REVIEW SUMMARY

HUMAN EVOLUTION

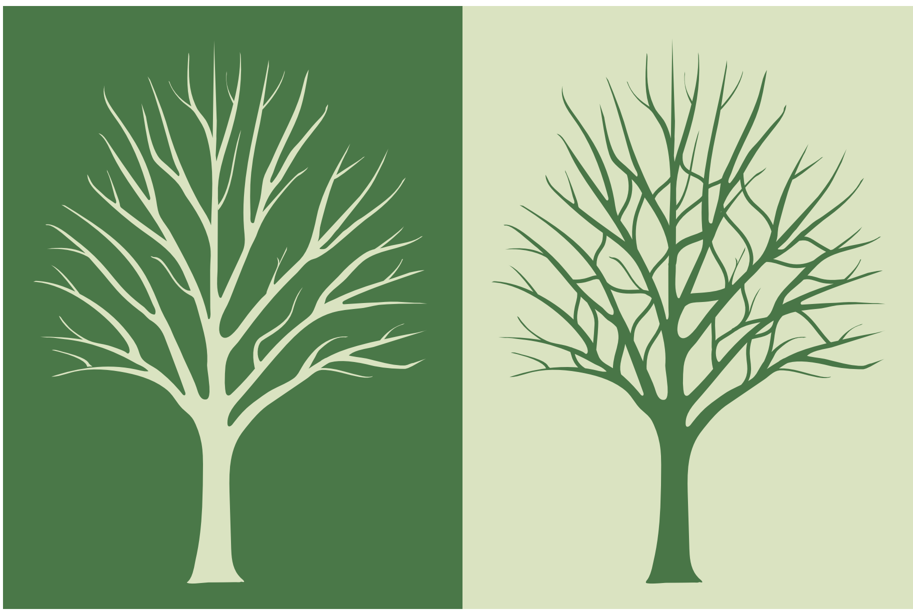
Modern theories of human evolution foreshadowed by Darwin's *Descent of Man*

Peter J. Richerson, Sergey Gavrilets*, Frans B. M. de Waal

BACKGROUND: Charles Darwin's *The Descent of Man*, published on 24 February 1871, laid the grounds for scientific studies into human origins and evolution. We look at the advances in our understanding of these processes through the lenses of modern speciation theory. Applying this theory to specific cases requires one to identify and understand the nature of (i) the ancestor and various preexisting adaptations and traits that it possessed that allowed or simplified the speciation process, (ii) evolutionary forces responsible for major differences between the emergent species and its close relatives, and (iii) the most salient adaptations characteristic of the new species and its evolutionary history (such as genetic, morphological, behavioral, spatial, and temporal).

ADVANCES: Modern research shows that we share many developmental, physiological, morphological, cognitive, and psychological characteristics as well as about 96% of our DNA with the anthropoid apes. We now know that since our last common ancestor with the other apes 6 million to 8 million years ago, human evolution followed the path common for other species with diversification into closely related species and some subsequent hybridization between them. Since Darwin, a long series of unbridgeable gaps have been proposed between humans and other animals. They focused on tool-making, cultural learning and imitation, empathy, prosociality and cooperation, planning and foresight, episodic memory, metacognition, and theory of mind. However, new insights from neurobiology, genetics, primatology, and behavioral biology only reinforce Darwin's view that most differences between humans and higher animals are "of degree and not of kind." What makes us different is that our ancestors evolved greatly enhanced abilities for (and reliance on) cooperation, social learning, and cumulative culture—traits emphasized already by Darwin. Cooperation allowed for environmental risk buffering, cost reduction, and the access to new resources and benefits through the "economy of scale." Learning and cumulative culture allowed for the accumulation and rapid spread of beneficial innovations between individuals and groups. The enhanced abilities to learn from and cooperate with others became a universal tool, removing the need to evolve specific biological organs for specific environmental challenges. These human traits likely evolved as a response to increasing high-frequency climate changes on the millennial and submillennial scales during the Pleistocene. Once the abilities for cumulative culture and extended cooperation were in place, a suite of subsequent evolutionary changes became possible and likely unavoidable. In particular, human social systems evolved to support mothers through the recruitment of males and nonreproductive females. The most distinctive feature of our species, language, appeared arguably driven by selection for simplifying cooperation. Reliance on social learning and conformity led to the emergence of new factors constraining and driving human behavior, such as morality, social norms, and social institutions. These forces often act against the immediate biological or material interests of individuals, promoting instead the interests of the society as a whole or of its powerful segments. Continuous engagement in cooperation has led to the evolution of strong coalitionary psychology, which can bring us together whenever we perceive that our identity group faces outside threats. Coalitionary psychology also has an undesirable byproduct: often negative or even hostile reaction to others who differ from us in their looks, behaviors, beliefs, caste, or class.

OUTLOOK: Our society faces challenges, including climate change; various types of inequality; economic crises; political, cultural, and religious conflicts; and pandemics. Similar challenges have repeatedly arisen and were dealt with in the past with varying success. What makes the current situation different is not only the scale of societal threats but also that modern science can provide guidance on how to respond to them. Adequately answering these challenges requires understanding humans' social behavior and the roles of cooperation, social learning, and culture for human decision-making. Evolutionary perspective is already helping to synthesize the contributions of social sciences, including anthropology, psychology, economics, political science, and history. The impact of *Descent* on the social sciences and on the development and implementation of different policies by practitioners and policymakers to improve our society will only grow. ■



Depictions of organic evolution versus cultural evolution. (Left) Organic evolution and (right) cultural evolution, as described in Alfred L. Kroeber's 1923 textbook *Anthropology: Cultural Patterns and Processes*. Biological inheritance is rigid from parents to offspring in eukaryotes, and species mostly do not exchange genes. Culture is potentially acquired from anyone in a person's social network, and ideas spread rather readily from culture to culture.

IMAGE: N. CARY/*SCIENCE*

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Peter J. Richerson[1], Sergey Gavrilets[2]*, Frans B. M. de Waal[3]

Charles Darwin's *The Descent of Man*, published 150 years ago, laid the grounds for scientific studies into human origins and evolution. Three of his insights have been reinforced by modern science. The first is that we share many characteristics (genetic, developmental, physiological, morphological, cognitive, and psychological) with our closest relatives, the anthropoid apes. The second is that humans have a talent for high-level cooperation reinforced by morality and social norms. The third is that we have greatly expanded the social learning capacity that we see already in other primates. Darwin's emphasis on the role of culture deserves special attention because during an increasingly unstable Pleistocene environment, cultural accumulation allowed changes in life history; increased cognition; and the appearance of language, social norms, and institutions.

