Darwin at 200

Francisco J. Ayala¹ and John C. Avise

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

harles Robert Darwin was born on February 12, 1809 (the same day as President Abraham Lincoln). In 1859 Darwin published *On the Origin of Species by Means of Natural Selection* (1), his most important book and the one by which he has become best known to posterity. Thus, 2009 is a double anniversary: the 200th of Darwin's birth and the sesquicentenary of *Origin*.

Darwin is deservedly credited as the originator of the modern theory of evolution. In Origin he gathered the best available evidence for evolution: 2 chapters dedicated to the geological record, 2 chapters to biogeography, and 1 chapter to comparative anatomy and embryology. The other 9 chapters (I-VIII and XIII) are mostly dedicated to natural selection, the process that accounts for the adaptation, common descent, and diversity of organisms. He explains how natural selection works, discusses the role of hereditary variation (the mechanics of which were not well understood in Darwin's time), and considers possible objections to his theory.

Darwin's "My Theory"

The discovery of natural selection, Darwin's awareness that it was a significant discovery, and Darwin's designation of natural selection as "my theory" can be traced to Darwin's Transmutation Notebook D, written between July and October 1838, not long after returning (on October 2, 1836) from his 5-year voyage around the world on the HMS Beagle. From then until his death in 1882, Darwin's life would be dedicated to substantiating natural selection and its companion postulates, mainly the pervasiveness of hereditary variation and the enormous fertility of organisms, which much surpassed the capacity of available resources. Natural selection became for Darwin "a theory by which to work." He relentlessly pursued observations and performed experiments to test the theory and resolve presumptive objections. These studies were reported in numerous papers and in volumes dedicated to barnacles (fossil and living), to orchids and their fertilization by insects, to insectivorous and to climbing plants, to earthworms, and much more.

The evolution of organisms was commonly accepted by naturalists in the middle decades of the 19th century. The

www.pnas.org/cgi/doi/10.1073/pnas.0900798106

distribution of exotic species in South America, in the Galápagos Islands and elsewhere, and the discovery of fossil remains of long-extinguished animals, confirmed the reality of evolution in Darwin's mind during his voyage on the Beagle. The intellectual challenge was to explain the origin of distinct species of organisms and how they adapted to their environments, that "mystery of mysteries," as it had been labeled by Darwin's older contemporary, the prominent scientist and philosopher Sir John Herschel (1792–1871). As Darwin wrote in his Autobiography, "I had always been much struck by such adaptations, and until these could be explained it seemed to me almost useless to endeavor to prove by indirect evidence that species have been modified" (2).

The advances of physical science accomplished by the "Copernican Revolution" of the 16th and 17th centuries had brought the workings of the universe under the domain of science: explanation by natural laws that can be tested by observation and experiment. The fundamental commitment was to the postulate that the universe consists of matter in motion governed by natural laws. All physical phenomena could be accounted for as long as the causes became adequately known. However, the origin and configuration of living creatures had been left out, because it seemed that the complex design of organisms could not have come about by chance, or by the mechanical laws of physics, chemistry, and astronomy. This notion had been argued at length by philosophers and theologians. William Paley, for example, made the case with considerable biological detail in his Natural Theology (1802), a book that Darwin read as part of his studies at Cambridge University (3).

It was Darwin's genius to resolve this exclusion with his theory of natural selection. 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 or extranatural agencies. The origin and adaptations of organisms in their profusion and wondrous variations were thus brought into the realm of science.

In his *Autobiography* (2), Darwin wrote,

The old argument of design in nature, as given by Paley, which formerly seemed to me so conclusive, falls, now that the law of natural selection has been discovered. We can no longer argue that, for instance, the beautiful hinge of a bivalve shell must have been made by an intelligent being, like the hinge of a door by a man.

Darwin's theory was, first and foremost, the theory of natural selection; or, at least, of evolution "by means of natural selection," as in the title of *Origin*.

Darwin to Molecular Biology

Darwin and other 19th-century biologists found compelling evidence for biological evolution in the comparative study of living organisms, in their geographic distributions, and in the fossil remains of extinct organisms. Since Darwin's time, the evidence from these sources has become stronger and more comprehensive, and biological disciplines that emerged more recently genetics, biochemistry, ecology, behavior (ethology), neurobiology, and especially molecular biology—have supplied powerful additional evidence and detailed confirmation.

