



Darwin's Living Legacy

A Victorian amateur undertook a lifetime pursuit of slow, meticulous observation and thought about the natural world, producing a theory 150 years ago that still drives the contemporary scientific agenda • • • **BY GARY STIX**

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hen the 26-year-old Charles Darwin sailed into the Galápagos Islands in 1835 onboard the HMS *Beagle*, he took little notice of a collection of birds that are now intimately associated with his name. The naturalist, in fact, misclassified as grosbeaks some of the birds that are now known as Darwin's finches. After Darwin returned to England, ornithologist and artist John Gould began to make illustrations of a group of preserved bird specimens brought back in the *Beagle's* hold, and the artist recognized them all to be different species of finches.

From Gould's work, Darwin, the self-taught naturalist, came to understand how the finches' beak size must have changed over the generations to accommodate differences in the size of seeds or insects consumed on the various islands. "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends," he noted in *The Voyage of The Beagle*, published after his return in 1839.

Twenty years later Darwin would translate his understanding of finch adaptation to conditions on different islands into a fully formed theory of evolution, one emphasizing the power of natural selection to ensure that more favorable traits endure in successive generations. Darwin's

theory, core features of which have withstood critical scrutiny from scientific and religious critics, constituted only the starting point for an endlessly rich set of research questions that continue to inspire present-day scientists. Biologists are still seeking experimental results that address how natural selection proceeds at the molecular level—and how it affects the development of new species.

Darwin's famed finches play a continuing role in providing answers. The scientist had assumed that evolution proceeded slowly, over "the lapse of ages," a pace imperceptible to the short lifetime of human observers. Instead the finches have turned into ideal research subjects for studying evolution in real time because they breed relatively rapidly, are isolated on different islands and rarely migrate.

Since the 1970s evolutionary biologists Peter R. Grant and B. Rosemary Grant of Princeton University have used the Galápagos as a giant laboratory to observe more than 20,000 finches and have shown conclusively how average beak and body size changes in a new generation as El Niños come and go, shifting climate from wet to arid. They have also been able to chronicle possible examples of new species that are starting to emerge.

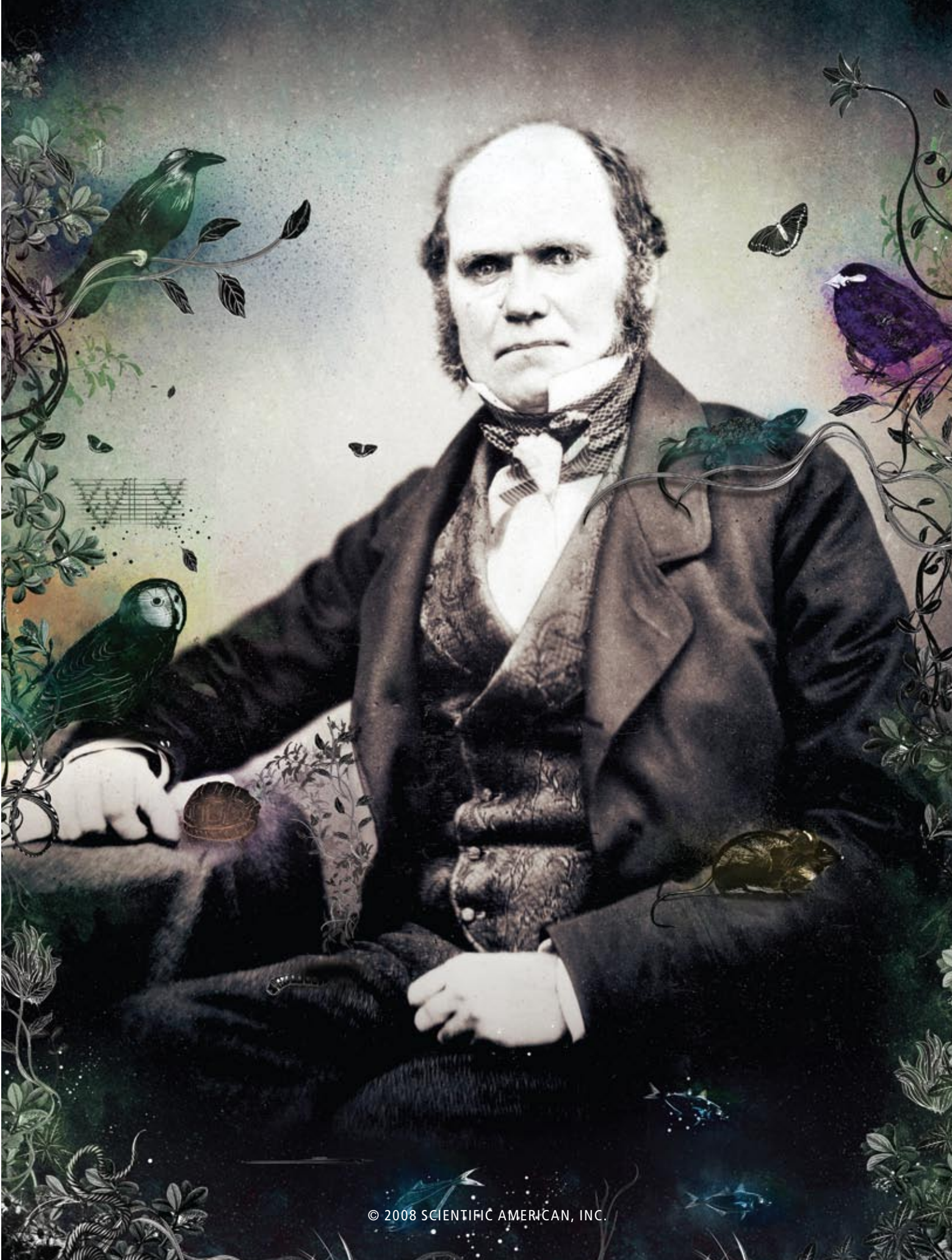
The Grants are just one among many groups that have embarked on missions to witness evo-