One hundred and fifty years ago, Charles Darwin published his opus on human evolution, *The Descent of Man* (hereafter *Descent*), together with *Selection in Relation to Sex* (Fig. 1) (*1*). In *On the Origin of Species*, Darwin (*2*) had promised that "light will be thrown on the origin of man and his history." Now it was time to deliver.

Descent is a sophisticated book that greatly influenced late 19th- and 20th-century investigations of human behavior and laid foundations for subsequent work. Perhaps most importantly, Darwin argued that anatomically and even behaviorally, humans were animals, vertebrates, mammals, and apes. These relationships, established by descent from a common ancestor, meant that our basic biology fits us tightly to the rest of the biological world. Moreover, Darwin already understood that humans are one species with only a limited amount of variation in anatomy and basic behavior. In chapter 7, "On the races of man," he argued against the racist theory that living humans belonged to different species. He did acknowledge that human behavior varied dramatically from place to place and time to time but attributed most of these differences to different cultural traditions rather than to the kinds of differences that biologists would use to classify species. The contemporary human sciences follow this distinction.

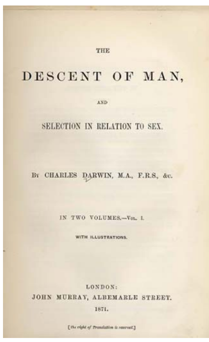
THE
DESCENT OF MAN,
AND
SELECTION IN RELATION TO SEX.
By CHARLES DARWIN, M.A., F.R.S., &c.
IN TWO VOLUMES.—Vol. I.
WITH ILLUSTRATIONS.
LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1871.
[The right of Translation is reserved.]

Fig. 1. The title page of *The Descent of Man*. [Image from https://en.wikipedia.org/wiki/The_Descent_of_Man,_and_Selection_in_Relation_to_Sex.]

The historical pathways of Darwin's influences on the human sciences is less direct than his influences on the rest of biology. Late-19th-century thinkers often incorporated ideas from *Descent* directly into their thinking. Robert Richards (*3*) and Geoffrey Hodgson (*4*) have traced its influence in psychology and economics, respectively. In both cases, as the modern disciplines emerged in the early 20th century, Darwinian evolutionary ideas vanished from the mainstream. The case of anthropology and sociology was more complex. The important late-19th-, early-20th-century anthropologist Franz Boas (*5*) was heavily influenced by Darwin's appreciation of the distinction between biological and cultural variation in humans. Boas (*6*) delivered a speech in appreciation of Darwin's contribution to anthropology on the 50th anniversary of the publication of *On the Origin of Species*. Boas was influential in the founding of American anthropology and trained major 20th-century figures, such as Alfred Kroeber, Ruth Benedict, and Margaret Mead. Boas's and his students' influence on sociology was also large (*7*). He advocated for the "four fields" approach to the study of humans, including the study of ethnographic (sociocultural), physical (biological), and linguistic anthropology plus archaeology. "Four fields" departments dominate academic anthropology in the United States to this day. Thus, Darwin's view that all humans are a single species was firmly entrenched in the social sciences by the middle of the 20th century, although despite Boas's essay, connection to *Descent* was lost. For example, Theodosius Dobzhansky (*8*) wrote inaccurately that Darwin "confined himself to biological matters" in *Descent*. Pioneering essays advocating a Darwinian approach to cultural evolution did not realize that Boasians' now dominant concept of culture owed so much to Darwin (*9*, *10*).

Applying modern speciation theory to humans

Darwin's (*2*) most famous book, *On the Origin of Species*, laid the foundation for studies of speciation. Our main goal here is to apply the framework of modern speciation theory (*11*, *12*) to human origins, summarizing some recent research. In doing so, we will highlight Darwin's insights contained in *Descent* that foreshadowed many recent scientific developments in this field.

In applying speciation theory to different cases, researchers usually focus on three main issues. The first is the identity of the ancestor and various preexisting adaptations and features it possessed that would make possible or simplify the speciation process. For example, tetrapod limbs evolved from fish fins, and birds' feathers initially evolved for heat insulation but later became essential for flight. The second is the nature of evolutionary forces responsible for major differences between the emergent species and its close relatives. The most common examples are ecological selection (for example, due to competition or predation or changing environmental conditions) leading to adaptation to a new ecological niche, sexual selection, sexual conflict, random genetic drift, and mutational order. The third issue is the nature of the most important traits and adaptations that make the new species distinct from its close relatives and various evolutionary patterns (such as genetic, morphological, behavioral, spatial, and temporal) that characterize it.

Three of Darwin's insights are of particular interest to modern science. The first is that humans, like every other species, are a "modified descendant of some preexisting form" [(*1*), p. 5], which for humans are the anthropoid apes. We share with them many characteristics (such as developmental, physiological, morphological, cognitive, and psychological) as well as about 96% of our DNA. The second is that culture and cultural evolution were particularly important in human evolution. He thought that laws, customs, and traditions were the main sources of variation in humans, and that these were transmitted by imitation and education. They evolved by such processes as teachings of innovators and the influence of public opinion. For example, in the second edition of *Descent*, Darwin stated that the evolution in civilized societies "depends to a subordinate degree on natural selection…. The more efficient causes of progress seem

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to consist of a good education during youth while the brain is impressible and of a high standard of excellence, inculcated by the best and ablest men, embodied in the laws, customs, and traditions of the nation, and enforced by public opinion" [(*13*) p. 192]. The third was that human cooperation and our moral sense, which Darwin viewed as "the best and highest distinction between man and the lower animals" [(*13*), p. 126], evolved from tendencies for mutual aid and self-sacrifice, which "are common to most social animals" [(*13*), p. 109].

