eventually converge on a consistent scenario for how our species came to be. “In the past, we’ve had a pretty simplistic view of what modern humans were,” says paleoanthropologist Leslie Aiello of University College London. “Now, we are entering a very exciting period where we are beginning to be able to piece things together.”

Modern skulls, modern brains?

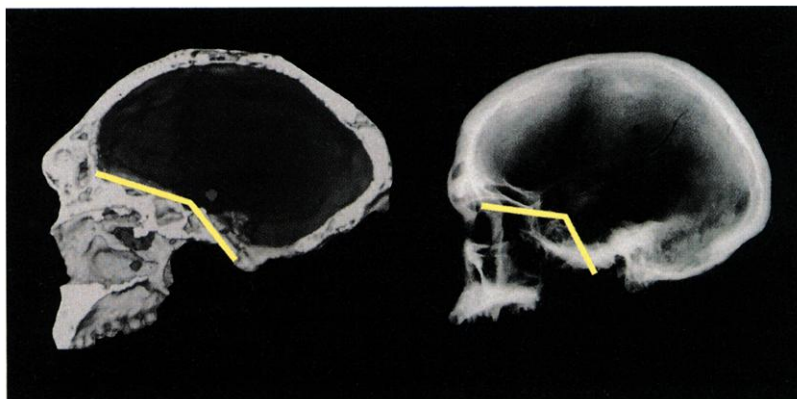
Over the past decade, the quest for modern human origins has crossed at least one critical Rubicon: Many researchers now think they know where, and roughly when, *H. sapiens* appeared. The place: Africa. The time: between 100,000 and 200,000 years ago. Geneticists, for their part, have analyzed current human genetic diversity across the world and then extrapolated backward, using mutation rates as a “molecular clock.” Their studies conclude that all modern humans are descended from an ancestral population that lived in Africa sometime after 200,000 years ago, with many dates con-

verging on about 130,000 years.

Many fossil experts come up with a similar story. Most agree that a 130,000-year-old human skeleton from Omo Kibish in Ethiopia and 100,000-year-old fossils from the Klasies River mouth in South Africa are “anatomically modern”: That is, on the evidence of the shape of these bones, they belong to our species.

Although this is now the majority view, some dissenters remain, including paleoanthropologist Milford Wolpoff of the University of Michigan, Ann Arbor. They continue to argue for the multiregionalism theory: that humans have belonged to the same species for nearly 2 million years and evolved simultaneously across the globe.

This has been a bitter conflict for 2 decades, and it is far from over. But the



Angling for brain space? A sharper flexion of the cranial base in modern humans (bold line, right) compared to archaic forms (left) tucked the face under the frontal lobes.

growing consensus on African origins means that “we can now devote our energies into delving into the African record and narrowing down where and why these changes happened,” says paleoanthropologist Chris Stringer of the Natural History Museum in London, a leading Out-of-Africa advocate.

Indeed, for those who subscribe to the Out-of-Africa hypothesis, it might seem a fairly straightforward matter to zero in on what happened on that continent about 130,000 years ago or earlier, particularly with respect to the skull and brain. But life and evolution are not so simple.

Take overall brain size, a feature long thought to be roughly correlated with thinking power. Modern humans, with an average cranial capacity of 1300 to 1400 cubic centimeters (cc), do have somewhat larger brains than those of most earlier humans; the brains of *H. heidelbergensis*, for example, a species that some researchers think was ancestral to both humans and Neandertals, weigh in at 1000 to 1300 cc.

But top honors for brain size, at 1400 cc, go to the Neandertals, considered by many researchers to be a separate species from us. Even when researchers adjust for Neandertals’ more robust bodies, their brains were

still only slightly smaller than ours.

This has led some researchers to suggest that Neandertals, who coexisted for thousands of years with *H. sapiens* until they went extinct about 30,000 years ago, could have been as smart as modern humans. “It might be good to think of Neandertals as the other modern species,” says anthropologist Christoph Zollikofer at the University of Zürich. “The large brains of Neandertals and modern humans might represent parallel evolutionary achievements, and their different cranial shapes would reflect different evolutionary strategies to pack a large brain into a small space.”