Darwin surely would have been pleased by the enormous accumulation of paleontological evidence, including the discovery of fossils of organisms transitional between major groups, such as Archaeopteryx, intermediate between reptiles (dinosaurs) and birds, and Tiktaalik, intermediate between fish and tetrapods (4), and the numerous fossils and diverse species of hominins, intermediate between apes and Homo sapiens (e.g., refs. 5-7). But there are good reasons to believe that Darwin would have been most pleased and most impressed with the overwhelming evidence for evolution provided by molecular biology, a compelling and precise source of documentation that Darwin could not have imagined.

Throughout 2009 PNAS will publish several collections of articles examining various aspects of evolution and evolutionary theory. These collections include In Light of Evolution III: Two Centuries of Darwin; Biogeography, Changing Climate, and Niche Evolution; Out of Africa; Plant and Insect Biodiversity; and Evolution in Health and Medicine.

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

It is now possible to make an assertion that would have delighted Darwin: Gaps of knowledge in the evolutionary history (phylogeny) of living organisms no longer need exist. Molecular biology has made it possible to reconstruct the "universal tree of life," the continuity of succession from the original forms of life, ancestral to all living organisms, to every species now inhabiting the Earth. The virtually unlimited evolutionary information encoded in the DNA sequence of living organisms allows evolutionists to reconstruct phylogenetic relationships (including occasional reticulate events) leading to present-day organisms with as much detail as desired. The only limitation is logistical: a capacity to invest the necessary resources (time and laboratory expenses).

In the Light of Evolution

The theory of biological evolution by natural selection, as first proposed by Darwin, is the central organizing principle of biology. Indeed, as the great evolutionist Theodosius Dobzhansky asserted in 1973 in an address to the American Association of Biology Teach-

- 1. Darwin C (1859) On the Origin of Species by Means of Natural Selection (John Murray, London).
- 2. Barlow N (1958) The Autobiography of Charles Darwin (Collins, London).
- 3. Paley W (1802) Natural Theology (R. Fauldner, London).

ers, "Nothing in biology makes sense except in the light of evolution." Yet, in the United States, evolution is not generally accepted by the public.

According to a Gallup poll of 1,016 US adults, taken in November 2004, 45% of those surveyed favored the statement that "God created human beings in their present form within the last 10,000 years"; 38% favored that "Man developed over millions of years, but God guided the process"; and only 13% opined that "Man developed over millions of years from less advanced life forms." Teaching creationism rather than evolution in the schools is preferred by a large number of American citizens. In a CNN/USA Today Gallup poll conducted in March 2005, 76% of 1,001 adult respondents would not "be upset if public schools in [their] community taught creationism," compared with 63% who would not "be upset if the schools taught evolution"; and only 22% would be upset if creationism was taught, whereas 34% would be upset if evolution was taught. Other polls yield similar statistics.

In 1959, at a symposium celebrating the 100th anniversary of the publication

 White TD, et al. (2006) Asa Issie, Aramis and the Origin of Australopithecus. Nature 440:883– 889. of the Origin of Species, the eminent geneticist and Nobel Laureate H. J. Muller proclaimed "One hundred years without Darwin are enough!" Fifty years later, the science of evolution is far from universally accepted by the American public, and activists throughout the country are advancing creationist or "intelligent design" alternatives to explain the origin, diversity, and adaptation of organisms, seeking that these "theories" be taught in science classrooms. Our educational system and society as a whole are best served when we teach science, not religious faith masquerading as science, in the schools. Scientists, educators, and the media have an obligation to convey to the American public that the evolution of organisms is well-established scientific knowledge and has important applications in agriculture, medicine, and much more. As biologists commemorate "two centuries of Darwin" with numerous festivals and colloquia during 2009, let us remember that an energetic commitment to enlighten the public about evolution, and thereby fulfill that obligation, would be a fitting celebration of Darwin's work.

7. Cela-Conde CJ, Ayala FJ (2007) Human Evolution. Trails from the Past (Oxford Univ Press, Oxford, UK).



Ayala and Avise

^{4.} Ahlberg PE, Clack JA (2006) Palaeontology: A firm step from water to land. *Nature* 440:747–749.

^{6.} Dalton R (2006) Feel it in your bones. *Nature* 440:1100–1101.