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The Darwin Legacy

An examination of Charles Darwin's On the Origin of Species — and how, 150 years after publication, his ideas have been applied and adapted in a host of different areas.

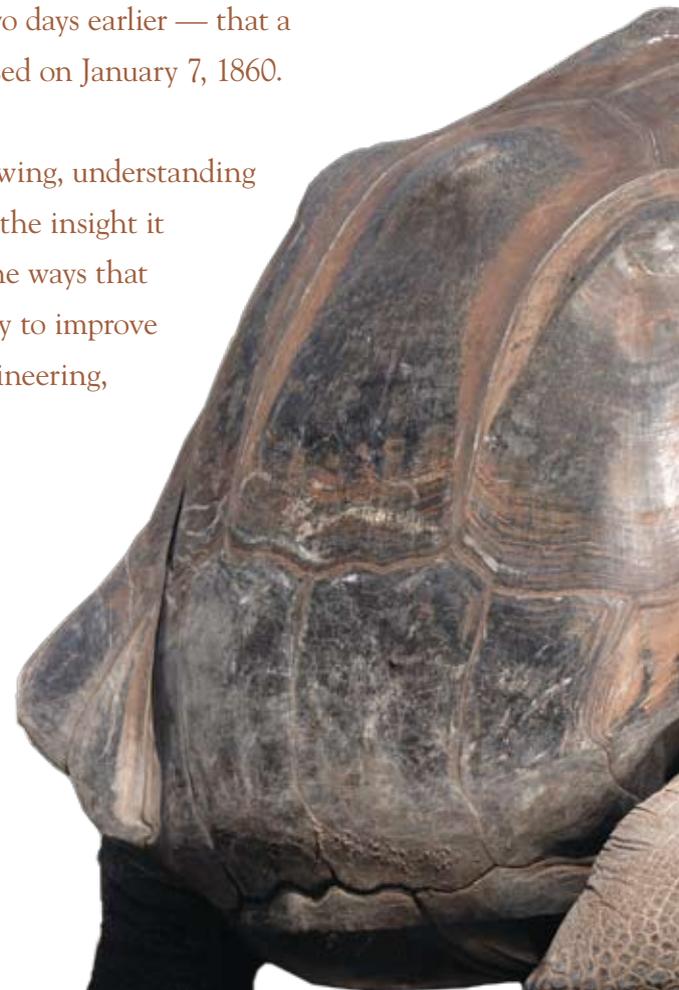
BY WADE WORTHEN

Earlier this year, we marked the 200th anniversary of the day when Abraham Lincoln and Charles Darwin were both born: February 12, 1809.

But 2009 also marks another important and related milestone. One hundred and fifty years ago, on November 24, 1859, the first edition of Darwin's *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, went on sale to the public. Sales were so brisk — booksellers had purchased all available copies two days earlier — that a second edition of more than 3,000 copies was released on January 7, 1860.

Given that this is a milestone year, it is worth reviewing, understanding and celebrating Darwin's work, not only because of the insight it provides to understanding biology, but because of the ways that the concepts of natural selection are employed today to improve systems in fields as diverse as computer science, engineering, chemistry and business.