Deep biological roots of many human traits

Darwin speculated that because man's nearest relatives—the gorilla and chimpanzee—live in Africa, humanity came out of Africa as well: "... [I]t is somewhat more probable that our early progenitors lived on the African continent than elsewhere." [(*13*), p.199]. However, there was no proof at his time, and many biologists and anthropologists favored the idea that "Man" arose in Europe. In *Descent*, Darwin remarked in a few passages on the origin and antiquity of humans, but he and his contemporaries had almost no relevant fossils to work with and very underdeveloped archaeological and paleoecological records. We now know that the human lineage has undergone a rather dramatic series of changes since our last common ancestor with the other apes 6 million to 8 million years ago (Fig. 2 and 3) (*14*). Human evolution followed the path common for other species, with diversification into closely related species and some subsequent hybridization between them (*15*). DNA and fossil remains suggest that our ancestors diverged from Neanderthals and Denisovans more than half a million years ago. Anatomically modern humans were present in Africa 200,000 years ago. Around 70,000 years ago, up to six highly distinctive subspecies of humans coexisted (*16*). Since then, we have been a single species that emerged from Africa about 50,000 years ago (*17*). Some of our derived features, especially bipedal locomotion, are fairly ancient (*18*); others, especially stone tool knapping, evolved a little before the first fossils attributable to our genus *Homo* appears in the fossil record around 2 million years ago (*19*); and still others appeared after 250,000 years ago (*20*). Human behavior was substantially modern by 30,000 years ago, but both biological and especially cultural changes have been dramatic right up to the present. In the Holocene, cultures evolved a whole series of new ecological niches based on cultural adaptations and symbolic markers of tribes and tribe-like social units that partially isolate ecologically different populations (*21*, *22*).

There exists a long tradition of elucidating human evolution through comparisons with other primates, other mammals, and animals further afield phylogenetically [for example, (*23*)]. Initially, these efforts focused on baboons because these monkeys share with our ancestors an adaptation to the savanna environment. Today, we favor comparisons with fellow hominids, such as chimpanzees and bonobos, not only because of the much closer genetic relationship and higher intelligence of these apes but also because they live in fission-fusion societies. Instead of permanent spatial cohesion among their members, such as in most group-living animals. Fission-fusion societies are marked by subgroupings of which the size and composition adjust to resource distribution. This flexible social system, which also marks our lineage, places special demands on cognition and communication (*24*).

Since Darwin, a long series of unbridgeable gaps have been proposed between humans and other animals—gaps relating to tool-making, cultural learning and imitation, empathy and prosociality, planning and foresight, episodic memory, metacognition, and theory of mind. The last claim was ironic given that the concept of theory of mind originated in chimpanzee research (*25*). None of these claims of uniqueness has held up, however. Tool manufacture, for example, has been experimentally shown in apes and corvids (*26*). Cultural transmission of habits and knowledge is a growing area of research in fish, birds, whales, and primates (*27*, *28*). Empathy and the tendency to help others are now considered mammalian capacities (Fig. 4). When theory of mind was tested with a false belief task and eye-tracking technology, apes responded similarly to human children (*29*).

Increasingly, students of animal cognition agree with Darwin that human cognition is continuous with animal cognition (*30*). New insights from neurobiology, genetics, primatology, and behavioral biology only reinforce Darwin's views about most differences between humans and higher animals being those "of degree and not of kind." Only one widely recognized difference remains, which is the human language capacity. Some aspects of language are found in the communication of other species, but not the syntax, recursiveness, and rich meaning of our learned symbolic communication (*31*).

Social comparisons with other primates have traditionally emphasized aggression and warfare. In both the popular press and the scientific literature, humans have been described as xenophobic "killer apes." These scenarios, which describe males as "fierce" and "demonic," feature only one of our two nearest relatives, however. Whereas chimpanzees are hostile to neighbors and regularly show lethal aggression, bonobos mingle with neighbors and are strikingly peaceful. Given the lack of fossilization in the forest, it remains unknown whether the last common ancestor of humans and apes resembled chimpanzees, bonobos, or some extinct hominid. Scenarios postulating a

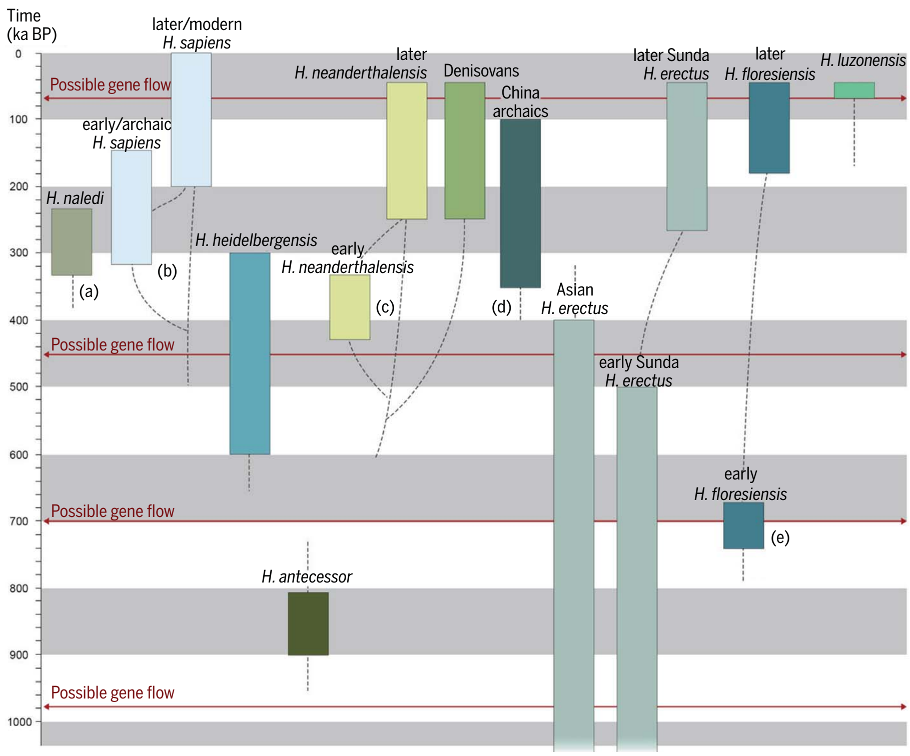

Fig. 2. Inferred ages of hominin lineages during the past million years. Colors reflect designations referenced in the literature. [Reproduced from (*16*) with permission.]