KEY CONCEPTS

- Charles Darwin's insights about evolution have withstood 150 years of scrutiny.
- But evolutionary theory has broadened and changed as his ideas have been melded with genetics.
- Evolutionary biology still must contend with some of the same questions that preoccupied Darwin: What, for one, is a species?

—The Editors

DOUG ALVES (illustration); GRANGER COLLECTION (Darwin)



○○○ Evolution before and after Darwin

The concept of evolution stretches back to ancient times. Here are some key events in a history that has been marked by continual change.



1838: Charles Darwin formulates the theory of natural selection, which is not published for more than 20 years.

1859: *On the Origin of Species* sells out as soon as it is published.



1865: Czech monk Gregor Mendel publishes his research on inheritance, but the importance of his work is not recognized for 35 more years.

610–546 B.C.: Greek philosopher Anaximander suggests that all life-forms evolved from fish in the seas and went through a process of modification once they were established on land.



1735: Carl Linnaeus publishes the first volume of *Systema Naturae*, which laid the foundations for taxonomy. Later he suggested that plants descend from a common ancestor.

1871: In *The Descent of Man*, Darwin ties the human lineage to primate ancestors, provoking outrage in some quarters and the caricaturing of his image.



1882: Darwin dies.

1925: The Scopes Monkey trial in Tennessee tries a teacher based on a law that made it illegal to teach any theory that denies divine creation.



APPROACHABLE GENIUS

Darwin's writings were remarkably accessible to any literate person, as is evident in this description of natural selection from the introduction to *Origin of Species*:

"As many more individuals of each species are born than can possibly survive; and as, consequently, there is a frequently recurring struggle for existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be naturally selected. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form."

lution in action, exemplars of how evolution can at times move in frenzied bursts measured in years, not eons, contradicting Darwin's characterization of a slow-and-steady progression. These studies focus on the cichlid fish of the African Great Lakes, Alaskan sticklebacks, and the *Eleutherodactylus* frogs of Central and South America and the Caribbean, among others.

Ruminations on evolution—often musings on how only the fittest prevail—carry an ancient pedigree, predating even Socrates. The 18th and 19th centuries produced fertile speculations about how life had evolved, including ideas forwarded by Darwin's grandfather, Erasmus Darwin, who lived between 1731 and 1802.