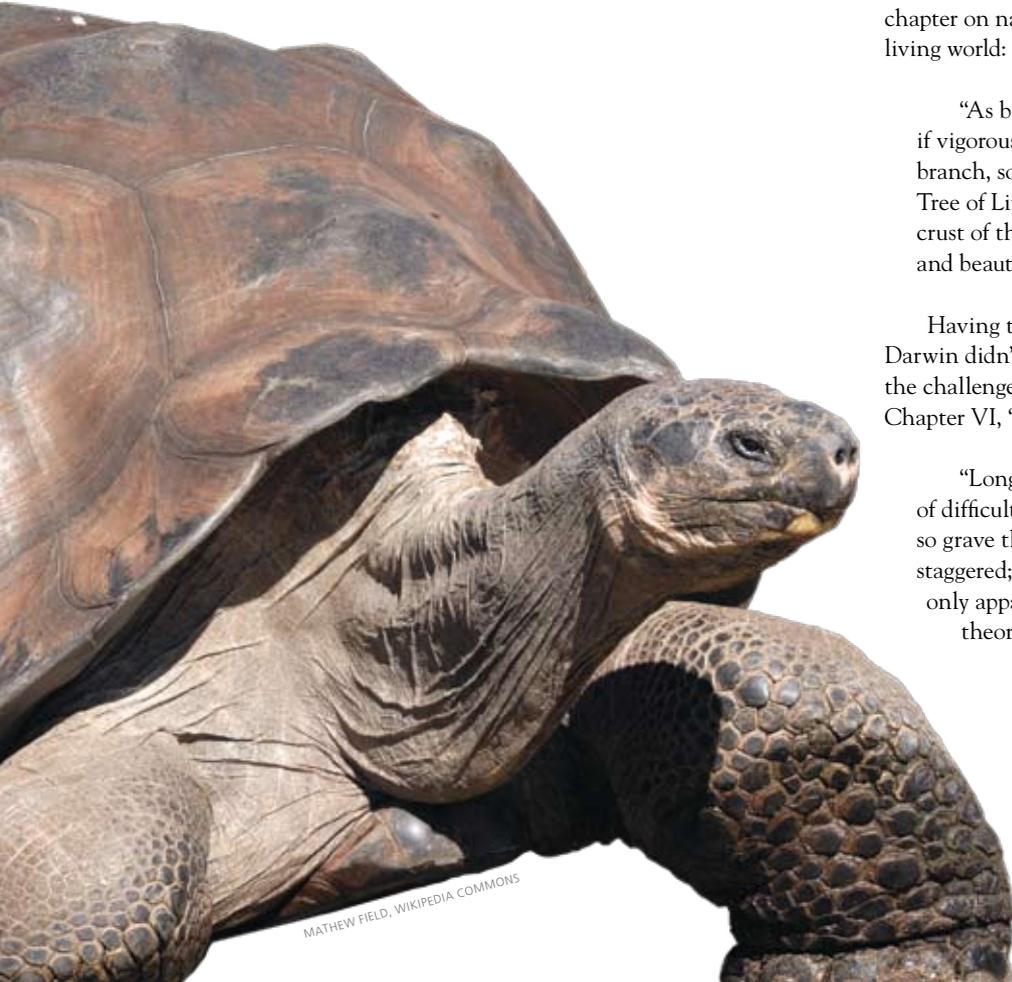
Darwin visited the Galápagos Islands in the 1830s. His studies there served as the basis of his theories. The variation in shell characteristics of tortoises in the Galápagos influenced his belief in a causal relationship between the characteristics of organisms and their environments.



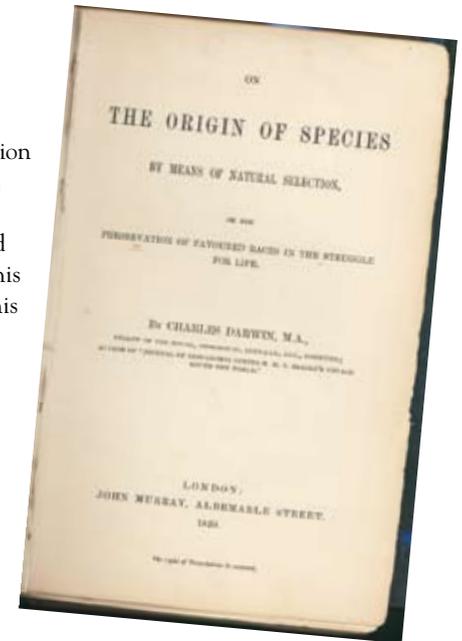
Darwin summarized his thesis of evolution by natural selection in his book's introduction:

“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. . . .

