# In the light of evolution III: Two centuries of Darwin

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Charles Darwin's enthusiasm and expertise in natural history contributed hugely to his elucidation of evolution by natural selection, which stands as one of the grandest intellectual achievements in the history of science. Darwin was a lifelong observer of nature, stating in correspondence that some of his happiest times in youth were spent fishing on rainy days and "entomologizing" when England's weather was nice. At the age of 22, he boarded the *HSM Beagle* for a 5-year stint as Captain Fitzroy's traveling companion and the ship's naturalist, an appointment that introduced him to biodiversity on a global geographic scale. Darwin's breadth and depth of natural-history experience would later be on full display in his most defining scientific works (3–5) in his detailed treatises on orchids, insectivorous plants, coral reefs, barnacles, and earthworms (6–10).

The year 2009 marks the 200th anniversary of Charles Darwin's birth and the 150th anniversary of his most influential publication (3). 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 celestium* ("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*, 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.

Darwin's impacts have been felt far beyond science. Before Darwin, most scientists and 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 in the 5th century B.C. (see ref. 11), and it was expressed again in a thoughtful and elegant treatise (*Natural Theology*) published in 1802 by the Reverend William Paley (12). Darwin later recalls in his autobiography (13) that Paley's logic "gave me as much delight as did Euclid" and that it was the "part of the Academical Course [at the University of Cambridge] which . . . was the most use to me in the education of my mind." Darwin was still a natural theologian when he boarded the *Beagle* in 1831 on what would become a fateful voyage, for Darwin and for humanity, into uncharted philosophical (as well as scientific) waters.

In the articles of this Colloquium, leading evolutionary biologists and science historians reflect on and commemorate the Darwinian Revolution. The authors of these Proceedings canvass modern research approaches and current scientific thought on each of the 3 main categories of selection (natural, artificial, and sexual) that Darwin addressed during his career. Although his legacy is associated primarily with the illumination of natural selection in *The Origin*, Darwin also contemplated and wrote extensively about what we would now term artificial selection and sexual selection, as reflected for example in two books titled, respectively, *The Variation of Animals and Plants Under Domestication* (1869) and *The Descent of Man and Selection in Relation to Sex* (1871). In a concluding section of these Proceedings, several science historians comment on Darwin's seminal contributions. Thus, these Proceedings are organized in 4 parts: *Natural Selection, or Adaptation to Nature*; *Artificial Selection, or Adaptation to Human Demands*; *Sexual Selection, or Adaptation to Mating Demands*; and *The Darwinian Legacy, 150 Years Later*.

## Natural Selection, or Adaptation to Nature

The concept of natural selection—as the unconscious broker of adaptive evolution—is Darwin's seminal contribution. It provided a materialistic account of nature's operations that contrasted sharply with the traditional invocations of supernatural causation that predominated before *The Origin*. The basic logic of natural selection is astonishingly simple. As phrased by Darwin in *The Origin*, "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." Darwin's clear elucidation of natural selection launched a revolutionary new paradigm in biology wherein organismal traits could be studied and interpreted as products of natural (rather than supernatural) forces amenable to rational scientific inquiry. Scientific studies of natural selection are now more popular and powerful than ever, and they have revealed the evolutionary origins and trajectories of numerous biological features and taxa.

A major limitation in Darwin's characterization of evolution concerned hereditary mechanisms, a difficulty that the field began to rectify early in the 20th century by incorporating Mendelian genetics and population genetics into the emerging evolutionary synthesis (14). Today, in the genomics era, scientists routinely extend studies of natural selection and trait evolution to the level of DNA itself, as several papers in these Proceedings will attest. Genomic dissections are also providing fresh insights into the ancient mystery alluded to in the title of Darwin's seminal work: how species originate. Ironically, *The Origin* says relatively little about the evolution of reproductive isolating barriers, which under the modern biological species concept are key to understanding cladogenetic (speciational) processes.