Yet other scientists doubt that Neandertals were as intelligent as modern humans, given their less sophisticated tools and limited symbolic behavior. This debate too is far from resolution (*Science*, 14 September 2001, p. 1980), but it’s clear that overall brain size is not the whole story.

If modern human brains aren’t outstanding in overall size, then what are our distinguishing characteristics? Lieberman is one of a long line of physical anthropologists to focus on the shape of our skulls. In 1982, for example, Stringer and paleoanthropologist Michael Day, now

also at London’s Natural History Museum, proposed seven skull characteristics—such as the rounded shape of the parietal bones on the roof of the skull and very reduced brow ridges—as diagnostic for *H. sapiens*. Other researchers have since added other items to the list. “This is the only guide we’ve had for the past 20 years,” says Aiello.

Using these criteria, several skulls fall on the borderline between modern and “archaic” forms. This has led many researchers to conclude that the first anatomically modern humans represent a continuum of gradual changes that began hundreds of thousands of years earlier—not a sudden speciation event. “I see a rather gradual evolution from an ancestral early archaic grade of *Homo sapiens* ... to early anatomically modern humans,” says paleoanthropologist Günter Bräuer of the University of Hamburg in Germany.

When Lieberman approached the problem in a new way, however, he came up with a much more clear-cut difference between archaic and modern skulls. In a study published online last month by the *Proceedings of the National Academy of Sciences*, Lieberman and his co-workers measured the Stringer and Day characteristics and other features of more than 119 skulls. They included 100 re-

cent *H. sapiens* from around the world, 10 older anatomically modern humans, five Neandertals, four *H. heidelbergensis*, and a number of modern human children and chimpanzees at various growth stages.

The group performed a series of computer-based analyses on these raw data. First they identified those combinations of traits that best account for the variation in shape between modern human and other hominid skulls. Much of the variation could be boiled down to the two features of globularity and facial retraction, or how tightly the face is tucked under the braincase, says Lieberman. And these two characteristics appear sufficient to distinguish modern from archaic skulls, with no overlap.

What's more, the growth patterns of humans and chimpanzees showed that these uniquely human features stem from early developmental shifts in the bones making up the cranial base. For example, the anterior (forward) segment of the cranial base is 15% to 20% longer relative to cranial size in modern humans than in either extinct species, and the base is bent at a much sharper angle in moderns. That flexing allows the face to grow tucked under the braincase rather than jutting forward, explains Lieberman (see figure on p. 1221).

The fact that these traits arise almost entirely during prenatal and infant development is important, he says: This kind of early alteration in growth pattern, rather than later developmental tinkering, can create major changes in body form.

That argument was bolstered by a study of Neandertal and modern human infants and children, published last year in *Nature* by Zollikofer and anthropologist Marcia Ponce de León, also at the University of Zürich. They too found that key differences between Neandertals and modern humans, including the angle of the cranial base, emerge very early, probably before birth. "Their analysis fits my model perfectly," says Lieberman. Zollikofer agrees: "[We] start from different ends to reach similar conclusions."

As for what triggered this alteration in skull shape, Lieberman proposes that the crucial factor may have been a relative expansion of the frontal or temporal lobes. Physical anthropologists argue about whether that expansion is proportionately greater than the overall brain expansion in humans. But neuroscientists, who have spent decades probing and scanning the frontal lobe, do associate this region with

many of the hallmarks of modern human behavior, such as creative thinking, artistic expression, planning, and language; the temporal lobe is linked to hearing and memory.

Expansion of those areas would lengthen the anterior segment of the cranial base as well as push the face into a more vertical position, Lieberman notes. And, he says, studies of brain deformations in living infants show that "the shape of the brain changes the shape of the braincase and not vice versa"—making it likely that natural selection acted on the brain and that braincase shape followed.

