

In the light of evolution IV: The human condition

John C. Avise¹ and Francisco J. Ayala

Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697

The year 2009 marked the 200th anniversary of Charles Darwin's birth and the 150th anniversary of his most influential publication. Darwin transformed the biological sciences in much the same way that Nicolaus Copernicus, Galileo Galilei, and Isaac Newton, centuries earlier, transformed the physical sciences—by demonstrating that the universe operates according to natural laws that fall within the purview of rational scientific inquiry. In 1543, Copernicus published *De Revolutionibus Orbium Coelestium* (“On the Revolutions of the Celestial Spheres”) that challenged conventional wisdom that the Earth was the center of creation and instead promoted the idea that natural laws govern the motion of physical objects in the universe. In 1859, in *On the Origin of Species* (4), Darwin developed the equally revolutionary concept that a natural but nonrandom process—natural selection—yields biological adaptations that otherwise can give the superficial impression of direct intelligent craftsmanship.

Actually, Darwin barely mentioned *Homo sapiens* in *On the Origin of Species*, cautiously stating only that “much light will be thrown on the origin of man and his history.” More than a decade later, however, Darwin addressed human evolution at considerable length in *The Descent of Man and Selection in Relation to Sex* (5) wherein can be found many thoughtful passages, such as, “Man may be excused for feeling some pride at having risen, though not through his own exertions, to the very summit of the organic scale; and the fact of his having thus risen, instead of having been aboriginally placed there, may give him hope for a still higher destiny in the distant future.”

Of course, much has been learned about humanity's evolutionary origins and biological conditions since Darwin's time, not least from the evidence of paleontology, comparative vertebrate biology, and genomics. An emerging field known as “anthropogeny” (6) seeks to understand the evolutionary origins of humans and their biological and cultural traits. In the articles of this Colloquium, leading evolutionary biologists, anthropologists, and philosophers of science reflect upon and commemorate the Darwinian Revolution as it relates to the human condition at levels ranging from the molecular to the phenotypic to the social and philosophical. The articles in these Proceedings are organized into three parts: (I) Human Phylogenetic

History and the Paleontological Record; (II) Structure and Function of the Human Genome; and (III) Cultural Evolution and the Uniqueness of Being Human. The diverse topics addressed in these articles give some indication of the vast breadth and depth of modern scientific research into the Darwinian evolution of the human state.

Human Phylogenetic History and the Paleontological Record

Precious few nonhuman fossils in humanity's recent “family tree” were known to science in the mid-1800s, but, interestingly, Darwin once briefly held in his hands one of these treasures: a Neandertal skull that had been excavated from Gibraltar in 1848. As additional hominid fossils of various geological ages gradually were unearthed in the ensuing decades (e.g., in Java, Africa, and Europe), anthropologists grappled with naming and classifying such remains and interpreting their proper places in prehuman evolutionary history. Such paleontological finds can be of two general types: fossilized body parts such as leg bones, the pelvic girdle, or the cranium (giving glimpses into humanity's anatomical heritage), and non-biotic physical artifacts such as stone tools or cave paintings that can offer important clues about humanity's cultural heritage. A different but complementary approach to studying human origins has entailed evolutionary reconstructions based on morphological, molecular-genetic, or other features of modern *Homo sapiens* compared with those of other extant primates. In these reconstructions, phylogeneticists take advantage of the voluminous biological information currently on display in living organisms to deduce the evolutionary ages and properties of the ancestors that humans shared with various other primates, thereby in effect delving back through time, indirectly.

In the opening presentation of these Proceedings, Wood (7) describes some of the special challenges that have confronted anthropologists wishing to reconstruct human evolution based on morphological evidence (from fossils and extant primates). One fundamental limitation has been the relative paucity of fossilized hominin material, but additional complications have come from shifting taxonomic paradigms and nomenclatural practices within the systematics community itself, as well as from continuing debates about phylogenetic methods and species concepts, especially as they apply

to fossil material. The net result has been an often confusing proliferation of species names and taxonomic realignments for putative human ancestors. To help simplify this imbroglio, Wood compiles, describes, and provides geological dates for all named fossil taxa in the human clade, ranging from anatomically modern *Homo sapiens* back to various archaic hominins and “possible hominins” that lived several million years ago and many taxa temporally in-between. The author also addresses several looming opportunities for the field of comparative primate morphology, such as the use of new imaging technologies that should help clarify (by permitting more detailed levels of examination) the situations in which anatomical traits in different taxa register genuine homology (shared ancestry) versus homoplasy (evolutionary convergence from separate ancestors).