In the opening presentation of these Proceedings, Via (15) takes a fresh perspective on the origin of species by characterizing genomic regions that appear to be diverging early in a speciation pro-

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cess. She calls this the "magnifying glass" approach for speciation in action, and contrasts it with the more traditional "spyglass" approach in which each completed speciation is characterized retrospectively by scrutinizing genetic differences between established sister taxa. Via develops and presents genetic evidence for a model in which incipient species become, in effect, genealogical mosaics in which ecologically important genomic regions (i.e., those under divergent ecological selection, sometimes even in sympatry) become resistant to genetic exchange, whereas gene flow remains possible over most of the genome. The key genomic regions under divergent selection become focal points for "divergence hitchhiking" by linked loci, because they reduce the porosity of the emerging species boundary to gene exchange. Under this scenario, Via views divergent selection as the motivator of genealogical differences (in these particular genomic regions) that later will crystallize into the branching pattern in the species phylogeny. Eventually, in responses to selection, genetic drift, and mutation, gene genealogies in the remainder of the genome will come into topological concordance with the species phylogeny, but these additional genetic differences will have been the effect of speciation rather than its cause.

Some of the richest biological quarries for extracting information about natural selection and speciation involve clades (monophyletic groups) that have arisen via rapid adaptive radiations. Darwin presaged such evolutionary analyses in his considerations of different forms of mockingbirds in the Galapagos Islands, and in the various finch species he collected there that now bear Darwin's name (but whose evolutionary appraisal mostly awaited later researchers). Hodges and Derieg (16) take a modern approach to speciation analysis by integrating observations from field studies with molecular and phylogenetic dissections of genes for traits (especially flower color) that probably played key cladogenetic roles in a spectacular evolutionary radiation of *Aquilegia* (columbine) plants. The authors describe how molecular investigations of genomes can complement traditional approaches and contribute to a better mechanistic understanding of how new species arise.

Schluter and Conte (17) emphasize a theme—ecological speciation—that would please Darwin. Under ecological speciation, reproductive isolation between populations emerges from the effects of ecology-based divergent natural selection. The authors address this speciation mode generally (with respect to the genetics of postzygotic isolation and prezygotic isolation under gene flow, and the role of standing genetic variation in the process) and specifically (with reference to speciation in stickleback fishes). For the sticklebacks, they develop an interesting "transporter model" of ecological speciation in which ecological selection pressures in freshwater streams consistently select for alleles different from those normally present in marine populations. However, occasional hybridization between freshwater and marine forms ensures a continual supply of freshwater alleles in the sea, at low frequency and disassembled by genetic recombination. When marine fish colonize a newly opened stream, natural selection can act on this standing pool of genetic variation to reconstitute the freshwater genotype. The analogy in the title of their model is to a fictional process in the movie *Star Trek*, wherein an organic body placed in the transporter is disintegrated only to be reassembled at a future time in a distant location.

The vast majority of phylogenetic diversity in eukaryotes is to be found not in the lineages of multicellular plants and animals, but rather in unicellular microbes (protists). Perhaps it is not surprising, therefore, that these microeukaryotes provide a wealth of opportunities (heretofore relatively untapped) for scientific investigations into natural selection and evolutionary operations. Lukeš, Leander, and Keeling exemplify the utility of protists for providing evolutionary insights by summarizing numerous phenotypic and genomic features in representatives of two huge protistan phylads: Alveolata and Euglenozoa. They underscore the mind-boggling diversity in protists of molecular genetic and phenotypic features, ranging from cellular ultrastructures to mechanisms of mRNA processing and the organization of organellar genomes. The picture that emerges is one of extraordinary evolutionary experimentation in these protists, sometimes channeled into convergent outcomes by natural selection, sometimes constrained by the idiosyncrasies of phylogeny, but always tinkered endlessly by various mixes of both chance and necessity.

## Artificial Selection, or Adaptation to Human Demands

Darwin titled the first chapter in *The Origin of Species*"variation under domestication," probably because he felt that developing a case for the effectiveness of human-mediated selection in generating new domestic varieties would facilitate his efforts in later chapters to communicate the concept of how natural selection can generate new varieties and species in nature. In chapter 1 of *The Origin*, Darwin discussed several domesticated plant and animal species, ranging from beans, melons, and plums to dogs, cattle, and horses. He devoted a long section to how selective breeding had altered the domestic pigeon, fancy varieties of which were widely prized in the Victorian era. Ten years later, he would expand greatly on these themes in *The Variation of Animals and Plants Under Domestication*.