Darwinian evolution was the first capable of withstanding rigorous tests of scientific scrutiny in both the 19th century and beyond. Today investigators, equipped with sophisticated cameras, computers and DNA-sampling tools thoroughly alien to the cargo hold of the *Beagle*, demonstrate the continued vitality of Darwin's work. The naturalist's relevance to basic science and practical pursuits—from biotechnology to forensic science—is the reason for this year's worldwide celebration of the bicentennial of his birth and the sesquicentennial of the publication of his masterwork, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life*.

Darwin's theory represents a foundational pillar of modern science that stands alongside relativity, quantum mechanics and other vital support structures. Just as Copernicus cast the earth out from the center of the universe, the Darwinian universe displaced humans as the epicenter of the natural world. Natural selection accounts for what evolutionary biologist Francisco J. Ayala of the University of California, Irvine, has called "design without a designer," a term that parries the still vigorous efforts by some theologians to slight the theory of evolution. "Darwin completed the Copernican Revolution by drawing out for biology the notion of nature as a lawful system of matter in motion that human reason can explain without recourse to supernatural agencies," Ayala wrote in 2007.

In this anniversary year, Darwin's greatest bequest can be found in the enormous body of research and theorizing that extends directly from his writings. It also serves to underline how evolution itself has undergone radical alteration in the past 150 years, a merger of the original theory with the science of the gene, which Darwin had as little understanding of as the ancients did.

This special issue of *Scientific American* highlights major questions that are still being addressed: How common is natural selection? To what extent does natural selection actually occur at the molecular level of the gene? What is



1809: Darwin (shown opposite his younger sister) is born in Shrewsbury, England, into the comfort of a wealthy family.

1830: Charles Lyell publishes *Principles of Geology*, a formative influence on Darwin's thinking about the gradualism of natural processes as can be witnessed in the Grand Canyon (right).



1831: Darwin leaves on a five-year around-the-world journey on the HMS *Beagle*.

1936–1947: The modern synthesis combines Darwin's evolutionary theory with Mendelian genetics.

1953: James D. Watson and Francis Crick discover the structure of DNA, making it possible to study the molecular biology of evolution.



Mid-2000s: Genetic analyses have shown evidence of relatively recent human evolution—dating back several thousand years.

2009: Darwin Day marks the naturalist's birthday on February 12 and will be observed with dozens of events in at least 10 countries. Stay abreast of what's happening at www.darwinday.org



the origin of the genetic variation on which natural selection operates? Does it work by administering a fitness test to individual genes, whole organisms, or even entire groups of animals, plants or microbes? Does it apply to humans if they are able to exercise a rigid control over their environment and even their biology?

A Naturalist by Nature

Like Albert Einstein and others gifted with genius, Darwin marched to his own drumbeat. He showed no signs of academic precociousness. Born into a well-to-do family in the English countryside, the young Darwin was a decidedly mediocre student who hated the regimentation of a curriculum centered on the classics. (Einstein was a rebellious youth and an erratic university student.) Following his father's desire, Darwin entered medical school but was repulsed by cutting open a human cadaver and never finished his studies. Paradoxically, he had little problem killing birds and small animals when hunting, just one of the tasks he set for himself on forays to watch wildlife and collect specimens.

Despairing that Charles would ever amount to anything, Robert Darwin ordered his second son to apply to the University of Cambridge to obtain a degree that would allow him to join the clergy. The man whose ideas are viewed by some clerics as a fundamental insult to religious faith graduated (barely) with a degree in theology.

Although his father tried to dissuade him, Darwin jumped at the offer to become a naturalist onboard a survey ship named the *Beagle*, an experience he would later characterize as “the first real training or education of my mind.” The five-year, around-the-globe journey provided exposure to the natural world—and ample time for contemplation—that shaped his later thinking.

Milestones along the way included experiencing the great diversity of species in tropical Brazil and discovery of fossils, including a giant sloth 400 miles south of Buenos Aires, which caused him to ponder how these creatures became extinct. Accounts by gauchos on the Argentine pampas of their killing of indigenous peoples taught him about the primal, territorial impulses of the human animal. And of course, there was the relatively brief, five-week stay in the “frying hot” Galápagos, where he was able to contemplate how closely related species of turtles and mockingbirds inhabited neighboring islands, implying a common ancestry for both groups.