Next, Arsuaga (8) reviews the history of one longstanding scientific debate, beginning in Darwin's era, about the precise phylogenetic interrelationships among modern humans and the various great apes of Africa and Asia. Another longstanding debate in anthropology is whether two or more species of more recent human ancestry ever inhabited the planet at the same time (a scenario that might seem unlikely based on general ecological considerations for competitive, large-brained primates). Traditionally, fossil-based assessments of this question relied heavily on rather meager population-level data from craniodental anatomy, but more comprehensive morphotypic descriptions are

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¹To whom correspondence should be addressed. E-mail: javise@uci.edu.

becoming possible now as the number of known postcranial hominin fossils has swelled. Arsuaga reviews these recent fossil-based discoveries about anatomical variation within and among particular proto-human populations dating to more than 0.5 Mya and concludes that the data are consistent with the more-or-less contemporaneous presence either of different species (depending on one's definition of species) or, perhaps, of morphologically distinct populations within a single species that seems to have been much more polytypic in anatomy than are modern humans.

Increasingly, in recent years the field of physical anthropology has shifted much of its attention from morphology-based appraisals of human evolution to historical reconstructions based on molecular-genetic and genomics data. Goodman and Sterner (9) review the history of molecular approaches in refining our understanding of primate phylogeny, for example in revealing the branching orders of lineages that led to extant great apes and humans. They then argue that a modern "phylogenomic approach" can go well beyond phylogeny reconstruction per se by helping identify Darwinian (positively selected) genetic changes (in expression profiles as well as in protein-coding sequences) that might mechanistically underlie the evolution of such distinctive human features as expanded cognitive ability, sociality, and language. The authors illustrate this phylogenomic approach by recent work that implicates particular loci in the adaptive evolution of high levels of aerobic energy metabolism that a large mammalian brain necessitates.

Hancock et al. (10) extend this general phylogenomic perspective in their population-genetic analyses of genome-wide scans of SNPs in numerous human populations that represent distinct ecoregions or that differ in their fundamental subsistence mode with respect to diet. In principle, genetic variation among humans living in different geographic areas might register adaptive differences promoted by environmental selection or, alternatively, historical population-demographic effects that mostly are independent of the ecological selective regime per se. The authors attempt to distinguish these two classes of historical causation by searching for consistent distributions of SNPs *vis-à-vis* human diet and ecoregion, after applying analytical methods designed to control for gene-environment associations that might result from historical population demography. The authors conclude that strong signals of natural selection related to diet and climate exist for SNPs at particular genes that are centrally involved in carbohydrate utilization and energy metabolism. The authors also compare their phylogenomic approach and its findings with those

of previous genome-wide association studies in humans.

Africa is humanity's evolutionary cradle, and its contemporary populations retain extraordinary genetic and linguistic diversity that offers anthropologists a wellspring of biological and cultural information about human history on that continent during the past 200 millennia. For example, with respect to languages, researchers recognize more than 2,000 ethno-linguistic groups that can be classified into four major African language families. With respect to genetic lineages, both mtDNA (which is inherited maternally) and the Y-chromosome (which is transmitted paternally) display higher genealogical diversity and evolutionary depth in Africa than in many other regions of the planet combined (as might be expected under a model of African ancestry for all modern humans). Scheinfeld et al. (11) address the demographic history of human populations in Africa by compiling and comparing scientific information from archeology (including cultural artifacts), comparative linguistics, and molecular genetics. Their synthesis reveals various signatures of past population movements on the continent, sometimes registered in particular genetic markers (either neutral or under selection), sometimes registered in cultural practices (such as agriculture and pastoralism), sometimes relatable to geophysical changes in the environment, and sometimes reflected to varied degrees in the current spatial distributions of languages. The net result is a fascinating but complex picture of African human demographic history presented in a broad framework that can be tested further as additional archaeological, linguistic, and genetic analyses (especially from autosomal loci) eventually are incorporated into the synthesis.