But, although Lieberman's study may suggest a sharp distinction between archaic and

modern and extinct humans, says Stringer. Although they haven't won universal acceptance yet, Lieberman's new criteria for anatomical modernity "advance the debate" and "are probably as good as anything we have right now," says Aiello of University College London.

But physical anthropologists have yet to deal with a remaining issue, Aiello notes: Do these innovations in skull anatomy really add up to making modern humans a truly different species, that is, a separate group that could not breed with Neandertals or other extinct humans? That's the definition of species on which many evolutionary biologists insist.

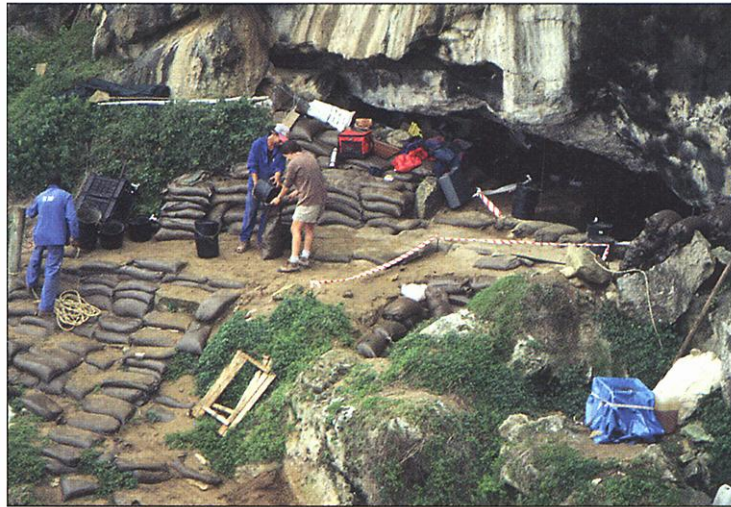
"Nobody's cracked this question yet," she says.

Revolution or evolution?

While anatomists ponder the link between modern skulls and modern brains, archaeologists are cataloging what may seem to be more direct clues to ancient minds: the tools, hearths, artwork, and other traces that early humans left behind. "A species is as a species does," says anthropologist Stanley Ambrose of the University of Illinois, Urbana-Champaign. But the archaeological record has led to a perplexing puzzle: There is relatively little evidence for dramatic changes in behavior until long after the appearance of modern anatomy.

Many researchers have thought that the first signs of truly modern behavior did not appear until about 50,000 years ago, during the so-called Later Stone Age (LSA) in Africa. This was soon followed by what some have called a "human revolution" starting about 40,000 years ago during the Upper Paleolithic period in Europe. The archaeological record seems to explode with creative activity, including personal ornaments, elaborate ritualistic burials, and fantastic cave paintings, such as the 32,000-year-old artworks at the Grotte Chauvet in France (*Science*, 12 February 1999, p. 920).

This burst of culture has led some scientists, notably archaeologist Richard Klein of Stanford University in California, to propose that about 50,000 years ago, the human lineage underwent a genetic change that boosted the brain's cognitive powers. This mutation, Klein argues, unleashed many of the abilities we associate with modern humans, including



Haven of modernity? Discoveries at South Africa's Blombos Cave may push evidence for sophisticated behavior back to 77,000 years.

modern skulls, other researchers question some of his assumptions. Stringer cautions that Lieberman's analysis requires using fossil specimens that have relatively complete faces and crania. That leaves out a number of incomplete—and perhaps transitional—skulls that might represent early moderns. And Brauer comments that some fossils in Lieberman's sample may not be modern human ancestors. "If you took 10 different skulls, perhaps you would see an overlap" between archaic and modern human forms, he says.

Others take issue with the notion of narrowing the Stringer-Day criteria to just two traits. Other, independent features, such as reduced brow ridges, are important too, says paleoanthropologist Ian Tattersall of the American Museum of Natural History (AMNH) in New York City. Stringer says that "other parts of the skeleton, such as the pelvis, may also be relevant" in distinguishing our species.

