How Scientists Discovered the Staggering Complexity of Human Evolution

Darwin would be delighted by the story his successors have revealed

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Credit: *Pascal Blanchet*

In 1859, 14 years after the founding of this magazine, Charles Darwin published the most important scientific book ever written. *On the Origin of Species* revolutionized society's understanding of the natural world. Challenging Victorian dogma, Darwin argued that species were not immutable, each one specially created by God. Rather life on earth, in all its dazzling variety, had evolved through descent from a common ancestor with modification by means of natural selection. But for all of Darwin's brilliant insights into the origins of ants and armadillos, bats and barnacles, one species is conspicuously neglected in the great book: his own. Of *Homo sapiens*, Darwin made only a passing mention on the third-to-last page of the tome, noting coyly that "light will be thrown on the origin of man and his history." That's it. That is all he wrote about the dawning of the single most consequential species on the planet.

It was not because Darwin thought humans were somehow exempt from evolution. Twelve years later he published a book devoted to that very subject, *The Descent of Man*. In it, he explained that discussing humans in his earlier treatise would have served only to further prejudice readers against his radical idea. Yet even in this later work, he had little to say about human origins per se, instead focusing on making the case from comparative anatomy, embryology and behavior that, like all species, humans had evolved. The problem was that there was hardly any fossil record of humans at that time to provide evidence of earlier stages of human existence. Back then, "the only thing you knew was what you could reason," says paleoanthropologist Bernard Wood of George Washington University.

To his credit, Darwin made astute observations about our kind and predictions about our ancient past based on the information that was available to him. He argued that all living humans belong to one species and that its "races" all descended from a single ancestral stock. And pointing to the anatomical similarities between humans and African apes, he concluded that chimpanzees and gorillas were the closest living relatives of humans. Given that relationship, he figured, early human ancestors probably lived in Africa.

Since then, Wood says, "the evidence has come in." In the past century and a half, science has confirmed Darwin's prediction and pieced together a detailed account of our origins. Paleoanthropologists have recovered fossil hominins (the group that comprises *H. sapiens* and its extinct relatives) spanning the past seven million years. This extraordinary record shows that hominins indeed got their start in Africa, where they evolved from quadrupedal apes into the upright-walking, nimble-fingered, large-brained creatures we are today.

And the archaeological record of hominin creations, which encompasses roughly half that time, charts their cultural evolution—from early experiments with simple stone tools to the invention of symbols, songs and stories—and maps our ancestors' spread across the globe. The fossils and artifacts demonstrate that for most of the period over which our lineage has been evolving, multiple hominin species walked the earth. Studies of modern and ancient DNA have generated startling insights into what happened when they encountered one another.

Neandertals were the first extinct hominin species to be recognized in the fossil record and the first to yield ancient DNA. Credit: Javier Trueba *Science Source*

The human saga, we now understand, is far more intricate than scholars of yore envisioned. The tidy tropes of our prehistory have collapsed under the weight of evidence: there is no single missing link that bridges apes and humankind, no drumbeat march of progress toward a predestined goal. Our story is complicated, messy and random. Yet it still can be accommodated under Darwin's theory of evolution and in fact further validates that framework.

This is not to say scientists have it all figured out. Many questions remain. But whereas the origin of humans was once an uncomfortable speculation in Darwin's big idea, it is now among the best-documented examples of evolution's transformative power.

We humans are strange creatures. We walk upright on two legs and possess supersized brains, we invent tools to meet our every need and express ourselves using symbols, and we have conquered every corner of the planet. For centuries scientists have sought to explain how we came to be, our place in the natural world.

This quest was often distorted by racist ideologies. Consider the era leading up to the birth of Darwin's bombshell theory. In the 1830s, while a young Darwin was making his momentous voyage onboard the *Beagle*, a movement was underway to promote the idea that the various modern human groups around the globe—races—had separate origins. To build the case for polygenism, as the theory is known, scientists such as Samuel Morton in Philadelphia collected skulls from people across the world and measured their sizes and shapes, falsely believing those attributes to be proxies for intelligence. When they ranked the specimens from superior to inferior, Europeans would conveniently come out on top and Africans on the bottom. “There was a desire to provide scientific justification for political and power structures," says anthropological geneticist Jennifer Raff of the University of Kansas. "It was science in the service of slavery and colonialism."