Structure and Function of the Human Genome

The first published reports of the complete nucleotide sequence of a human genome appeared near the turn of the 21st century (12, 13), and the full sequence of a chimpanzee genome was unveiled soon thereafter (14). Overall, humans and chimpanzees proved to be about 99% identical in the nucleotide regions they share (which include most of the genome and essentially all genes). Thus, somewhere within that "other 1%" of the nucleotide sequence must reside all the genetic changes that biologically differentiate humans from our closest living relatives. The "smallness" of the genetic divergence can be deceptive: A 1% sequence difference means that the human and chimpanzee genomes differ at about 30 million among their 3 billion pairs of nucleotides. A monumental challenge for the field of evolutionary genetics is to pinpoint the specific

genomic alterations that causally underlie various unique features that make us human (and to explain precisely how they do so).

Varki (15) describes an apparent "hot-spot" in human genomic evolution involving multiple loci that encode or regulate the expression of sialic acids (Sias) and the receptors that recognize them. The Sias are ubiquitous molecules that "decorate the canopy of the glycan forest" on cell surfaces and thereby play several key roles in human health and disease (e.g., by serving as cell-surface signals for "self" recognition in the vertebrate immune system or as cell-surface targets for the extrinsic receptors of many pathogens). By comparing the suite of human sialic acids and their associated binding proteins with those of nonhuman primates, the author details the molecular bases and the putative functional consequences of more than 10 evolutionary genetic changes that seem to be specific to the human lineage. Overall, Varki's analyses reveal multifaceted and often unexpected roles for cell-surface molecules in human biology and evolution. The sialic acid story also has broader evolutionary ramifications. For example, it suggests that evolutionary "arms races" between hosts and pathogens can promote a form of "molecular mimicry" whereby different microorganisms convergently "reinvent" the use of Sias to help mask themselves from the surveillance of vertebrate immune systems. The Sias system also illustrates the profound challenges as well as the opportunities that are likely to attend many attempts to dissect other complex structural and functional components of human genome evolution.

Conventionally, "the human genome" refers to the full suite of DNA within the cellular nucleus. However, the nuclear genome has a diminutive partner: mtDNA, which is housed in the cellular cytoplasm. The prototypical human mitochondrial genome is only 16,569 base pairs in length (roughly 0.5-million-fold smaller than each nuclear genome), but what mtDNA lacks in size it more than makes up for in copy number (thousands of mtDNA molecules reside in a typical somatic cell) and functional significance. Proteins and RNAs coded by the mitochondrial genome contribute critically to mitochondrial operations, which provide the cell with its chemical energy. The first complete sequence of human mtDNA was published 30 years ago (16), and since then this "other" genome has become a model system for genealogical reconstructions of human demographic history (17, 18) as well as for detailed mechanistic appraisals of genomic structure and function in relation to human health (19, 20). Wallace (21) uses such extensive informational background on

mtDNA as the basis for a bioenergetic hypothesis that ascribes a central role to energy flux in generating and maintaining complex biological structures such as the human brain. The author envisions a cyclical evolutionary process in which complex adaptations arise from a synergy between the information-generating power of energy flow and the information-accumulating capacity of selection-winnowed DNA. In this evolutionary scenario, bioenergetic genes (notably those contributing to mitochondrial function) play key roles.

The ongoing genomics revolution in biology that began little more than decade ago is opening new windows not only to the genes that make us human but also to the nature and significance of genetic differences between extant human populations now living in different geographical regions of the planet. As a part of this global monitoring effort by the scientific community (22, 23), Bryc et al. (24) provide a detailed case study involving mostly Hispanic/Latino populations in Central and South America. The authors compile and analyze genotypic information for several thousand individuals at several tens of thousands of SNPs scattered across the human nuclear and mitochondrial genomes. The results reveal a complex genetic signature of recent sex-biased admixture superimposed on a potentially ancient substructure involving source populations of Native American, European, and West African ancestry. In addition to illuminating the genealogical heritage of particular human populations, genomic surveys of this sort, when interpreted in combination with detailed epidemiological data, should be helpful in studies of the spatial distributions and evolutionary-genetic etiologies of particular human heritable diseases.