But Tattersall agrees with Lieberman's overall conclusion that the modern human skull may be the result of a small number of evolutionary events. "I would be very surprised if the distinctions between *Homo sapiens* and its closest relatives were not due to a relatively small genetic change with ma-

language, abstract thought, and symbolic expression. "The [anatomy] stayed the same," Klein says. "But look what happens to the cultural record. Before, [the brain] had just one simple sort of software. Now, you get hardware that can run all kinds of software."

But the conclusion that modern behavior came so late—and so suddenly—is now under attack. Perhaps the most dramatic onslaught came last month, when a team led by archaeologist Christopher Henshilwood of the South African Museum in Cape Town reported what it claims is the world's oldest art—two 77,000-year-old pieces of red ochre engraved with geometrical designs, found at Blombos Cave on South Africa's south coast (*Science*, 11 January, p. 247, and p. 1278 of this issue). "This is a fantastic discovery," says GWU's Brooks. "It is really proof of symbolic behavior at this early date."

Indeed, even before the Blombos research was published, Brooks, together with paleoanthropologist Sally McBrearty of the University of Connecticut, Storrs, had thrown down the gauntlet to those who espoused the cultural explosion idea.

In an article 2 years ago in the *Journal of Human Evolution* (*JHE*), entitled "The Revolution That Wasn't," the pair argued that the real roots of modernity could be found long before 50,000 years ago. They cited a number of recent excavations in Africa, including Blombos, that reveal sophisticated stone- and bone-tool manufacture, advanced hunting and fishing skills, and well-developed exchange networks—evidence, they claim, for modern behavior tens of thousands of years earlier.

Although they agree that such evidence is much more abundant during the Upper Paleolithic, the cognitive transition "wasn't sudden," says Brooks. "It was improving on a basic plan that was already there." Most advances in behavior during this later period, they argue, were due to cultural rather than genetic evolution—the genetic changes had already happened.

Henshilwood adds that the Blombos finding might turn out to be the "tip of the iceberg" once more pre-LSA African sites are excavated. Brooks agrees: "We see numerous intimations that humans ... already had these abilities," she says, including ancient ostrich eggshell beads from Mumba Rock Shelter in Tanzania and barbed bone points from Katanda in the Congo. Indeed, last December in *JHE*, Henshilwood's team reported

ed finding a cache of elaborately worked bone tools (often interpreted as evidence of modern behavior) in Blombos layers also dated to about 70,000 years ago.

But such artifacts are considered by many to be less convincing than, say, actual art. And some researchers are unwilling to draw broad conclusions from the red ochre designs. Klein, who has worked at Blombos as an animal-bone analyst, says that "the meaning of these pieces will remain debatable so long as they are unique."

New York University archaeologist Randall White argues that neither the isolated red ochre designs nor the bone tools represent "evidence of organized symbolic systems shared across space and through time"—the hallmark, he believes, of the kind of fully modern behavior seen in the Upper Paleolithic. White says that the earlier finds cannot be equated with full-blown symbolic representations such as the paintings of horses, lions, and rhinos in the Grotte Chauvet.

Yet White, unlike

But is it art? Archaeologists debate whether these very ancient ochre engravings (*below*) are evidence of symbolism as seen in the younger Grotte Chauvet paintings (*right*).



case the archaeological record may be a poor guide to the timing of genetic and neurological changes.

"The big bang" of genetically determined cognitive advances "came with modern humans," suggests psychologist Michael Tomasello of the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. But what followed, he suggests, was a "ratcheting effect": cultural evolution fueled by improved transmission of knowledge, especially via language. Says AMNH's Tattersall: "We didn't go from the first blade tool or

Blombos geometric engraving to moon shots overnight, and we are still learning new ways to deploy our capacities today."

Earlier hominids, adds anthropologist C. Owen Lovejoy of Kent State University in Ohio, "may well have been every bit as intelligent as we are today, but they lacked the shoulders of giants on which to perch."