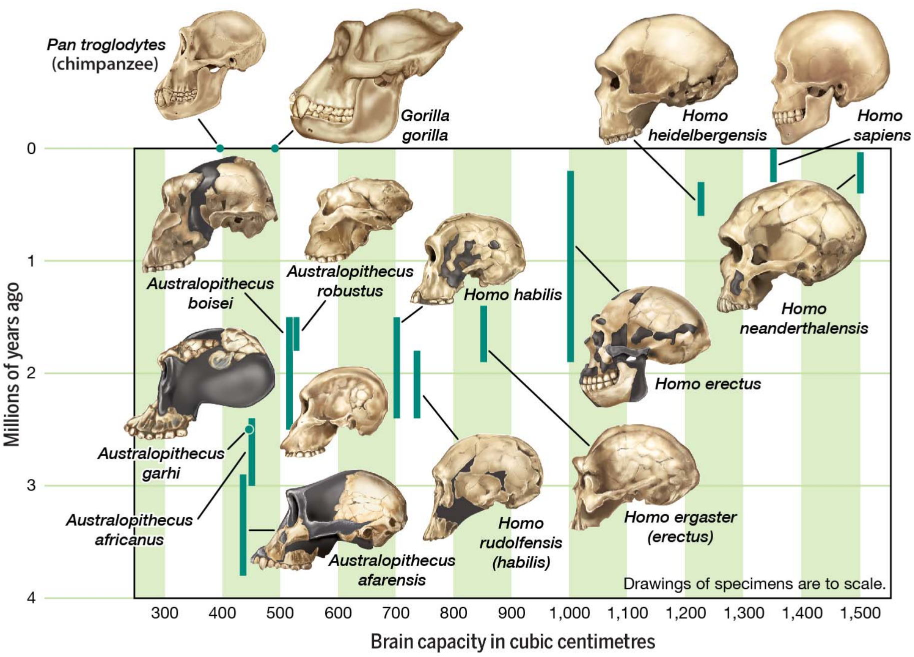

Fig. 3. Brain size evolution. [Reprinted with permission from Encyclopaedia Britannica, 2016 (Encyclopædia Britannica).]

long evolution of human warfare are therefore highly speculative, also in view of the archeological data. Evidence for warfare (such as graveyards with weapons embedded in a large number of skeletons) goes back only a little further than the origins of agriculture about 11,000 years ago (*32*). Given that human populations only began to increase substantially about 50,000 years ago (*33*, *34*), it is likely that warfare was unimportant until the Mesolithic.

Both of our closest primate relatives are highly cooperative. They engage in tit-for-tat exchanges of benefits and have ways to overcome and suppress competition for the sake of cooperation. Exchanged benefits range from grooming, food-sharing, and anti-predator defense to support in fights. Cooperation is also by no means limited to kin relations. DNA evidence shows that political partnerships among unrelated chimpanzee males are common (*35*). In bonobos, collective female dominance over males is established by a "sisterhood" of unrelated females (*36*).

Although Darwin appreciated the existence of social learning in animals, the possibility that animals might have a second inheritance system, now known as culture, was for a long time largely ignored in evolutionary biology under the influence of the Modern Synthesis, which rather dogmatically focused on genetic evolution. With Western anthropology having firmly declared culture as that which makes us human, it was perhaps no accident that the possibility of animal culture originated with a Japanese scientist, Kinji Imanishi (*37*). Since then, there have been many studies, both observational and experimental, of how animals transmit habits and knowledge to each other. The first well-known example was sweet-potato washing by Japanese macaques on Koshima island, but we now have a rich array of passed-on traditions, and not only for the primates. Examples range from local bird dialects to nut-cracking with stones by chimpanzees, and from whales' hunting techniques to pinecone-opening by wild rats (*27*, *38*, *39*). As a result, biologists recognize that vertebrate animal populations possess knowledge reservoirs that are essential for survival and passed on to the next generation through nongenetic means.

The difference with our species is not so much the existence of culture, therefore, but its scale and partially its method of transmission. There is evidence for conformity, emulation, and imitation in other species, but intentional teaching, in which competent individuals actively scaffold the acquisition of habits by naïve individuals, has been documented in only a few species. There is also scant evidence in other species for elaborately cumulative culture in that new habits build on old ones to arrive at ever more complex outcomes (*40*). Both differences may not be absolute, but they are substantial enough for human culture to have taken flight to an unprecedented degree. Moreover, the symbolized nature of human culture and its linguistic support make its transmission more efficient and widespread.

The complex cognition and social emotions needed in the highly differentiated societies of apes has been documented both in the field and experimentally (*30*, *41*). Apart from hierarchical relations and networks of friends and relatives, we know about conflict resolution, well-developed reciprocity, and a range of traditions and customs. The basic primate psychology that we share with these apes also underpins human behavior, from politics to economics and from morality to culture. The moral continuity emphasized by Darwin in *Descent* is increasingly supported by research.

Whereas many scholars have tried to drive a wedge between morality and biology, including Darwin's public defender Thomas Henry Huxley, Darwin himself made an explicit effort to point out the continuities between human morality and animal sociality: "Besides love and sympathy, animals exhibit other qualities connected with the social instincts which in us would be called moral" [(*1*), p. 103].

Rooting morality in the emotions, instead of the reasoning and logic emphasized by many moral philosophers, derives from David Hume and Adam Smith, both of whom influenced Darwin. These Scottish philosophers emphasized sympathy, which Darwin saw as an evolved capacity. To be vicariously affected by the emotions of others must be very basic because this capacity has been reported for a great variety of animals and is immediate and spontaneous. For example, rats display distress in response to perceived distress of a conspecific and terminate stress manipulations that negatively affect others in laboratory procedures. A wide variety of reports on ape empathic reactions suggests that apart from emotional connectedness, apes show "consolation behavior," which is defined as reassuring body contact (such as a kiss or embrace) by an uninvolved bystander toward the loser of an aggressive incident (Fig. 2). Since these early reports, the study of animal empathy has taken off (*42*).

Selective forces driving human origins

Humans represent a peak in a continuous trend of increasing brain size and social competencies observed in primates and many other mammalian and bird lineages. But what were the selective forces responsible for us becoming such a large-brained species, and how did it happen?