Next, Jablonski and Chaplin (25) show how, even in the age of genomics, much still can be learned about adaptive human evolution from comprehensive geographical analyses of phenotypes, in this case involving one of the most obvious of all human polymorphisms: skin pigmentation. Although the precise mechanistic action of the full suite of pigmentation genes underlying human skin-color variation remains incompletely known, the authors erect a compelling adaptationist scenario explaining why humans generally evolved dark skins near the equator and depigmented but tannable skins at intermediate and higher latitudes. This striking latitudinal pattern appears to reflect selection-mediated responses to two distinct challenges related to exposure to UV radiation (UVR), major forms of which (UVA and UVB) vary predictably with latitude and season. In the tropics, where UVA is high throughout the year, dark pigmentation tends to be selectively advantageous because it protects

the body against damaging UVR exposure. At higher latitudes, where UVB levels generally are lower and peak only once per year, natural selection has tended to favor light but tannable skin that can capture UVB for the cutaneous production of vitamin D, which otherwise must come from a suitable diet. As detailed by the authors in their opening comments, this modern understanding of skin color variation in humans is strikingly different not only from some of the racially prejudiced ideas formerly in vogue but also from the sexual-selection hypothesis for skin pigmentation originally favored by Darwin in *The Descent of Man* (5).

Before Darwin, most scientists as well as theologians accepted what seemed obvious: That divine intervention must have underlain nature's design. The traditional "argument from design" traces back at least to the classical Greek philosopher Socrates (469–399 BC) (26), and it was expressed again, in 1802, in a thoughtful treatise entitled *Natural Theology* by the Reverend William Paley (27). Darwin read Paley and later recalled in his autobiography (28) that Paley's logic "gave me as much delight as did Euclid" and that it was the "part of the Academic Course [at the University of Cambridge] which . . . was the most use to me in the education of my mind." Darwin himself was a natural theologian when he boarded the *Beagle* in 1831 on what would be a fateful voyage into previously uncharted scientific waters. Darwin's discoveries were revolutionary for philosophy and theology as well as science, because they identified a nonsentient directive agent (natural selection) that apparently could craft complex and beautiful biological outcomes that otherwise could be interpreted as direct handiworks of a supernatural God. However, Avise (29) asks whether the human genome actually does display the kinds of artistry of molecular design that natural theologians might wish to claim (30) as definitive proof for *ex nihilo* craftsmanship by a caring and omnipotent Deity. To the contrary, modern genetic and biochemical analyses have revealed, unequivocally, that the human genome is replete with mistakes, waste, dead-ends, structural and functional imperfections, and other molecular flaws ranging from the subtle to the egregious with respect to their negative impacts on human health (29, 31). These imperfections are the kinds of biological outcomes that are expected from nonsentient evolutionary processes but surely not from an intelligent designer. The author argues, nevertheless, that theologians should welcome rather than disavow these genomic discoveries. The evolutionary sciences can help to emancipate mainstream religions from the age-old theodicy dilemma (the

theological "problem of evil") and thereby return religious inquiry to its rightful realm—not as the ill-equipped interpreter of biological minutiae of our physical existence but rather as a potentially respectable counselor on grander philosophical matters that have always been of "ultimate concern" (32) to theologians and to humanity.

Cultural Evolution and the Uniqueness of Being Human

Darwin closed *The Descent of Man* (5) by noting two fundamental aspects of the human condition that at face value might seem contradictory: ". . . man with all his noble qualities, with sympathy which feels for the most debased, with benevolence which extends not only to other men but to the humblest living creature, with his god-like intellect— . . . still bears in his bodily frame the indelible stamp of his lowly origin." Ever since that time, philosophers as well as biologists have sought to reconcile these two sides of human nature, at times emphasizing our biological similarities and close evolutionary ties to other primate species and at other times accentuating the features that seem to separate *Homo sapiens* from the remainder of the biological world. Indeed, some have argued that Darwin might better have entitled his treatise *The Ascent of Man*. Among the characteristics that might be deemed uniquely human are extensive tool-use, complex symbolic language, self-awareness, death-awareness, moral sensibilities, and a process of cultural evolution that, although necessarily rooted in biology, goes well beyond standard biological evolution per se. Following the reasoning and terminology of the French philosopher Teilhard de Chardin, Dobzhansky (32) argued that two transcendent events have occurred to date in the Earth's history: the ancient emergence of life, which initiated the biosphere and enabled biological evolution, and the recent emergence of intelligence in *Homo sapiens*, which initiated the noosphere ("thinking arena") and enabled cultural evolution. In Part III of these Proceedings, leading academicians with backgrounds ranging from genetics to linguistics and the other humanities reflect in diverse ways upon what it can mean to be uniquely human.