Although Darwin's work came down firmly on the side of monogenism—the idea that all humans share a common ancestor—it was nonetheless co-opted to support notions about racial superiority. Social Darwinism, for one, misapplied Darwin's ideas about the struggle for existence in natural selection to human society, providing a pseudoscientific rationalization for social injustice and oppression. Darwin himself did not subscribe to such views. In fact, his opposition to slavery may have been a driving force in his research agenda, according to his biographers Adrian Desmond and James Moore.

By the time Darwin published *The Descent of Man*, in 1871, the idea that humans had evolved from a common ancestor with apes was already gaining traction in the scientific community thanks to books published in the 1860s by English biologist Thomas Henry Huxley and Scottish geologist Charles Lyell. Still, the fossil evidence to support this claim was scant. The only hominin fossils known to science were a handful of remains a few tens of thousands of years old that had been recovered from sites in Europe. Some were *H. sapiens*; others would eventually be recognized as a separate but very closely related species, *Homo neanderthalensis*. The implication was that fossils of more apelike human ancestors were out there somewhere in the world, awaiting discovery. But the suggestion by Darwin, like Huxley before him, that those ancestors would be found in Africa met with resistance from scholars who saw Asia as a more civilized birthplace for humankind and emphasized similarities between humans and Asia's gibbons.

Perhaps it should come as no surprise, then, that when the first hominin fossil significantly older and more primitive than those from Europe turned up, it came not from Africa but from Asia. In 1891 Dutch anatomist Eugène Dubois discovered remains on the Indonesian island of Java that he thought belonged to the long-sought missing link between apes and humans. The find, which he named *Pithecanthropus erectus*, spurred further efforts to root humankind in Asia. (We now know that Dubois's fossil was between 700,000 and one million years old and belonged to a hominin that was much more humanlike than apelike, *Homo erectus*.)

Two decades later the search turned to Europe. In 1912 amateur archaeologist Charles Dawson reported that he had found a skull with a humanlike cranium and an apelike jaw in an ancient gravel pit near the site of Piltdown in East Sussex, England. Piltdown Man, as the specimen was nicknamed, was a leading contender for the missing link until it was exposed in 1953 as a fraudulent pairing of a modern human skull with an orangutan's lower jaw.

Piltdown so seduced scholars with the prospect of making Europe the seat of human origins that they all but ignored an actual ancient hominin that turned up in Africa, one even older and more apelike than the one Dubois discovered. In 1925, 43 years after Darwin's death, anatomist Raymond Dart published a paper describing a fossil from Taung, South Africa, with an apelike braincase and humanlike teeth. Dart named that fossil—a youngster's skull now known to be around 2.8 million years old—*Australopithecus africanus*, "the southern ape from Africa." But it would take nearly 20 years for the scientific establishment to accept Dart's argument that the so-called Taung Child was of immense significance: the fossil linked humans to African apes.

Evidence of humanity's African origins has accumulated ever since. Every hominin trace older than 2.1 million years—and there are now quite a few of them—has come from that continent.

Even as fossil discoveries proved Darwin right about the birthplace of humanity, the pattern of our emergence remained elusive. Darwin himself depicted evolution as a branching process in which ancestral species divide into two or more descendant species. But a long-standing tradition of organizing nature hierarchically—one that dates back to Plato and Aristotle's Great Chain of Being—held sway, giving rise to the notion that our evolution unfolded in linear fashion from simple to complex, primitive to modern. Popular imagery reflected and reinforced this idea, from a caricature in *Punch's Almanack* for 1882 showing a progression from earthworm to Darwin, to the iconic monkey-to-man illustration that appeared in the 1965 Time-Life book *Early Man* and became known as the March of Progress.