“Although much remains obscure, and will long remain obscure, I can entertain no doubt, after the most deliberate study and dispassionate judgment of which I am capable, that the view which most naturalists entertain, and which I formerly entertained — namely, that each species has been independently created — is erroneous. I am fully convinced that species are not immutable; but that those belonging to what are called the same genera are lineal descendants of some other and generally extinct species, in the same manner as the acknowledged varieties of any one species are the descendants of that species. Furthermore, I am convinced that Natural Selection has been the main but not exclusive means of modification.”



MATHEW FIELD, WIKIPEDIA COMMONS



Darwin knew natural selection was a provocative — even heretical — idea. And he knew that its acceptance would depend both on the weight of his evidence and the structure of his argument.

For this reason, he began *On the Origin of Species* with observations and principles that his readers already knew — that through selected breedings humans had created different domesticated breeds and varieties from common ancestral stocks. Although references to breeds of cattle, sheep and pigeons can be tough going for the modern reader, these breeds were well known in Victorian England, and this common knowledge created a solid foundation for his argument.

Darwin then extrapolated from animal husbandry and horticulture to nature, suggesting that populations diverged from one another when naturally selected by different environmental conditions. He ended the chapter on natural selection with a new vision of a dynamic, responsive, living world:

“As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications.”

Having taken the reader to new and perhaps uncomfortable ground, Darwin didn't push the issue. Rather, he used several chapters to address the challenges, shortcomings and apparent inconsistencies with his theory. Chapter VI, “Difficulties of the Theory,” opens:

“Long before having arrived at this part of my work, a crowd of difficulties will have occurred to the reader. Some of them are so grave that to this day I can never reflect on them without being staggered; but, to the best of my judgment, the greater number are only apparent, and those that are real are not, I think, fatal to my theory.

“These difficulties and objections may be classed under the following heads: Firstly, why, if species have descended from other species by insensibly fine gradations, do we not everywhere see innumerable transitional forms? Why is not all nature in confusion instead of the species being, as we see them, well defined?”

“Secondly, is it possible that an animal having, for instance, the structure and habits of a bat, could have been formed by the modification of some animal with wholly different habits? Can we believe that natural selection could produce, on the one hand, organs of trifling importance, such as the tail of a giraffe, which serves as a fly-flapper, and, on the other hand, organs of such wonderful structure, as the eye, of which we hardly as yet fully understand the inimitable perfection?”

Darwin argued that transitional forms between species are rare because, through natural selection, better adapted forms supplant their more poorly adapted ancestors and neighbors. This creates the divergence and discontinuity between the species that we see in nature.

For a theory that described change through time, however, the absence of continuous sequences of transitional fossils was more disturbing. Darwin addressed this in two ways. First, he suggested that intermediates might not be what one might expect:

“In the first place it should always be borne in mind what sort of intermediate forms must, on my theory, have formerly existed. I have found it difficult, when looking at any two species, to avoid picturing to myself, forms directly intermediate between them. But this is a wholly false view; we should always look for forms intermediate between each species and a common but unknown progenitor; and the progenitor will generally have differed in some respects from all its modified descendants. To give a simple illustration: the fantail and pouter pigeons have both descended from the rock-pigeon; if we possessed all the intermediate varieties which have ever existed, we should have an extremely close series between both and the rock-pigeon; but we should have no varieties directly intermediate between the fantail and pouter; none, for instance, combining a tail somewhat expanded with a crop somewhat enlarged, the characteristic features of these two breeds.”

In other words, we should not expect the common ancestor of whales and cows to look like “Bossie,” but with a tail fluke and flippers. Rather, the common ancestor, which modern genetic and paleontological evidence places at approximately 65 million years ago, was probably a small, non-descript herbivore that looked nothing like a modern cow or whale.

But the real culprit, Darwin argued, was the “imperfection” of the fossil record. Because fossilization is rare and because strata are laid down discontinuously at a given place, it is impossible for the rock record to preserve a history of the continuous changes that have occurred in a lineage over time.