With respect to life-history traits, humans tend to live longer and mature later than our nearest living relatives, the great apes; paradoxically, however, humans and great ape females lose the last of their fertility at similar ages. In other words, human females have exceptional postmenopausal longevity. Hawkes (33) addresses the history of scientific speculation about this evolutionary conundrum, including an elaboration of senescence theories, resource-allocation theories, and especially the "grandmother

hypothesis” that emphasizes the key supportive roles that postreproductive women can play in rearing grandchildren. The author then focuses on life-history comparisons between humans and chimpanzees and describes variation in aging patterns within and among populations of both species that may seem inconsistent with some of the standard assumptions of life-history theory (e.g., that tradeoffs inevitably exist between current and future female reproductive success). To help reconcile these apparent contradictions, Hawkes proposes that individuals differ substantially in their overall “frailties,” so that those who are more robust can enjoy both higher fertility and better survival. Incorporating this idea into life-history theory may offer some fresh insights on human aging.

Culture, which can be defined as the deployment of socially learned information, has been a part of the “human condition” for more than 2 million years (as judged, for example, by the early appearance of stone tools), and it is the proximate reason for our remarkable success as a species. Cultural evolution emerged from biological evolution, and the two processes are similar in some respects but are very different in others (such as in the speeds at which they operate and in their modes of information transmission). Richerson and Boyd (34) develop the case that human genes and human culture co-evolve, with cultural innovations often precipitating environment-mediated changes in natural selection and social selection with feedback effects on gene evolution. They further argue from paleontological and other evidence that gene-culture coevolution has been a dominant process underlying human evolution, perhaps since the initial divergence of hominins from their last shared ancestor with the great apes. Looking forward, the authors see great promise that modern genomic tools may help clarify gene-culture coevolution in several ways: by providing better marker-based assessments of human paleodemography; by detecting genomic footprints of selection and thereby revealing exactly where and when selection took place in the human genome; and by yielding mechanistic insights into the structures and functions of particular genes that have been under natural or social selection (or both).

Culture and cultural evolution are greatly facilitated by another uniquely human characteristic: complex grammatical language, which allows people to share acquired knowledge, to negotiate agreements, and otherwise to interact readily in social contexts. The net result is that our ancestors were able to colonize a previously unoccupied “cognitive niche,” one hallmark of which is enhanced survival

resulting from environmental manipulation through cause-and-effect reasoning and social cooperation. However, even if the evolution of general intelligence and the capacity for language are explicable in terms of the physical and social selective advantages they afforded our ancestors, the question remains as to why our evolved cognitive capabilities extend also to the kinds of abstract reasoning sometimes displayed in, for example, science, philosophy, law, government, and commerce. Pinker (35) reviews the history of speculation about the emergence of abstract intelligence, ranging from standard evolutionary scenarios for how physical and social evolution might have favored bigger brains, to supernatural causation (as was invoked by Alfred Russel Wallace, the codiscoverer of natural selection). The author then develops a somewhat different perspective on abstract intelligence that builds on a longstanding observation in linguistics: People often extend word constructions based on concrete scenarios to more abstract concepts, by analogy. Under Pinker’s scenario of “metaphorical abstraction,” cognitive schemas and social emotions that were important in promoting the capacity for language and adapting humans to the cognitive niche eventually became assembled into increasingly complex mental structures that have been co-opted to perform abstract mental functions they had not originally evolved to promote directly.

Language also is the topic of discussion by Deacon (36), who recounts a long history of often tortuous speculation about how a social capability that appears to be as complex and variable in expression as language might have arisen and come to occupy such a central position in human evolution. The basic problem, as Deacon and some other authors have seen it, is somewhat akin to explaining the emergence of other extravagantly complicated traits that in their initial evolutionary stages are not necessarily of clear utility to their bearers in the struggle for existence; indeed, as discussed by Deacon, at least one well-known modern linguist has argued that language competence did not evolve by standard natural selection because the rudiments of language would not likely have facilitated effective communication. In *The Descent of Man* (5), Darwin at one point resorted to the concept of sexual selection to explain the emergence of language in proto-humans, suggesting that human vocal complexity and the mental capacity it reflects might have evolved in part as a means to attract mates. On the other hand, even a prelinguistic symbolic communication or proto-language probably could have contributed to a novel cognitive niche (34) that in turn imposed novel selective demands for more effective communication on the proto-human brain and on our vocal apparatus. In any event, to add another perspective to the deliberations, Deacon (36) suggests that a relaxation (rather than accentuation)