From the rich assortment of fossils and artifacts recovered from around the world in the past century, however, paleoanthropologists can now reconstruct something of the timing and pattern of human evolution. The finds clearly show that this single-file scheme is no longer tenable. Evolution does not march steadily toward predetermined goals. And many hominin specimens belong not in our direct line of ancestry but on side branches of humankind—evolutionary experiments that ended in extinction.

From the outset, our defining traits evolved not in lockstep but piecemeal. Take our mode of locomotion, for example. *H. sapiens* is what anthropologists call an obligate biped—our bodies are built for walking on two legs on the ground. We can climb trees if we need to, but we have lost the physical adaptations that other primates have to arboreal life. Fragmentary fossils of the oldest known hominins—*Sahelanthropus tchadensis* from Chad, *Orrorin tugenensis* from Kenya and *Ardipithecus* *kadabba* from Ethiopia—show that our earliest ancestors emerged by around seven million to 5.5 million years ago. Although they are apelike in many respects. all of them exhibit characteristics associated with walking on two legs instead of four. In *Sahelanthropus*, for example, the hole in the base of the skull through which the spinal cord passes has a forward position suggestive of an upright posture. A bipedal gait may thus have been one of the very first traits that distinguished hominins from ancestral apes.

Yet our forebears appear to have retained traits needed for arboreal locomotion for millions of years after they first evolved the ability to walk on two legs. *Australopithecus afarensis*, which lived in eastern Africa from 3.85 million to 2.95 million years ago and is famously represented by the skeleton known as Lucy, discovered in 1974, was a capable biped. But it had long, strong arms and curved fingers—features associated with tree climbing. It would be another million years before modern limb proportions evolved and committed hominins to life on the ground, starting with early *H. erectus* in Africa (sometimes called *Homo ergaster*).

The brain evolved on quite a different schedule. Over the course of human evolution, brain size has more than tripled. A comparison of the braincase of *A. afarensis* with that of the much older *Sahelanthropus*, however, shows that hardly any of that growth occurred in the first few million years of human evolution. In fact, most of the expansion took place in the past two million years, perhaps enabled by a feedback loop in which advances in technology—stone tools and the like—gave hominins access to more nutritious foods such as meat, which could fuel a larger and thus more energetically demanding brain, which in turn could dream up even better technology, and so on. Shifts in the shape and structure of the brain accompanied these gains, with more real estate allocated to regions involved in language and long-range planning, among other advanced cognitive functions.

This mosaic pattern of hominin evolution in which different body parts evolved at different rates produced some surprising creatures. For instance, *Australopithecus sediba* from South Africa, dated to 1.98 million years ago, had a humanlike hand attached to an apelike arm, a big birth canal but a small brain, and an advanced ankle bone connected to a primitive heel bone.

Sometimes evolution even doubled back on itself. When one examines a hominin fossil, it can be difficult to discern whether the species retained a primitive trait such as small brain size from an earlier ancestor or whether it lost the characteristic and then re-evolved it. But the strange case of *Homo floresiensis* may well be an example of the latter. This member of the human family lived on the island of Flores in Indonesia as recently as 50,000 years ago yet looked in many ways like some of the founding members of our genus who lived more than two million years earlier. Not only did *H. floresiensis* have a small body, but it also possessed a remarkably tiny brain for *Homo*, about the size of a chimp's. Scientists' best guess is that this species descended from a brawnier, brainer *Homo* species that got marooned on Flores and evolved its diminutive size as an adaptation to the limited food resources available on its island home. In so doing, *H. floresiensis* seems to have reversed what researchers once considered a defining trend of *Homo*'s evolution: the inexorable expansion of the brain. Yet despite its small brain, *H. floresiensis* still managed to make stone tools, hunt animals for food and cook over fires.