At sea, Darwin also read avidly two volumes of Charles Lyell's *Principles of Geology* that embraced the idea of “uniformitarianism” in which the processes of erosion, sedimentation and volcanic activity occurred in the past at about the same rates as they do now. Lyell rejected the then prevailing catastrophism, which holds that sudden, violent events driven by supernatural forces had driven the shaping of the landscape.

THE QUOTABLE MR. DARWIN

Darwin's wit extended from the natural sciences to his own work habits. Here is a sampling:

“Man still bears in his bodily frame the indelible stamp of his lowly origin.”

“It is a cursed evil to any man to become as absorbed in any subject as I am in mine.”

“My mind seems to have become a kind of machine for grinding laws out of large collections of facts.”

“To kill an error is as good a service as, and sometimes even better than, the establishing of a new truth or fact.”

SOCIAL DARWINISM and the eugenics movement that flourished in the late 19th and early 20th centuries were pseudoscientific attempts, now discredited, to apply Darwin's ideas to social planning. Below, a German anthropologist attempts to ascertain ethnic characteristics from the eye.



A trek inland in the Andes, where the explorers found an ancient marine deposit uplifted to 7,000 feet, helped to bring Lyell's ideas vividly to life.

Darwin had no awareness that he had embarked on a trip that would forever transform the biological sciences. The 57-month journey produced no moment of sudden realization, nothing equivalent to Einstein's "*annus mirabilis*" of 1905 in which he published papers about special relativity, Brownian motion and other themes. The treasure trove of the journey was what today could be called an immense database: a collection of 368 pages of zoology notes, 1,383 pages of geology notes, a 770-page diary, in addition to 1,529 species in bottles of alcohol and 3,907 dried specimens, not to mention live tortoises caught in the Galápagos.

By the time the *Beagle* returned to England in October of 1836, Darwin's letters, along with some specimens, had circulated among British scientists, cementing his reputation as a peer. This recognition assured that his father's aspirations for his son's place in the clergy were cast aside. Within a few years Darwin married a first cousin, Emma Wedgwood, and then moved to a country estate whose gardens and greenhouses would provide a living laboratory for his work until his death, an existence made possible by the family's substantial wealth. Unexplained illness, with symptoms ranging from headaches to heart flutters to muscle spasms, plagued Darwin after the expedition until he died in 1882, quashing any thoughts of further expeditions.

Origins of a Theory

Darwin had begun to formulate his theories by the late 1830s, but he waited for two decades to publish (and then only under pressure from a competitor, Alfred Russel Wallace) because he wanted to ensure that his facts and arguments were beyond reproach.

The process of theory building crept along at an almost glacial tempo. From his readings of Lyell, Darwin took the idea of gradual change in the geological landscape and reasoned that it must also apply to biological organisms: one species must beget another. The recognition of biology's mutability was shared by some other evolutionary thinkers of the day. But it was conceived as a *scala naturae*—an ascending ladder in which each lineage of plant or animal arose by spontaneous generation from inanimate matter and then progressed inexorably toward greater complexity and perfection.

Darwin rejected this straight-line progression in favor of what is now called branching evolution, in which some species diverge from a common ancestor along separate pathways, contradicting the prevailing view that there are fixed limits on how far a new species can diverge from an ancestral one. Darwin recalled that three species of mockingbird he observed in the Galápagos could be traced to a single colonization of a related species he had observed in Latin America. His sketch of a branching "tree of life" is the only illustration in *Origin of Species*.

The concept of a tree of life still begged a "how" for evolution, a gap that led to Darwin's most revolutionary idea, the theory of natural selection. From reading the work of Thomas Malthus, Darwin recognized that populations tend to grow quickly, thereby overwhelming limited resources. He also had an obsession with animal and plant breeding. He would visit agricultural markets and collected plant catalogues.

In 1838 he came to the realization (shared at first with only a few friends) that the natural world, instead of deliberately choosing favorable traits as if it were a cattle breeder, has its own way of addressing a bulging demographic that threatens to exhaust an ecological niche. From the vast hereditary diversity within a given species, natural selection blindly weeds out those individuals with less favorable traits: in essence, Ayala's concise "design without a designer." Moreover, if two populations of the same species remain isolated—one in a desert, the other in the mountains—they may over long periods develop into wholly separate species, no longer able to breed.