A number of trigger hypotheses have been proposed that focus on a particular breakthrough innovation, after which a positive-feedback process drove relentless progress. These include transition to bipedalism (*43*, *44*), cooperative breeding (*45*), cooking (*46*), language (*47*), and sexual selection for large brains (*48*). Alexander (*49*) developed a comprehensive theory postulating that at some point in the past, our ancestors had achieved a state of "ecological dominance," leading to competition between humans to become the dominant selective force. All of these proposals must be true in some sense. If humans were still quadrupeds, did not assist mothers with children, did not cook, did not have language, did not have large brains, and did not compete with one another, we would be a rather different species than we are.

Biological research convincingly shows that there are a myriad of pathways for organisms to adapt to their environment by optimizing their viability, survivorship, fertility, and mating success. The consensus over the past couple of decades is that the path taken by our ancestors was the path of increased reliance on cooperation, social learning, and cumulative culture—the traits already present in a comparatively advanced form in our primate ancestors (*14*, *50*, *51*). Specifically, cooperation allowed for environmental risk buffering, cost reduction, and the access to new resources and benefits through the "economy of scale." Learning and cumulative culture allowed for the accumulation and rapid spread of beneficial innovations between individuals and groups. The evolved abilities to learn from others and cooperate became a universal tool, removing the need to evolve specific biological organs for specific environmental challenges. Next, we discuss social learning and cooperation as well as a special role of an unstable Pleistocene environment in making these two traits crucial in our evolution.

A fundamental role for cultural processes in human evolution

As discussed above, whereas some culture exists in many other species, humans are unusually dependent on culture and have unusually specialized mechanisms for its acquisition, curation, and transmission (Fig. 5). Human culture is cumulative; that is, knowledge and habits accumulate over time within and between generations (*52*). Humans exhibit preferences and abilities for social learning at very early ages (*53*), show a striking level of conformity with opinions of others (*54*), and over-imitate even perceivably unnecessary actions in relation to the given goal (*55*). We deeply internalize the systems of religious and political beliefs (*56*) and are strongly influenced by various types of propaganda (such as political or commercial) (*57*).

The Modern Synthesis (*58*) heavily focused on genetic evolution, natural and sexual selection, mutation, random genetic drift, and migration as evolutionary forces moving gene frequencies. The Modern Synthesis founders fought a strong and largely winning battle against the inheritance of acquired variation at the core of Jean-Baptiste Lamarck's theory. This, however, is all very far from Darwin's picture of evolution generally and human evolution in particular. In the preface to the 2nd edition of *Descent* in 1874, Darwin remarks that his critics frequently assume that he attributed all change to natural selection and spontaneous variation, "whereas, even in the first edition of the *Origin of Species*, I distinctly stated that great weight must be attributed to the inherited effects of use and disuse, with respect to both the body and the mind." In modern terms, Darwin thought that evolution was powerfully influenced by the agency of actors. From the point of view of the Modern Synthesis, Darwin's emphasis on inheritance of acquired variation and agency-based forces more generally was his greatest mistake. However, from the point of view of the modern theory of cultural evolution, it meant that Modern Synthesis theorists had forsworn interest in the special properties of cultural evolution that were highly salient to Darwin himself.

Fig. 4. A juvenile chimpanzee reassures a screaming adult male who has just lost a fight by embracing and holding him. Consolation behavior is used in both human and nonhuman studies as an index of empathy. [Photograph: Frans B. M. de Waal.]

Cultural evolution differs from genetic evolution structurally as well as in the array of forces that affect it. Structurally, culture can be acquired from anyone in the acquiring individual's social network: parents, other relatives, peers, teachers, prestigious figures, and so forth (*59*). Because cultural transmission through teaching or imitation is based on phenotypic performances, any acquired modifications of the phenotype of teachers or models will be transmitted to learners.

The array of forces that affect cultural evolution can be divided into two types: those that have close analogs in the Modern Synthesis version of evolutionary biology and those that involve agency (*52*). Analogs of mutation, drift, migration, recombination, and selection all generate or prune cultural variation much as in genetic evolution. Boyd and Richerson (*60*) divided the agentic forces into guided variation, new variations that are not random with respect to fitness, and bias forces, selective adoption of existing variants, subdividing the bias forces into subtypes with different dynamic properties. Many authors follow their scheme, with various modifications (*61*).

Cultural evolutionists have proposed that culture-led gene-culture coevolution can in theory, and arguably in practice, drive genetic evolution as much as gene-based biases can drive cultural evolution (*43*, *62*–*64*). The best understood example is the evolution of adult lactase persistence in traditionally dairying populations in western Eurasia and Africa (*65*). Aside from natural selection created by human-modified environments, such as in the adult lactase persistence case, cultural conventions and norms can generate agentic social selection on genes (*66*). Punishment for social rule violations is an example. Punishment for social rule violations will select against any selfish genes, and social selection that favors rule followers selects for genes favoring prosocial behavior. By such mechanisms, the human species might have been completely transformed by the processes of cultural evolution (*14*, *67*).

Cooperation

Research on cooperation has burgeoned in recent decades owing to the growing appreciation of its importance in both biological and social processes. This view can be traced back to Kropotkin's *Mutual Aid: A Factor of Evolution* published 30 years after *Descent* (*68*). Kropotkin argued against both Social Darwinism, which overemphasized "survival of the fittest" and "struggle for existence," and depictions of "human nature" as good, virtuous, and moral in the vein of Rousseau (*69*). In Kropotkin's view, which is consistent with contemporary interpretation, cooperation and mutual aid are one of the mechanisms of adaptation and increased survival common across all branches of life. For our ancestors, the advantages of cooperation included greatly improved effectiveness and efficiency of hunting and defense from predators as well as increased survival of offspring through cooperative breeding.

Cooperation is common across all branches of life. Examples range from within-cell cooperation of organelles, to cooperation of cells in biofilms, to colonies of social insects, to cooperative hunting in some mammals (*47*). In many biological systems, cooperation

Fig. 5. Examples of learning manual skills. (**A**) Learning through observation in chimpanzees. Recent studies demonstrate cultural transmission of knowledge and habits in many animal species. The mechanism varies, however. Chimpanzees in Bossou, Guinea, crack tough nuts with stones. This is a difficult technique that young apes learn from watching their elders. [Photograph: Noriko Inoue-Nakamura and Tetsuro Matsuzawa.] (**B** to **D**) Humans learning through observation and instruction, which makes transmission more efficient. (D) Hadza women processing Baobab seeds into flour with children practicing the technique. Notable is the use of the human power grip that is so important in tool use and manufacture. [Credit: Caren Apicella.] (B) A drawing class in Germany. [Photograph: Julia Budka, CrossBorders.] (C) Basket weaving in Ecuador. [Photograph: Jerónimo Zuñiga, Amazon Frontlines.]

is based on genetic relatedness, as explained by Hamilton (*70*). In humans, cooperation is distinctive both in the diversity of its types (matching the diversity of human behavior), in scale (from dyadic interactions to collaborations between nations), and that it regularly involves nonrelatives (Fig. 6) (*71*). Humans start exhibiting cooperative tendencies at very early ages (*72*), they often cooperate by default (*73*), and they are often willing to pay substantial personal costs to make collaboration successful, both in the laboratory and real life (*74*).