Adding to the complexity of our story, it is now clear that for most of the time over which humans have been evolving, multiple hominin species walked the earth. Between 3.6 million and 3.3 million years ago, for example, at least four varieties of hominins lived in Africa. Paleoanthropologist Yohannes Haile-Selassie of the Cleveland Museum of Natural History and his team have recovered remains of two of them, *A. afarensis* and *Australopithecus deyiremeda*, as well as a possible third creature known only from a distinctive fossil foot, in a single area called Woranso-Mille in Ethiopia's Afar region. How they managed to share the landscape is a subject of current investigation. “Competing species could co-exist if there were plenty of resources or if they were exploiting different parts of the ecosystem,” Haile-Selassie says.

Later, between roughly 2.7 million and 1.2 million years ago, representatives of our genus, *Homo*—large-brained tool users with dainty jaws and teeth—shared the grasslands of southern and eastern Africa with a radically different branch of humanity. Members of the genus *Paranthropus*, these hominins had massive teeth and jaws, flaring cheek bones and crests atop their heads that anchored powerful chewing muscles. Here the co-existence is somewhat better understood: whereas *Homo* seems to have evolved to exploit a wide variety of plants and animals for food, *Paranthropus* specialized in processing tough, fibrous plant foods.

H. sapiens overlapped with other kinds of humans, too. When our species was evolving in Africa 300,000 years ago, several other kinds of hominins also roamed the planet. Some, such as the stocky Neandertals in Eurasia, were very close relatives. Others, including *Homo naledi* in South Africa and *H. erectus* in Indonesia, belonged to lineages that diverged from ours in the deep past. Even as recently as 50,000 years ago, hominin diversity was the rule, with the Neandertals, the mysterious Denisovans from Asia, tiny *H. floresiensis* and another small hominin—the recently discovered *Homo luzonensis* from the Philippines—all at large.

Such discoveries make for a much more interesting picture of human evolution than the linear account that has dominated our view of life. But they raise a nagging question: How did *H. sapiens* end up being the sole surviving twig on what was once a luxuriant evolutionary bush?

Here are the facts of the case. We know from fossils found at the site of Jebel Irhoud in Morocco that our species originated in Africa by at least 315,000 years ago. By around 200,000 years ago it began making forays out of Africa, and by 40,000 years ago it had established itself throughout Eurasia. Some of the places *H. sapiens* colonized were occupied by other hominin species. Eventually the other folks all disappeared. By around 30,000 to 15,000 years ago, with the end of the Neandertals in Europe and the Denisovans in Asia, *H. sapiens* was alone in the world.

Researchers have often attributed the success of our species to superior cognition. Although the Neandertals actually had slightly larger brains than ours, the archaeological record seemed to indicate that only *H. sapiens* crafted specialized tools and used symbols, suggesting a capacity for language. Perhaps, the thinking went, *H. sapiens* won out by virtue of sharper foresight, better technology, more flexible foraging strategies and bigger social networks for support against hard times. Alternatively, some investigators have proposed, maybe *H. sapiens* waged war on its rivals, exterminating them directly.

But recent discoveries have challenged these scenarios. Neandertal technology, archaeologists have learned, was far more varied and sophisticated than previously thought. Neandertals, too, made jewelry and art, crafting pendants from shells and animal teeth and painting abstract symbols on cave walls. Moreover, they may not have been our only enlightened kin: a 500,000-year-old engraved shell from Java suggests that *H. erectus* also possessed symbolic thought. If archaic hominins had many of the same mental faculties as *H. sapiens*, why did the latter prevail?

The conditions under which *H. sapiens* got its start may have played a role. Fossil and archaeological data suggest that our species mostly stayed in Africa for the first couple of hundred thousand years of its existence. There, some experts argue, it evolved as a population of interconnected subgroups spread across the continent that split up and reunited again and again over millennia, allowing for periods of evolution in isolation followed by opportunities for interbreeding and cultural exchange. This evolutionary upbringing may have honed *H. sapiens* into an especially adaptable hominin. But that is not the whole story, as we now know from genetics.