TREE OF LIFE, originally sketched by Darwin in 1837 (below), still exists as a highly intricate, multi-dimensional computer model (left) that shows how evolution proceeds in branching descent but also through lateral transfer of genes among microorganisms (red lines).

Origin of Species was rushed to publication in 1859 because Wallace had a manuscript that came to virtually identical conclusions. The first 1,250 copies of the 155,000-word “abstract” immediately sold out. The clarity and accessibility of Darwin’s argument stood out. No quips came forth, as they did for Einstein’s theories, about how only three people on the rest of the planet could understand his work.

Darwin spent the rest of his life continuing to explore natural selection firsthand with orchids and other plants at his country estate in Downe, 16 miles south of London. He left it to others to defend his work. The publication provoked controversy that continues to this day in the form of creationist debates that still dog public school boards. An article that appeared in *Scientific American* on August 11, 1860, described a meeting of the British Academy of Sciences at which a “Sir B. Brodie” rejected Darwin’s hypothesis, saying: “Man had a power of self-consciousness—a principle differing from anything found in the material world, and he did not see how this could originate in lower organisms. This power of man was identical with the divine intelligence.” But even then, Darwin had many defenders among leading scientists. At the same conference, the periodical reported, the renowned Joseph Hooker told the bishop of Oxford, another critic in attendance, that the cleric simply lacked any understanding of Darwin’s writings.

Darwin had avoided discussion of human evolution in *Origin of Species*, but his *The Descent of Man, and Selection in Relation to Sex* attributed human beginnings to Old World monkeys, an assertion that also offended many and made



MORE TO EXPLORE

What Evolution Is. Ernst Mayr. Basic Books, 2002.

The Cambridge Companion to Darwin. Edited by Jonathan Hodge and Gregory Radick. Cambridge University Press, 2003.

On the Origin of Species: The Illustrated Edition. Charles Darwin. Edited by David Quammen. Sterling, 2008.

The Complete Works of Charles Darwin Online can be accessed at <http://darwin-online.org.uk>

its way into cartoonish newspaper caricatures of the scientist as half-man, half-ape. Even in the 1860s Darwin’s cousin, Francis Galton, and others had begun to complain that modern society protects its “unfit” members from natural selection. The distortion and misunderstanding of Darwinism, from Nazi ideologues to neoliberal economists to popular culture, have yet to cease. American novelist Kurt Vonnegut once remarked that Darwin “taught that those who die are meant to die, that corpses are improvements.”

The concept of evolution as a form of branching descent from a common ancestor achieved a relatively rapid acceptance, but accommodation for natural selection came much more slowly, even within the scientific community. The hesitation was understandable. In his work, Darwin had not described a mechanism for inheritance, attributing it to minuscule, hypothetical “gemmules” that ejected from each tissue and traveled to the sex organs, where copies were made and passed to subsequent generations. It took until the decades of the 1930s and 1940s for natural selection to gain broad acceptance.

It was then that the modern synthesis emerged as an expansive framework that reconciled Darwin’s natural selection with the genetics pioneered by Gregor Mendel. In 1959, the centennial of the publication of *Origin of Species*, the place of natural selection seemed assured.

But in the ensuing years, the scope of evolutionary biology has had to broaden still further to consider such questions as whether the pace of evolution proceeds in fits and starts—a paroxysm of change followed by long periods of stasis. Do random mutations frequently get passed on or disappear without enhancing or diminishing fitness, a process called genetic drift? Is every biological trait an evolutionary adaptation, or are some characteristics just a random by-product of a physical characteristic that provides a survival advantage?

The field has also had to take another look at the notion that altruistic traits could be explained by natural selection taking place across whole groups. And as far as the origin of species, what role does genetic drift play? Moreover, does the fact that single-celled organisms often trade whole sets of genes with one another undermine the very concept of species, defined as the inability of groups of organisms to reproduce with one another? The continued intensity of these debates represents a measure of the vigor of evolutionary biology—as well as a testament to Darwin’s living legacy. ■