The literature on the evolution of human cooperation is far too large to review in detail here. Its mechanisms include pure altruism, helping kin, direct and indirect reciprocity, punishment, group selection, social norms, and institutions (*73*, *75*).

Recent research suggests a particularly important role for selection on culturally transmitted institutions in the evolution of human cooperation. Richerson *et al.* (*76*) contrast the reciprocity and cultural group selection and review the evidence that supports a major role for cultural group selection. Cultural evolution is generally faster than genetic evolution, altering the balance between adaptive forces and migration and allowing cultural relatedness to build up in large groups in a way that genetic relatedness normally cannot. Thus, selection on cultural variation can favor cooperation on the scale observed in human societies. Institutions are particularly prone to cultural group selection because they vary between groups, suppress selection for selfish behavior within groups, and play a crucial role in success or failure in intergroup competition. Throughout their history, human groups have cooperated not only against environmental challenges but also against other human groups. As a result, we have evolved strong coalitional psychology (*77*), which can bring us together whenever we perceive that our identity group faces outside challenges. Coalitionary psychology also has a darker byproduct: often negative or even hostile reaction to others who differ from us in their looks, behaviors, or beliefs (*78*).

Pleistocene environment and evolution of cognition and culture

Identifying the most important selective forces and mechanisms that were driving human evolution is not enough. Ideally, we need to explain the timing of the appearance of humanity's greater reliance on cooperation and the ascent of cumulative culture.

Why did human cumulative culture evolve during the Pleistocene and not earlier? An evolutionary-functional analysis and mathematical modeling of culture suggests that it is a system for adapting to relatively fine-grained spatial and temporal variation (*60*). Since the 1990s, increasingly detailed climate records resolving high-frequency climate variation have been recovered from ice, ocean, and lake cores (*79*–*81*). They show abundant evidence of millennial and submillennial scale variation, which produced increasing spatial heterogeneity, with closed canopy forests being replaced with mosaics of open woodlands, grasslands, and deserts in many parts of the world. Therefore, it seems plausible that the evolution of humans' massive dependence on complex, cumulative culture and cooperation was driven by increasing high-frequency climate change (*82*). Humans' learning and cooperative abilities would then coevolve with their cognitive abilities, driving brain expansion (*83*–*85*).

But of course many other species experienced the same climate variation, so the question is whether it affected only our lineage or other species as well. In mammals, brain size has increased in many mammalian lineages over the whole 65 million years of the Cenozoic, most rapidly in the past 3 million years (*86*). Thus, our lineage, in which brain size more than doubled in the past 2 million years (Fig. 3), is part of a broad progressive trend of adaptation to variable environments by using individual and social learning.

A more recent environmental change was extremely consequential for our species. The Pleistocene-Holocene transition rather abruptly created warm, wet, relatively stable conditions that made farming a feasible adaptation (*87*). At the very end of the Pleistocene, some specialized hunter-gathers in the Near East had become semisedentary owing to the exploitation of wild wheat, rye, and barley and the hunting of wild sheep and goats. After the

Fig. 6. Examples of human cooperation. (**A**) Plains Indian buffalo drive. Tens or even hundreds of personnel were often employed historically and prehistorically by hunter-gatherers in drive lines kilometers long to push herds of animals into natural or specially constructed traps—here, a cliff. [Painting: Alfred Jacob Miller, https://commons.wikimedia.org/wiki/File:Alfred_Jacob_Miller_-_Hunting_Buffalo_-_Walters_371940190.jpg.] (**B**) Amish barn raising, Holmes County, Ohio. Recruiting large numbers of community volunteers for common projects is nearly ubiquitous. Modern civil society organizations organize such things as food banks, blood drives, and civic celebrations. Hunter-gatherers organize the quotidian communal cleaning of their camps. [Reprinted with permission from Ian Adams Photography.]

final major Pleistocene abrupt climate excursion ended 11,700 years ago, these hunter-gatherers fairly rapidly evolved into farmers and began to migrate westward along the Mediterranean littoral and northwestward into Central and eventually Western Europe, reworking their agricultural adaptations as they went to suit new environments (*21*). Similar processes were happening in east Asia, where cultivation and domestication of millets (in the north and west of China) and rice (in the south of China) started about 9000 years ago, and sedentary farming villages subsequently developed after 5000 BCE (*88*, *89*). It is not entirely clear what has regulated the pace of cultural change over the past 12 millennia (*90*), but the time scale of progressive change in the Holocene is millennial.

Why us?

What triggered our species' evolution of special abilities for cumulative cultural learning, extensive cooperation, prosocial motivation, and sophisticated cognition? As argued above, humans are part of a broad trend of adaptation to variable environments using individual and social learning. As noticed by Darwin, with regard to cognition, "the difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind" [(*1*), p.85]. Nevertheless, as he pointed out in *Descent*, the gap in mental powers between humans and even the most advanced animals is "enormous" [(*1*), p. 65]. Darwin was reluctant to admit gaps, especially enormous gaps, because they are incompatible with his theory of evolution through descent with modification. This is certainly true of our highly complex cultures, even if we now realize that many nonhuman cultures are much more sophisticated than we once thought. Because several vertebrate lineages seem to have independently converged on the ape level of brain size and cognitive sophistication, arguably in response to increasing environmental variability, what might account for the even greater expansion in humans?