Analyses of DNA have revolutionized the study of human evolution. Comparing the human genome with the genomes of the living great apes has shown conclusively that we are most closely related to chimpanzees and bonobos, sharing nearly 99 percent of their DNA. And large-scale studies of DNA from modern-day human populations across the globe have illuminated the origins of modern human variation, overturning the centuries-old notion that races are biologically discrete groups with separate origins. "There have never been pure populations or races," Raff says. Modern human variation is continuous, and most variation actually exists within populations rather than between them—the product of our demographic history as a species that originated in Africa with populations that mixed continuously as they migrated around the world.

More recently, studies of ancient DNA have cast new light on the world of early *H. sapiens* as it was when other hominin species were still running around. In the late 1990s geneticists began recovering small amounts of DNA from Neandertal and early *H. sapiens* fossils. Eventually they succeeded in getting entire genomes not only from Neandertals and early *H. sapiens* but also from Denisovans, who are known from just a few fragmentary fossils from Siberia and Tibet. By comparing these ancient genomes with modern ones, researchers have found evidence that our own species interbred with these other species. People today carry DNA from Neandertals and Denisovans as a result of these long-ago encounters. Other studies have found evidence of interbreeding between *H. sapiens* and unknown extinct hominins from Africa and Asia for whom we have no fossils but whose distinctive DNA persists.

Mating with other human species may have aided *H. sapiens'* success. Studies of organisms ranging from finches to oak trees have shown that hybridization with local species can help colonizing species flourish in novel environments by giving them useful genes. Although scientists have yet to figure out the functions of most of the genes people today carry from extinct hominins, they have pinpointed a few, and the results are intriguing. For instance, Neandertals gave *H. sapiens* immunity genes that may have helped our species fend off novel pathogens it encountered in Eurasia, and Denisovans contributed a gene that helped people adapt to high altitudes. *H. sapiens* may be the last hominin standing, but it got a leg up from its extinct cousins.

Scientists have many more pieces of the human-origins puzzle than they once did, but the puzzle is now vastly bigger than it was previously understood to be. Many gaps remain, and some may never close. Take the question of why we evolved such massive brains. At around 1,400 grams, the modern human brain is considerably larger than expected for a primate of our body size. “The singularity is why it's interesting—and why it's impossible to answer scientifically,” Wood observes. Some experts have suggested that hominin brains ballooned as they adapted to climate fluctuations between wet and dry conditions, among other explanations. But the problem with trying to answer “why” questions about the evolution of our unique traits, Wood says, is that there is no way to evaluate the proposed explanations empirically. “There isn't a counterfactual. We can't go back to three million years ago and not change the climate.”

Other mysteries may yield to further investigation, however. For example, we do not yet know what the last common ancestor of humans and the *Pan* genus that includes chimps and bonobos looked like. Genomic and fossil data suggest that the two lineages diverged between eight million and 10 million years ago—up to three million years before the oldest known hominin walked the earth—which means that paleoanthropologists may be missing a substantial chunk of our prehistory. And they have hardly any fossils at all of *Pan*, which has been evolving along its own path just as long as we have. Insights may come from a project currently underway in central Mozambique, where Susana Carvalho and René Bobe of the University of Oxford and their colleagues are hunting for fossil primates, including hominins, in sediments older than the ones that yielded *Sahelanthropus, Orrorin* and *Ardipithecus*.