Box 1. In the Light of Evolution In

1973, Theodosius Dobzhansky penned a short commentary titled, “Nothing in biology makes sense except in the light of evolution” (39). Most scientists agree that evolution provides the unifying framework for interpreting biological phenomena that otherwise can often seem unrelated and perhaps unintelligible. Given the central position of evolutionary thought in biology, it is sadly ironic that evolutionary perspectives outside the sciences often have been neglected, misunderstood, or purposefully misrepresented. Biodiversity—the genetic variety of life—is an exuberant product of the evolutionary past, a vast human-supportive resource (aesthetic, intellectual, and material) of the present, and a rich legacy to cherish and preserve for the future. Two challenges, as well as opportunities, for 21st-century science are to gain deeper insights into the evolutionary processes that foster biotic diversity and to translate that understanding into workable solutions for the regional and global crises that biodiversity currently faces. A grasp of

evolutionary principles and processes is important in other societal arenas as well (e.g., education, medicine, sociology, and other applied fields including agriculture, pharmacology, and biotechnology). The ramifications of evolutionary thought extend into learned realms traditionally reserved for philosophy and religion. The central goal of the *In the Light of Evolution* series is to promote the evolutionary sciences through state-of-the-art colloquia and their published proceedings. Each installment explores evolutionary perspectives on a particular biological topic that is scientifically intriguing but also has special relevance to contemporary societal issues or challenges. Individually and collectively, the *In the Light of Evolution* series will aim to interpret phenomena in various areas of biology through the lens of evolution, to address some of the most intellectually engaging as well as pragmatically important societal issues of our times, and to foster a greater appreciation of evolutionary biology as a consolidating foundation for the life sciences.

of selective pressures at the organismal level may have been the source of many of the complex and synergistic features of the uniquely human capacity for language.

High intelligence, cognition, and the capacity for reasoning that the human brain enables are so central to the human condition as to be inseparable from what makes us uniquely human. These features also are highly adaptive; without them human culture could only be rudimentary at best. But is reasoning a single, all-purpose procedure of the human mind or, alternatively, is it an amalgam of special-purpose (i.e., “domain-specific”) operations, each of which evolved in response to a specific suite of adaptive challenges posed by particular social or physical environments that our ancestors routinely encountered? The former hypothesis is sometimes referred to as the “blank-slate” theory of cognition in traditional psychology, whereas the latter hypothesis tends to be favored by many evolutionary psychologists who envision the evolved architecture of the human mind to include multiple cognitive specializations, each molded by natural selection to solve a particular adaptive problem. Cosmides et al. (37) review the history of these and other ideas about the nature of the neurocognitive system and human intelligence. Based in part on the results of

psychological tests designed to distinguish experimentally between blank-slate and domain-specific operations of human cognition, the authors conclude that the human mind probably contains a multitude of different adaptive specializations for reasoning. One of the most salient of these specialized adaptations, the authors argue, is the hypertrophied human capacity to detect cheaters in social contracts.

Morality is a uniquely human attribute, to which Darwin (5) attached a special significance: “I . . . subscribe to the judgment of those writers who maintain that of all the differences between man and the lower animals the moral sense or conscience is by far the most important.” In the final chapter of these Proceedings, Ayala (38) makes a fundamental distinction between the capacity for ethics (i.e., the human capacity for a moral sense) and the expression of moral norms, which can vary from one human society to another. The former, Ayala argues, is an inevitable byproduct of the biological evolution of high intelligence, which itself arose from selection pressures for other fitness-enhancing capabilities such as bipedalism and tool use. The latter, by contrast, are products of cultural evolution rather than biological evolution. This distinction between morality and moral norms

generally parallels the obvious distinction between the capacity for creative language and the particular languages that happen to be spoken by particular societies. In developing this line of argument, the author invokes the distinction between an adaptation (something targeted quite directly by natural selection—in this case, higher intelligence) and an exaptation (something that arises by being co-opted to serve a positive role other than its original selection-promoted function). Ayala’s distinction between ethics and moral norms is helpful, but it nevertheless leaves open important questions regarding whether and to what extent particular moral norms (as well as a general moral sensibility) are genuinely adaptive for the human groups that display them (as opposed to being nonadaptive or perhaps even maladaptive on some occasions). Such questions no doubt will continue to intrigue sociobiologists and philosophers alike.

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