The quest for genes

While anthropologists and archaeologists opine about how many genetic changes may have led to the birth of *H. sapiens*, geneticists themselves have

been trying to gather data, but they face a difficult challenge. Teasing out ancient DNA is a formidable task that has been successfully performed on only a few relatively recent Neandertals. Fossils as old as 100,000 or more years remain out of reach. And, although a few geneticists are eagerly scanning primate and human genomes for differences in genes and gene expression, especially in the brain (*Science*, 6 April 2001, p. 44), those studies reveal differences between

apes and humans—not what separates modern humans from extinct ones.

"We are looking at less than a 2% genetic difference between chimps and humans, but vast differences in morphology and behavior," says paleoanthropologist Mark Collard of University College London. "I don't think the genetic data will be a panacea to solving [the origins of modern humans]."

Nevertheless, there have been a few recent breakthroughs. Last year in *Nature*, for

Klein, doesn't think that the Upper Paleolithic "revolution" was driven by genetic changes. In fact, he and many other researchers agree with Brooks that the Upper Paleolithic explosion was the result of "cultural and not biological changes," as paleoanthropologist Robert Foley of Cambridge University puts it. In other words, even if some sort of genetic speciation event gave rise to modern brains, that does not mean that fully modern behavior flowered immediately thereafter—in which

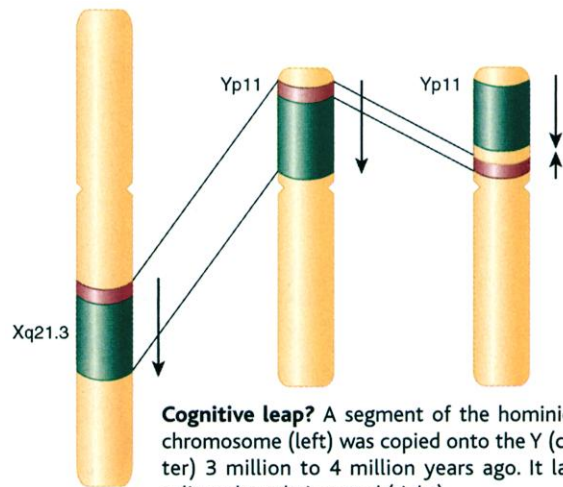
example, researchers reported finding a gene directly implicated in the ability to speak—an ability many, though not all, researchers believe is unique to modern humans. Researchers are now probing that gene's evolutionary history to see if it underwent mutations around the time of the birth of *H. sapiens* (*Science*, 5 October 2001, p. 32).

And one group of researchers has set out on what some believe is a quixotic quest to explicitly identify the genes that make us modern. They have even identified a candidate gene that, they say, might be responsible for language and other advanced cognitive abilities.

Back in the early 1990s, Oxford University psychiatrist Timothy Crow hypothesized that just such a gene, key to language and the brain asymmetries that many researchers believe accompany it, might be located on the sex chromosomes. Such a possibility might seem far-fetched, because there are few functional genes on the Y chromosome and most are involved with male fertility. But Crow already had a good

idea about where to look.

A decade earlier, geneticist David Page's team at the Massachusetts Institute of Technology (MIT) had identified a 4-million-base-pair block of DNA on the X chromosome, called Xq21.3, which was missing from the Y chromosome in all mammals except humans. Page and others found that about 3 million or 4 million years ago—that is, after the chimp and human lines split—this segment was copied onto the Y chromosome of the hominid lineage. The homologous Y chromosome segment then underwent a rearrangement called a paracentric inversion, in which it reversed direction and split into two parts (see diagram). Crow speculated that this second genetic event sparked genetic changes on both the X and Y segments that ultimately led to the speciation of modern humans. He



Cognitive leap? A segment of the hominid X chromosome (left) was copied onto the Y (center) 3 million to 4 million years ago. It later split and partly inverted (right).

predicted that one or more genes important to brain function would be found in these chromosomal segments.