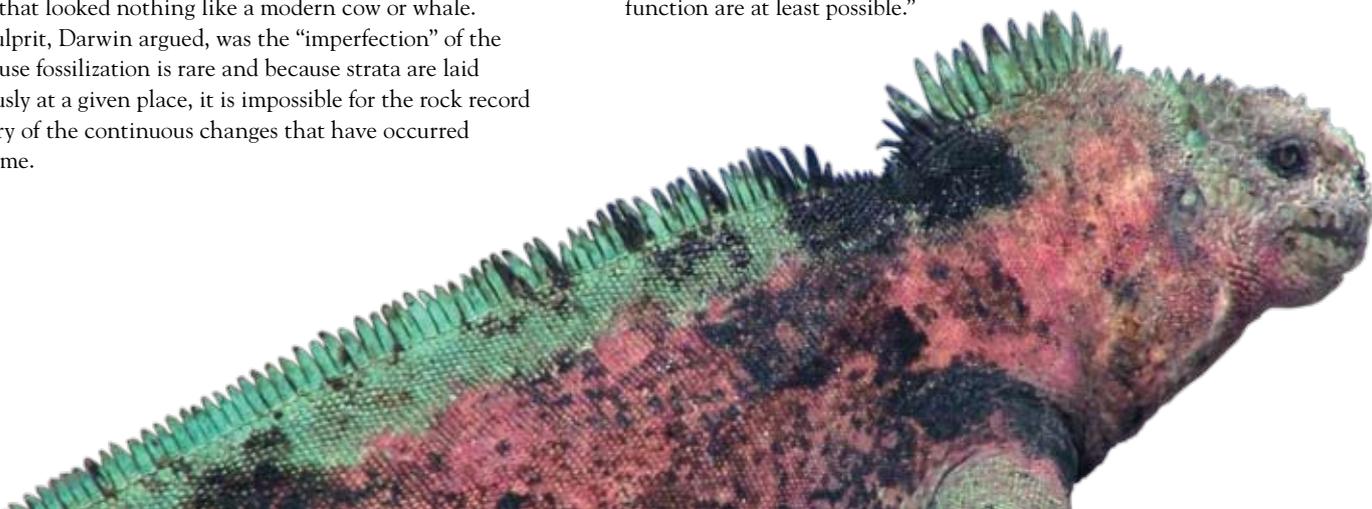
These chapters were critically important to Darwin’s argument. Even during his time there were strong, pre-existing, institutionalized arguments against evolution and transmutation.

Although evolutionary ideas were part of the general cultural discussion in Europe in the early 1800s, they had not gained much traction. The battle in France between the evolutionary “transformationist” Lamarck and the creationist “catastrophist” Cuvier had been won by Cuvier, and the tone in England was set by William Paley’s 1802 publication, *Natural Theology; or, Evidences of the Existence and Attributes of the Deity*. *Natural Theology* and Paley’s other great works, *The Principles of Moral and Political Philosophy* and *Evidences of Christianity*, were required reading at English universities, where all faculty were ordained in the Church of England.

Paley’s “watchmaker analogy” asserted that the complexity and interdependence of the natural world — from single complex structures, like the eye, to the entire economy of nature — required and proved the existence of a supreme designer, just as the existence of a watch composed of complex, integrated pieces implied the existence of a watchmaker. It was a powerful reiteration of the argument made in *Summa Theologica* by Saint Thomas Aquinas, who saw proof of God in the purposeful action of unintelligent things, “as the arrow is shot to its mark by the archer.”

Rather than ignoring these arguments, Darwin knew they must be rebutted. He used Paley’s exemplar of design — the eye — and referenced the variation that exists in the visual systems of mollusks, from light-sensitive cells in limpets to the camera eye of squid. When we see this continuity of structure among organisms today, it raises the possibility that this continuum could have occurred through time as an evolutionary sequence. In short, Darwin answered his critics with this admonition:

“Although the belief that an organ so perfect as the eye could have been formed by natural selection, is more than enough to stagger any one; yet in the case of any organ, if we know of a long series of gradations in complexity, each good for its possessor, then, under changing conditions of life, there is no logical impossibility in the acquirement of any conceivable degree of perfection through natural selection. In the cases in which we know of no intermediate or transitional states, we should be very cautious in concluding that none could have existed, for the homologies of many organs and their intermediate states show that wonderful metamorphoses in function are at least possible.”