In chapter 1 of *The Origin*, Darwin lamented that "We hardly know anything about the origin or history of our domestic breeds"; and "The origin of most of our domestic animals will probably for ever remain vague." Darwin would therefore be both pleased and surprised by recent scientific progress in deciphering the evolutionary origins of many domesticated plant and animal species. Much of this evidence has come from molecular genetic and phylogenetic analyses of domesticated breeds vis-à-vis their wild ancestors. Driscoll, Macdonald, and O'Brien (19) tabulate some of this evidence for various domestic animals, and then provide a detailed case-in-point by describing the phylogenetic and biological history of the domestic cat. The cat appears to be nearly unique among animal domesticates (including dogs) in the sense that it was initially self-selected for tolerance to humans, rather than actively selected by humans for tameness or for desired services such as companionship, hunting or guard duties, or food. According to the authors' reconstruction, cat domestication probably began near some of the earliest agricultural settlements of the Neolithic, in the Fertile Crescent region of the Near East, as wildcats became accustomed to feeding on rodents and refuse near human towns. If so, their evolution to companion animals, and their ecological isolation from wildcats, were initially a response to natural selection more so than to conscious artificial selection.

Apart from appraising the phylogenetic histories of domestic organisms, the field of molecular genetics is also uncovering the genes responsible for key phenotypes that have emerged from artificial selection. Tian, Stevens, and Buckler (20) provide cases-in-point involving domestic corn (maize), the ancestors of which are wild teosinte grasses native to Mexico. The evolutionary transformation from teosinte to maize ranks among the most impressive of all feats of artificial selection. For example, teosinte lacks a cob-like inflorescence and instead produces only 6–12 kernels in 2 rows protected by a hard covering, whereas each cob of modern maize consists of ≈20 rows with numerous exposed kernels; and teosinte has long lateral branches terminated by male tassels, whereas modern maize has short lateral branches tipped by female ears. The authors review current knowledge about the genetic loci responsible for these and other such morphological transitions. Several genes with major effect can be specified, and many others are implicated, including a newly discovered region on chromosome 10 that spans >1,000,000 base pairs and retains the molecular footprints of strong artificial selection during the domestication process.

Allendorf and Hard (21) describe another form of human-induced selection that they term unnatural selection. When breeders artificially select domestic animals for food or companionship, they purposefully try to propagate traits that people deem desirable. However, hunting and fishing (especially for trophies) routinely violate such ground rules by culling rather than propagating the animals that humans prize most. In other words, unnatural selection via hunting, unlike artificial selection by people (or natural selection by nature), often eventuates biotic outcomes that run counter to what humans (or nature) otherwise would strive to achieve. For example, the evolutionary responses to the continued selective removal of larger or healthier animals from a population of deer or fish could include, in principle, earlier sexual maturation and smaller adult body sizes. The authors review arguments and empirical evidence for unnatural selection imposed by human harvests of wild animal populations, and they discuss the management problems generated by such selective mortality. Darwin mostly overlooked this important topic, which continues to be neglected by many wildlife and fisheries agencies today. This article may help to rectify that situation by bringing to broader attention the important contrasts between standard hunting and fishing practices (unnatural selection) on the one hand and standard agricultural and aquacultural practices (artificial selection) on the other.

Artificial selection traditionally refers to human-mediated differential propagation of plants or animals with desirable hereditary traits. In the modern biotechnology era, an entirely different form of genetic engineering is possible in which particular proteins are subjected to repeated rounds of mutation and selection, in laboratory test tubes, for improved stability or biochemical function. Bloom and Arnold (22) review this form of directed evolution, which is becoming a powerful approach to the design of new proteins for medicine and pharmacology. Directed protein evolution has also yielded new insights into the fundamental nature of evolutionary processes. The authors emphasize 3 major conclusions from directed evolution experiments: (*i*) most desirable protein properties can be incrementally improved through successions of single mutation steps; (*ii*) much of the epistatic coupling between mutations is due to protein stability and its influence on mutational robustness and protein evolvability; and (*iii*) adaptive protein evolution is heavily reliant on the prevalence of promiscuous protein functions (initial traces of activity that proteins routinely display on foreign substrates) that in turn are routinely influenced by neutral mutations. Directed protein evolution goes far beyond the wildest imaginings of Darwin, who would doubtless be impressed that the general principles of selection he illuminated would prove to be so universal.

## Sexual Selection, or Adaptation to Mating Demands

In *The Descent of Man, and Selection in Relation to Sex*, Darwin defined sexual selection as the "advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction." Darwin appreciated that sexual selection could be mediated by intrasexual combat (e.g., between males) or by intersexual preferences (e.g., female choice of attractive mates). He also appreciated that sexual selection could be in opposition to natural selection with respect to particular phenotypic traits (such as a peacock's tail), but he generally viewed sexual selection as less effective than natural selection.