We still do not have a generally accepted answer. One explanation invokes cooperative breeding, which some researchers view as the most important step that created conditions for widespread cooperation, cumulative culture, and the appearance of language (*45*, *51*). Family structure is the most substantial difference between human societies and those of our closest relatives. Whereas in apes, offspring care is almost entirely shouldered by mothers, in humans, we find both high levels of female cooperation and substantial involvement of males. When our ancestors left the forest environment, males needed to get involved by carrying offspring as well as provisioning and defending them against predators. The need for cooperative breeding could also be generated by the nutritional demands of growing big brains and raising highly altricial offspring. Cooperative breeding could then lead to other types of cooperation and the appearance of language, which greatly simplifies cooperation.

The trouble with this argument is that one can easily reverse the arrow of causation. Once humans became cooperative for whatever reason, cooperative breeding would be easier to organize. Moreover, in modern humans cooperative breeding is heavily institutionalized, so its spread plausibly evolved gradually as human brains got larger and infants more altricial.

Perhaps the most obvious answer to the question "Why us?" is a modified version of Engels' (*44*) and Washburn's (*43*) proposal regarding hands, brains, and tools. They argued that the bipedal stance of Australopithecines freed their hands to become specialized for toolmaking. This set up a positive feedback because toolmaking favored larger brains, and larger brains favored an anatomy specialized for toolmaking. The long period over which the Australopithecines were bipedal before stone toolmaking became important suggests that the positive-feedback proposal itself is not correct. Rather, increasing climate variation could have favored the evolution of toolmaking sophistication and larger brains. Darwin in *Descent* has an extended discussion of the importance of hands that could be further specialized for precision toolmaking. All primates have hands, and whereas some hands are more specialized for climbing, others have opposable thumbs that allow them to handle and make tools. The study of intelligent tool use in the primates began with the chimpanzee studies of Wolfgang Köhler (*91*), who related this capacity to intelligence, untrained problem-solving (*Einsicht*), and planning. Since then, many studies on tool use have been conducted in both the field and captivity, resulting in an impressive body of knowledge about the relative capacities of apes, monkeys, corvids, parrots, dolphins, and other tool-using species. Most impressive perhaps is the planning involved, such as the way wild apes carry sets of tools with differing functions to feeding sites to use them in sequence (*92*).

Tool technology is one of the best archeological markers of human culture because tools made of stone or metal are preserved, a circumstance shared with the stone tools used for probably thousands of years by chimpanzees and capuchin monkeys documented by a new field named ethnoarcheology (*93*). The human hand is homologous with those of the primates' but evolved more of a precision grip required for the sophisticated tool manufacture and use by our species. Australopith hands seem to have evolved substantially in the direction of human hands in this regard. Biomechanical studies suggest that stone tool knapping and marrow extraction require a precision power grip that demands the greatest specialization of hands (Fig. 5) (*94*). Stone tools in turn are used to make other tools in wood and other perishable materials (*95*). Tools are a critical feature of most human cultural adaptations (*67*). Ape brains are relatively large, meaning that even before human brains began to expand toward their enormous size, australopithecines would already be capable of mastering a fair repertoire of tools. Hands and the technology they can make thus might have acted as a multiplier of the adaptive advantages of culture that in turn paid the huge overhead cost of our brains driving our evolution past the "gray ceiling" imposed on the other culturally advanced lineages (*96*).

Some other distinctively human traits

Once the abilities for cumulative culture and extended cooperation were in place, a suite of subsequent evolutionary changes became possible and likely unavoidable. Here, we discuss some of the most striking and consequential.

Life history

Our large brains, so foundational for complex cumulative culture, forced a revolution in our life history. In particular, social systems had to evolve to support mothers who could not alone marshal the resources to care for and feed our large-brained, helpless infants and slow-growing juveniles (*45*, *97*). In the end, the recruitment of males and nonreproductive females to alloparental roles through culturally transmitted social institutions became so efficient that interbirth intervals are nearly half that of other apes (*98*), whereas human lifespan is substantially longer (*99*).

Language

Language has always been seen as one of the most distinctive features of our species. Language origin has traditionally been a very controversial topic. The Linguistic Society of Paris famously banned publications about the origin of human language in 1866. We still do not know when and how language appeared. But its origins must be a result of gene-culture coevolution, with biological traits underlying linguistic abilities (speech organs and neurological mechanisms) coevolving with culturally transmitted features (sound patterns, words, and syntax). Pinker and Bloom's (*100*) pioneering article on the evolution of the innate aspects of language invokes the Baldwin effect, which is a hypothesis that learned abilities can acquire a genetic basis. The degree to which a cognitive substratum of language is gene based is controversial, but there is general acceptance of the idea that gene-culture coevolution is involved; language adapts to the brain, or the brain adapts to language, or both (*101*, *102*). What we do know is that all the necessary precursors for human speech motor control are present in closely related primate species. The emerging consensus is that adaptations for speech (or at least for complex vocal behavior such as song) must have evolved gradually and that they predate the last common ancestor with Neanderthals, who lived more than 400,000 years ago (*103*). Contrary to earlier results, forkhead box P2 (FOXP2), which was initially thought to be key to the evolution of language, did not undergo a rapid "selective sweep" as humans developed language (*104*).

An important question is why language is restricted to our species. Language is part of the extraordinary cooperation of humans, and linguistic communication is extremely useful in many contexts (*105*)—for example, in teaching others (*106*) and reaching collective decisions (*107*). Cooperation requires close matching of interests. Burkart *et al.* (*108*) argue that great apes possess many of the prerequisites for language but largely lack the motivation to share information. By contrast, our ancestors—being cooperative breeders, with all group members helping to raise offspring—had strong motivation to share information. Richerson and Boyd's (*109*) tribal social instincts hypothesis links the emergence of language to selection to simplify cooperation within large groups of distantly related or unrelated people. Such groups, already possessing both some protolanguage and a fairly advanced cultural system, would then be a subject of strong cultural group selection for improved communication and beneficial social norms and institutions.

We know much more about the evolution of languages. Darwin himself noted that "the formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously parallel…" [(*1*), p. 90]. Like species, languages evolve through a process of descent with modification (*110*). Although the ability to speak is clearly an adaptation, most language differences are not obviously adaptive at all. You can convey the same meanings by using the syntax and vocabulary of many different languages, although of course translation can be fraught because different cultures have unfamiliar concepts that cannot be simplistically rendered into a language that lacks the necessary vocabulary. One model of language evolution is that it is largely powered by limited neophilia (*111*). People must largely conform to the syntax and vocabulary of the languages they speak for communication to work. At the same time, old words and old grammatical constructions become boring, and new words and new constructions are attractive to the linguistically adventurous, and some of these are eventually adopted as new conventions (*112*). In this fashion, language families on the millennial time scale diverge as semi-isolated daughter languages explore huge spaces of neutral or near-neutral variation [for example, (*113*)]. At the same time, language variation is an important social marker, and social marking itself may be adaptive (*102*). Language evolution can also be influenced by selection. For example, frequently used words are shorter and, thus, easier to say. Moreover, larger populations have higher rates of gain of new words, whereas smaller populations have higher rates of word loss (*114*), which is a key signature of adaptive evolution.