Having offered his mechanism and addressed his critics, Darwin used the last portion of *Origin* to demonstrate the extraordinary explanatory power of his ideas. He showed how his model of common ancestry and descent with modification explained why the distribution of living species often correlated with the distribution of similar but extinct forms, and why very similar living species often have neighboring ranges. In this way, Darwin's evolutionary model provided a logical and testable explanation of the distribution of species in space and time.

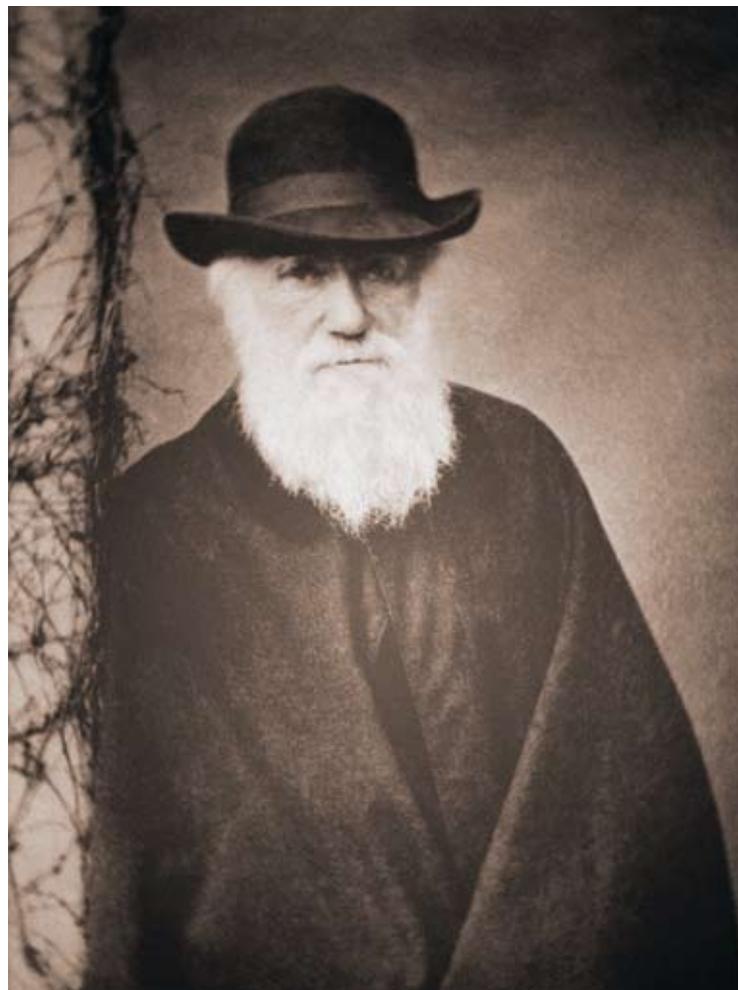
In addition, he showed that common descent explained the underlying structural and anatomical similarities within particular groups of organisms. Similarities between the limb-bones in mammals as different as whales and bats could be explained as a rather embarrassing limitation of design or as a historical product of common ancestry. Likewise, non-functional structures that are inconsistent with design arguments — like leg and hip bones in whales — could also be explained by common ancestry.