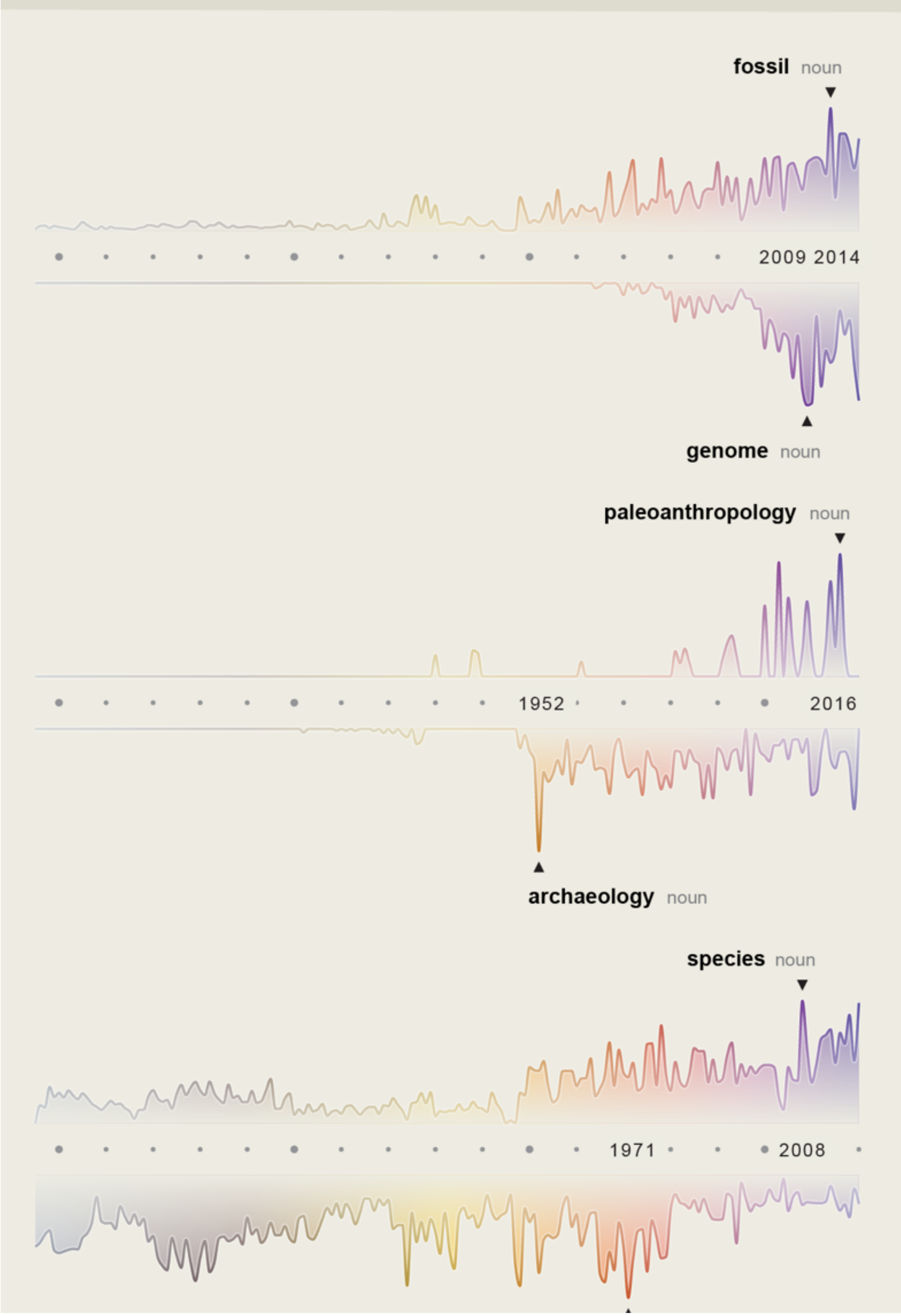
Later stages of the human story are riddled with unknowns, too. If *H. sapiens* was interbreeding with the other hominin species it encountered, as we now know it was, were these groups also exchanging culture? Might *H. sapiens* have introduced Neandertals to novel hunting technology and artistic traditions—or vice versa? New techniques for retrieving ancient DNA and proteins from otherwise unidentifiable fossils and even cave sediments are helping researchers determine which hominin species were active and when at key archaeological sites.

One wonders where the next 175 years will take us in the quest to understand who we are and where we come from. We may have found our place in nature, located our twig on the shrub, but we are still searching for ourselves. We're only human, after all.