Forces shaping human social behavior

Evolved reliance of humans on social learning and conformity has created conditions for the appearance of new factors constraining and driving their behavior: morality, social norms, and social institutions. These forces often act against immediate biological or material interests of individuals, promoting instead the interests of the society as a whole or of its powerful segments (*115*).

Morality

As discussed earlier, human morality has roots in the biology of social behavior. Darwin in *Descent* proposed a well-thought-out theory of human moral progress (*116*). It is a two-step theory. He hypothesizes that in primordial times, tribal-scale group selection endowed humans with prosocial emotions: "A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes… [A]s morality is one important element in their success, the standard of morality and the number of well-endowed men will thus everywhere tend to rise and increase" [(*1*), p. 148]. So endowed, all living people could use these emotions, aided by reason, as a basis for moral progress.

Modern research on the origins of morality returns to many of Darwin's first thoughts on this issue, such as studies of animal behavior that point out continuities between human morality and animal sociality. In the behavior of our close relatives, the apes, one can recognize certain "building blocks" of morality, such as empathy and sympathy, the need for conflict resolution, the following of unwritten social rules, the reciprocal exchange of benefits, and a sense of fairness (*117*). For example, experiments show negative reactions to unequal reward distributions in monkeys, apes, dogs, and birds (*118*).

Meanwhile, psychologists have begun to emphasize moral intuitions about harm and fairness as main ingredients of moral decision-making. Following Hume, Haidt (*119*) has called for a thorough reevaluation of the role played by rationality in moral judgment, arguing that most human justification seems to occur post hoc—that is, after moral judgments have been reached on the basis of quick, automated intuitions. Neuroimaging shows that moral judgment involves a wide variety of brain areas, some extremely ancient (*120*). These approaches stress the social functionality of human morality rather than the seeking of truth or of logically consistent normative principles. Neuroimaging studies indicate a two-pronged process that can switch between affective and consequentialist decisions, with the first relying more on the emotions and the second more on cognition (*121*). Churchland (*122*) further illustrates the promise of anchoring human morality in ancient neural circuitry and dopamine systems for bonding and care. Recent theory of "morality-as-cooperation" argues that morality helps solve the problems of cooperation. Its prediction that seven types of cooperative behavior—helping kin, helping your group, reciprocating, being brave, deferring to superiors, dividing disputed resources, and respecting prior possession—are considered morally good is supported by the analysis of 60 societies (*123*).

Social norms

The ability to learn social norms appears early in child development universally across societies (*124*). Social psychology makes a distinction between descriptive and injunctive (or prescriptive) norms (*125*). Descriptive norms are behaviors that are typically performed by people. Injunctive norms are behaviors that people ought to do in a given social situation, even if doing so is against their immediate interests. Injunctive norms represent perceived moral rules of the group. They are maintained by the threat of social disapproval or punishment for norm violations and/or by norm internalization (*126*, *127*). Descriptive norms are related to the general phenomenon of conformity, which, as discussed above, may extend to animals (*27*). Animals also have unwritten rules that mark behavior that they accept or reject and strive for certain outcomes in their social relationships that hint at a natural normativity (*128*). The importance of such norms for humans was well understood by Darwin himself, who wrote, "The expression of the wishes and judgment of the members of the same community… serves… as a most important secondary guide of conduct, in aid of the social instincts, but sometimes in opposition to them" [(*1*), p. 99]. Social norms govern our social life at all levels, from the way we greet each other, eat, and dress to norms of conduct in family, education, business, or politics. As Tomasello puts it, "Humans live in a sea of social norms that govern pretty much all aspects of their lives" [(*129*), p. 20]. This has been the case during all of human history (and likely also in prehistoric human groups and societies) and remains true now, when norms can change quickly because of increased connectedness of human societies and the rapid flow of information between them.

Institutions

The concept of institutions as used in anthropology, sociology, and economics refers to systems of injunctive norms. Marriage is a classic example. Marriage institutions specify two roles, wife and husband, or sometimes more, such as junior wife or secondary husband. Subsets of norms govern the rights and duties of each role. Norms and institutions are rooted in innate social emotions but are highly variable cross-culturally and historically (*130*, *131*). Our root social psychology is itself a likely candidate for culture-driven gene-culture coevolution (*132*). Social norms and institutions became a new selective force in the evolution of our species (*133*).

Conclusions

We discussed only some of the research areas influenced by *Descent*, leaving aside many others (such as sexual selection). The more we learn about human origins and evolution, the more we appreciate Darwin's genius. The Modern Synthesis has honored his biological insights but forgotten about his attention to the cultural side (acquired characteristics) of human evolution. As stressed by Darwin, humans are part of the biological world. The impact of *Descent* and the research on cultural and social evolution it has stimulated on social sciences and on the development and implementation of different policies by practitioners and policymakers to improve our society will only grow. One of the greatest current challenges is knowledge syntheses across biology and the social sciences (*134*). In the 20th century, the social sciences became isolated from the natural sciences and from each other, which is an impediment to scientific progress. Clearly, applied problems—such as climate change, the extinction crisis, various types of social conflicts, and pandemics—need to tap multiple disciplines that share a common body of theory.

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Modern theories of human evolution foreshadowed by Darwin's *Descent of Man*

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150 years of *The Descent of Man*

Charles Darwin's *The Descent of Man* was published in 1871. Ever since, it has been the foundation stone of human evolutionary studies. Richerson *et al.* reviewed how modern studies of human biological and cultural evolution reflect the ideas in Darwin's work. They emphasize how cooperation, social learning, and cumulative culture in the ancestors of modern humans were key to our evolution and were enhanced during the environmental upheavals of the Pleistocene. The evolutionary perspective has come to permeate not just human biology but also the social sciences, vindicating Darwin's insights.

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