With example after example, Darwin marched through geology, paleontology, biogeography, comparative anatomy and embryology, showing that the patterns that had been described by science were best explained by this new model of common ancestry and evolutionary divergence by natural selection. He summarized the details of his thesis in a powerful “recapitulation,” which begins:

“As this whole volume is one long argument, it may be convenient . . . to have the leading facts and inferences briefly recapitulated. That many and grave objections may be advanced against the theory of descent with modification through natural selection, I do not deny. I have endeavoured to give to them their full force. Nothing at first can appear more difficult to believe than that the more complex organs and instincts should have been perfected, not by means superior to, though analogous with, human reason, but by the accumulation of innumerable slight variations, each good for the individual possessor. Nevertheless, this difficulty, though appearing to our imagination insuperably great, cannot be considered real if we admit the following propositions, namely, — that gradations in the perfection of any organ or instinct, which we may consider, either do now exist or could have existed, each good of its kind, — that all organs and instincts are, in ever so slight a degree, variable, — and, lastly, that there is a struggle for existence leading to the preservation of each profitable deviation of structure or instinct. The truth of these propositions cannot, I think, be disputed.”

Throughout this chapter, Darwin directly challenged the opinions of those who supported the premise that species are independently created. He suggested that his model would stimulate new and exciting questions

Darwin published six editions of *Origin* before his death in 1882. He found that marine iguanas varied between the islands of the Galápagos, suggesting that divergence in species might occur in different, isolated environments.



about the source of heritable variation and the complex relationships among organisms that act as selective pressures. He thus predicted the explosive growth of genetics and ecology in scientific literature:

“It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us . . . Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.”

Among the wonders of the Galápagos are more than 120 species of crabs; seven different species of lava lizards are believed to have evolved from one species; male frigate birds puff out their red chests as courting displays. **Opposite:** Many species in the Galápagos, like the flightless cormorant, exist nowhere else on Earth. Darwin asked why this small, isolated archipelago would hold so many unique forms. Photos courtesy Yancey Greene and Wade Worthen except as noted.



Darwin provided a new, testable explanation for why living things are as they are. He suggested that the characteristics and origins of living species could be explained as a consequence of physical, natural processes that could be understood through careful examination, study and experimentation. In short, he moved questions about why organisms are as they are, and how they came to be that way, from the exclusive purview of theology to the domain of science.

In the ensuing 150 years, scientific investigations in paleontology, ecology, comparative anatomy, cell biology, genetics and molecular biology have confirmed, extended and illuminated Darwin's seminal ideas of common ancestry (pattern) and natural selection (process). But, like a living organism, Darwin's theory of evolution by natural selection did not arise spontaneously.

Its evolution was influenced both by ancestral ideas and the immediate cultural environment. Nor did it emerge in isolation; several other authors, most famously Alfred Russel Wallace, conceived of the process of natural selection in some form. Darwin recognized their ideas in "An Historical Sketch of the Recent Progress of Opinion on the Origin of Species" that was included in the third and later editions of *Origin*.

On the Origin of Species had a prolonged and difficult germination, and the wintry reception it at first received did not bode well for its long-term survival. But with each new test came confirmation, and the theory of evolution by natural selection grew stronger until it was finally unified with our understanding of genetics and heritable variation during the 1940s.

Darwin's model explains how living systems can become more complex and adapt to their environment over time. Selection can be a creative force that, by increasing the frequency of individuals with different but adaptive traits, also increases the frequency of matings between them and the frequency of organisms with combinations of adaptive traits that did not exist before. In this cumulative way, and with the continued production of new variations, selection favors organisms with better and better combinations of traits that work well together as a complex living system.

Improvement by natural selection will occur in any system in which

variation is induced, the different varieties are "evaluated" by some performance criteria, and the system that performs best is replicated with new variations. Through this repeated process of replication with variation, evaluation and selection, the performance of a system can be optimized.

The beauty of this process is that it is not constrained by the limited imagination of a designer who purposefully searches through possible designs. Rather, a broader, random search is more likely to find functional solutions that selection and new variations can improve. The power of natural selection, and the speed with which it acts, is limited only by the number of slightly different variants or recombinants that can be produced in a "generation," the time it takes to replicate a generation, the time it takes for the evaluation process, and the size of the design space.