Then, 2 years ago, Cambridge University molecular geneticist Nabeel Affara's group reported finding similar functional genes, called *PCDHX* and *PCDHY*, in this segment on both the X and Y chromosomes. The genes code for a member of the protocadherin family of proteins, biomolecules that play critical roles in the development of the nervous system. Sure enough, *PCDHX* and *PCDHY* "are expressed almost entirely in the brain," says Affara.

But because no one has yet been able to date the paracentric inversion, Crow's theory linking it to modern human origins remains speculation. Affara and Crow are working together to better characterize the *PCDH* genes and what they do, in the hopes of demonstrating that they are crucial to cognitive abilities associated only with modern humans. In the meantime, comments Tattersall, "I take my hat off to them for trying to come up with a mechanism" for the speciation of *H. sapiens*. "They may be wrong, but we need as many ideas as possible."

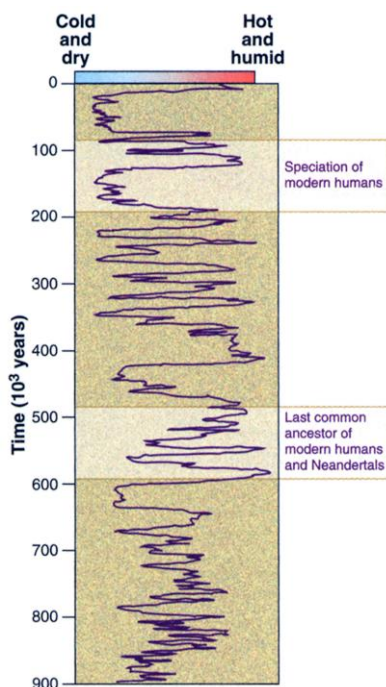
It may be some time before all of these new ideas in anthropology, archaeology, genetics, and other disciplines come together to create a coherent picture of modern human origins. But researchers are encouraged by the interdisciplinary attempts. "This new research will provide the springboard for a lot of other discoveries," says Aiello. "We are on our way."

There may be few sure answers so far, but one thing seems certain: Sometime during the last 200,000 years or so, evolution blessed us with the wisdom to ask the questions.

—MICHAEL BALTER

Why Get Smart?

To us humans, it may seem that smarter is always better. But only once in the history of life on Earth did natural selection favor the evolution of brains sophisticated enough to send people to the moon, paint the Mona Lisa, or wonder about their own origins. However that evolution unfolded (see main text), most anthropologists think that advanced human cognition was no evolutionary accident but an adaptation to a challenging environment.



Wild ride. Humans had to survive sudden, dramatic climate changes.

Experts have suggested that a series of wild global climate swings, which were especially intense beginning about 250,000 years ago (see graph), forced hominid species to adapt or go extinct. At times the African climate switched from very cold and dry to very hot and humid within a single century. "Imagine these human populations being shoved around by these tremendous changes," says anthropologist Chris Stringer of the Natural History Museum in London. "This would have had profound effects" on their survival.

But if conditions varied so often, what exactly were humans adapting to? To variation itself, says paleoanthropologist Richard Potts of the Smithsonian Institution in Washington, D.C. He argues that human evolution is marked by an increasing ability to deal with change—the result of a process he calls "variability selection"—rather than adaptation to specific habitats. And this ability, he believes, reached its height with modern humans. The hallmarks of *Homo sapiens*, he says, are "the use of complex symbolic codes and abstraction, [which] presented the potential for behavioral diversification and extraordinarily sophisticated alteration of the surroundings."

Many experts believe that this plasticity in responding to new environmental challenges laid the cognitive foundations for our ability to creatively solve new problems—like getting to the moon—that our ancestors never had to face. "The minds of our ancestors were not hardwired with specific strategies for felling mastodons but with more general categories such as 'person,' 'living thing,' 'action,' 'cause and effect,'" says cognitive neuroscientist Steven Pinker of the Massachusetts Institute of Technology. When these categories were recombined in the mind, Pinker adds, "an unlimited number of new ideas ... or courses of action could be formulated."

—M.B.