Wordplay

The relative frequency of revealing and interesting terms in *Scientific American* over time

Editors suggested word pairings related to the topics of each article in our 175th-anniversary issue that might uncover intriguing relationships. The resulting line charts compare the relative frequency of word occurrence each year—from 1845 (*far left*) to 2020 (*far right*)— scaled by maximum value. To search for your own favorite words and to explore other juxtapositions, visit the interactive portal at www.scientificamerican.com/interactive/science-words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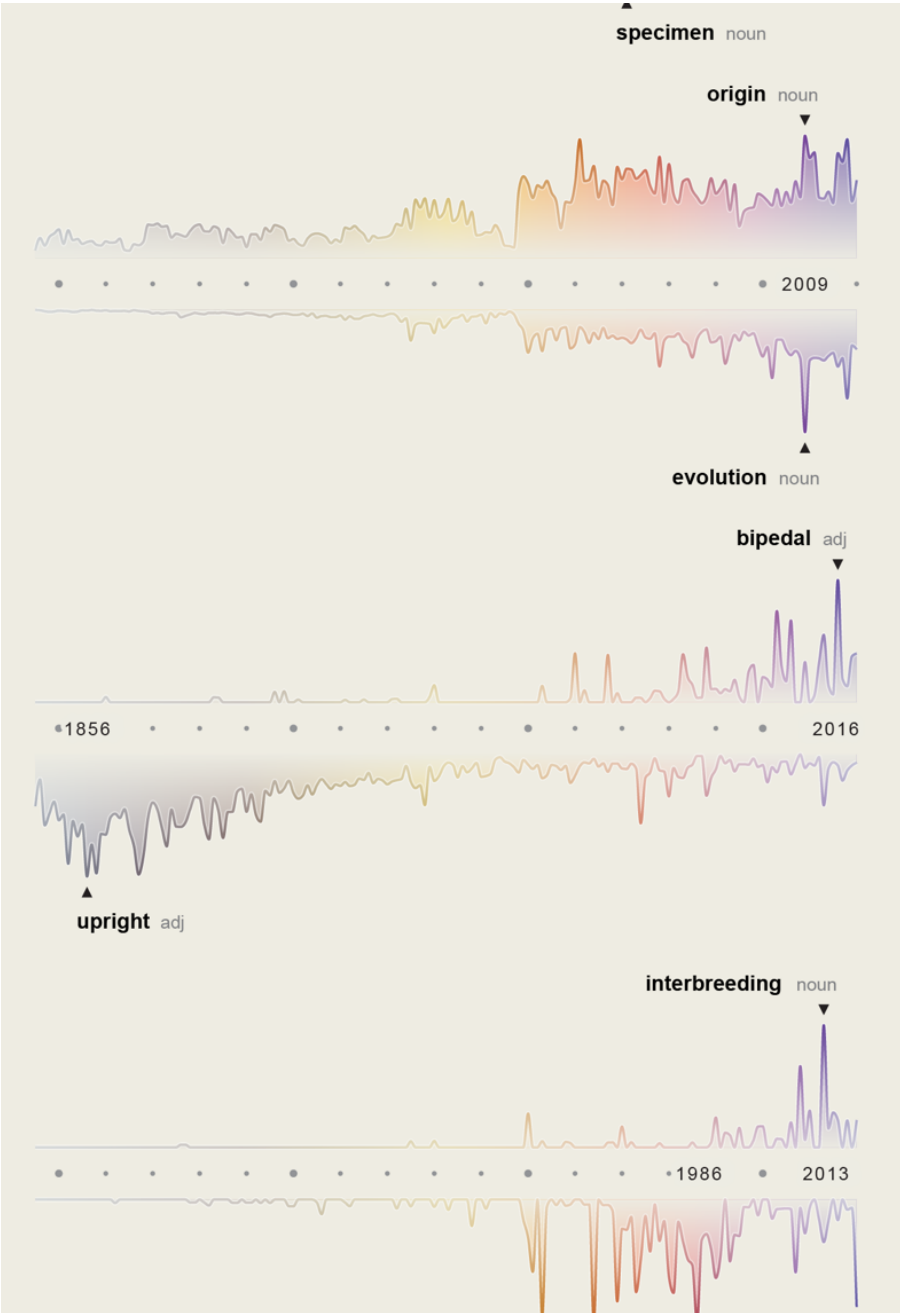
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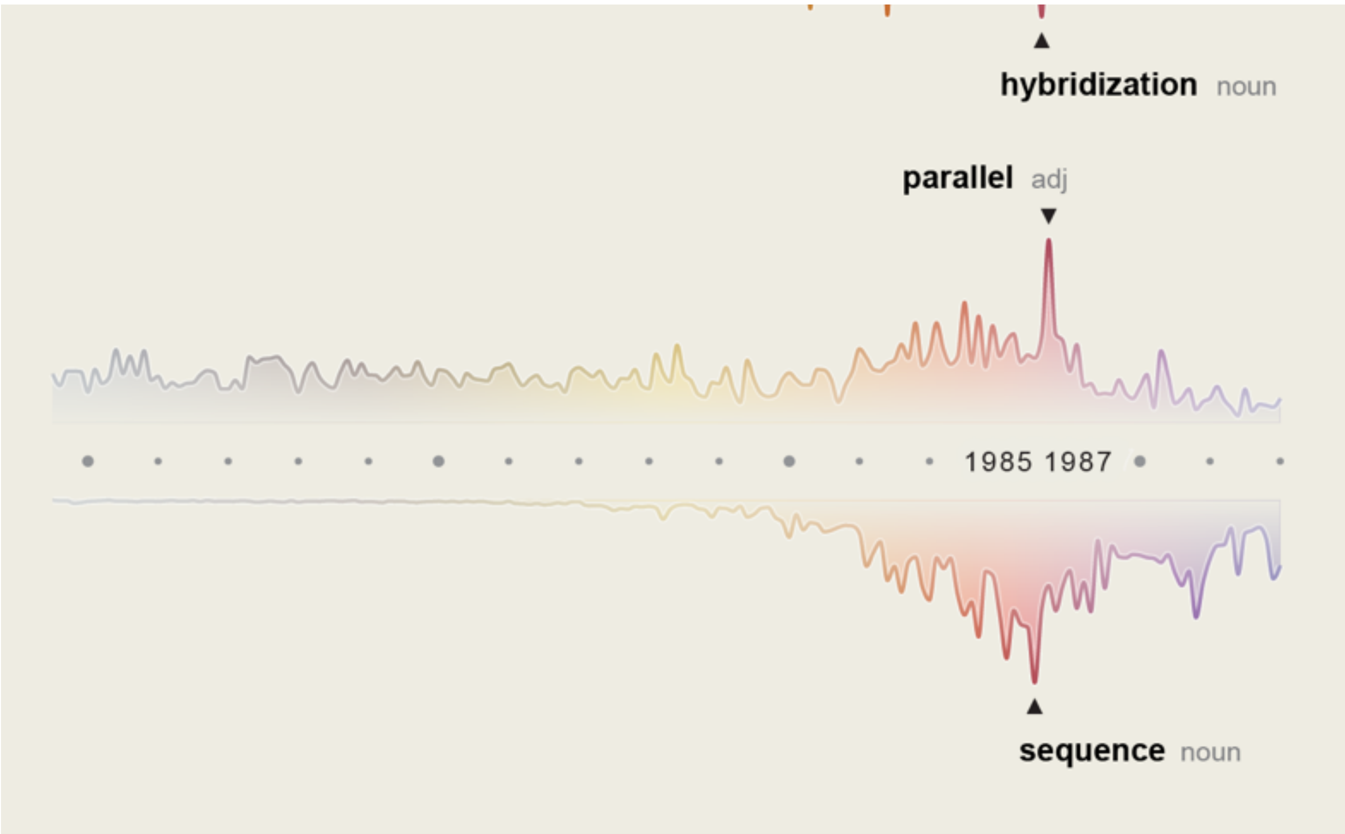

Credit: Moritz Stefaner and Christian Lässer

For more context, see "[Visualizing 175 Years of Words in Scientific American](https://www.scientificamerican.com)"