As the number of variables and the number of possible states of each variable increase, the design space gets much larger. Searching for an optimal solution in this design space is truly like searching for a functional needle in a stack of useless hay.

However, modern computers allow us to search the design space relatively rapidly. Many fields in both the natural and social sciences now apply natural selection as a design process, to search a vast design space for combinations of variables that maximize a system's performance. These search strategies are rightly called "genetic" or "evolutionary" algorithms. Like Darwinian selection in biological systems, computational algorithms can create designs where the pieces work well together in ways that a human designer may not have considered.

The idea of genetic algorithms originated in the 1960s with John Henry Holland and others, who realized that the advent of computing power would allow for an efficient search through a design space for an optimal solution by introducing variation, evaluating the products, selecting the best one, and repeating the process. Holland's books — *Adaptation in Nature and Artificial Systems* (1975), *Hidden Order: How Adaptation Builds Complexity* (1995) and *Emergence: From Chaos to Order* (1998) — are testimonies to the creative power of repeated selection acting on variable systems.



There are several examples of practical applications of evolutionary algorithms employed today. One comes from a field called evolutionary electronics, which was first employed to configure digital gates on computer chips to perform a particular function with greatest efficiency.

At first, the initial routing pattern was set by a human designer. Now, however, routing patterns can be fully automated from the outset, designed by the process of selection acting on novel variants. Many of these circuits outperform those of human design.

Evolutionary algorithms have been used in nearly every type of engineering to optimize such things as water flow and distribution through cities, load distribution and structural supports in bridge design, and the effectiveness of certain chemicals and drugs. Computers sort through the “design space” of particular molecular structures to create chemicals with certain characteristics and specific pharmacological or industrial applications.

In addition, genetic algorithms can adapt to changing environments. This is Artificial Intelligence, where computers learn to do new things by generating variable algorithms that achieve new goals with progressively greater efficiency. These adaptive algorithms are such a useful tool for improving production that they can be applied to nearly any business or production situation.

In this context, it is ironic that Darwin’s ideas are still stigmatized and rejected by people who remain committed to the ideas of independent creation and static design. For after 150 years of empirical testing and practical application, Darwin’s hypotheses have been confirmed, validated and applied.

In short, evolution by natural selection works — and there can be no higher praise for a scientific idea. So celebrate!

The author has taught biology at Furman since 1988. He thanks Kevin Treu, chair of the Department of Computer Science, for his assistance with this article.

For more information

The Complete Works of Charles Darwin on-line (<http://darwin-online.org.uk>). The site provides text, scans and PDF access to all of Darwin’s publications, including the first six editions (edited by Darwin) of *On the Origin of Species*; *Life, Letters, and Autobiography*; *The Voyage of the Beagle* (originally published as *Journal of Researches*); *Descent of Man*; and a collection of lesser known works that reinforced or extended his ideas.

Ernest Mayr, *One Long Argument: Charles Darwin and the Genesis of Modern Evolutionary Thought* (Harvard University Press, 1991).

On the evolution of Darwin’s thinking:

Ben Fry, <http://benfry.com/traces>. Uses color coding to depict the changes in Darwin’s thinking by highlighting his revisions over six editions of *On the Origin of Species*. The site was featured in the October 5, 2009, issue of *Newsweek*, which says Fry uses modern technology to allow readers to “Watch, in short, the theory of evolution evolve.” Fry is director of a laboratory in Cambridge, Mass., that focuses on understanding complex data.

On genetic algorithms in science and technology:

D.E. Clark, editor, *Evolutionary Algorithms in Molecular Design* (Wiley-VCH, 2000).

J.R. Koza, *Genetic Programming: On the Programming of Computers by Means of Natural Selection* (MIT Press, 1992).

R.S. Zebulum, M.A. Pacheco and M.M.B.R. Vellasco, *Evolutionary Electronics: Automatic Design of Electronic Circuits and Systems by Genetic Algorithms* (CRC Press, 2001).