After discussing Darwin's original ideas about sexual selection (especially as presented in *The Descent of Man*), Jones and Ratterman (23) identify 3 modern triumphs in sexual selection research: the introduction and widespread use of molecular markers to assess genetic parentage (the key to describing actual mating systems in nature) unequivocally; a better conceptual understanding (at least in formal models) of the mechanisms and consequences of mate choice by females (or by males in role-reversed taxa); and a better appreciation of why differences exist among lineages in the intensity of various forms of sexual selection. For the latter two topics, the histories of ideas on sexual selection—beginning with Darwin—are interwoven with how those notions laid the foundation for categorizing various forms of sexual selection, and for extending and expanding modern research into various aspects of sexual selection both in theory and empirically. The authors close by suggesting several lines of future research on sexual selection.

Shuster (24) provides a comprehensive overview (and contrast) of how sexual selection has been measured and studied in plant systems versus animal systems. One general theme that he emphasizes is the need to reconcile Darwin's idea that sexual selection tends to be less rigorous than natural selection with the observation that sexual selection would seem to be responsible for many if not most differences between the two genders (in features other than the primary sex organs). In *The Origin*, Darwin wrote that sexual selection "depends, not on the struggle for existence, but on a struggle between males for possession of the females; the result is not death of the unsuccessful competitor, but few or no offspring. Sexual selection is, therefore, less rigorous than natural selection." Shuster, by contrast, views sexual selection as being "among the most powerful of evolutionary forces." The author proposes to reconcile these two stances in evolutionary models that combine quantitative differences in the fitness variances between the sexes (an approach traditionally applied to animal systems) with phenotypic and genotypic correlations underlying reproductive traits among breeding pairs (an approach often taken in plant systems). The net result, he claims, will be the ability to predict the magnitudes of sexual dimorphism and classify mating systems using existing genetic and life history data.

Gowaty and Hubbell (25) offer a unique perspective on what underlies the individual decision-making process that in turn underlies patterns of mate choice and sexual selection in various species. Their central thesis is that even stochastic variation in various parameters that predict the time available for mating might promote considerable flexibility in individual decision-making with regard to mate choice; and that even consistent sex differences in these mating proclivities might therefore, in at least some cases, reflect ecological constraints (habits-of-life considerations) rather than behavioral differences that might otherwise be genetically hardwired between the sexes. The parameters that might impact available time for mating include the probabilities of encountering mates, individual survivorships, mating latencies (times-out between mating events), and fitness distributions, all of which are likely to vary as functions of the natural histories and the evolutionary histories of species. Such considerations lead the authors to their switch point theorem, which in principle can quantitatively evaluate what proportion of potential mates in a population a focal individual should find acceptable as mating partners if it is to maximize its relative lifetime fitness.

In an uncharacteristic conceptual lapse, Darwin failed to appreciate that sexual selection (including both male-male competition and female choice) can continue even after copulation has begun. The intrasexual (male-male) component can happen via sperm competition for the fertilization of ova, and the intersexual component can occur via cryptic female choice of alternative sperm, all within the female's reproductive tract. Eberhard (26) reviews the history of ideas for these underappreciated but nevertheless intense forms of postcopulatory sexual selection. The miniature worlds of gametic competition and gametic choice have proven to be every bit as fascinating and compelling as the macroscopic worlds of mating competition and mate choice that have been the traditional foci of sexual selection studies. Eberhard brings this miniature Kama Sutra realm to light by detailing fascinating examples of sexual selection in the time interval (which is often but not invariably brief) between the onset of copulation and the completion of fertilization.

## The Darwinian Legacy, 150 Years Later

Beyond his numerous books and autobiography (27), Darwin left a wealth of personal correspondence (28) and additional written material that science historians can now sift through to better understand Darwin's developing ideas at different stages of his life. Prominent among these were notebooks that Darwin wrote during the voyage of the *Beagle*, and a lettered series of Transmutation Notebooks that he wrote in the 2 years after his return. Several authors in this concluding part of the In the Light of Evolution III Proceedings scrutinize these writings to illuminate Darwin's thought processes and thereby better appreciate and contextualize his scientific legacy.

Ayala (29) describes a fundamental discrepancy between Darwin's scientific methodology and how Darwin portrayed his methods to the general public. The version for public consumption emphasized how Darwin proceeded on the principles of Baconian induction, which at that time were favored by British philosophers such as John Stuart Mill. Under this approach, facts are collected wholesale—presumably without the bias of preconceived notions—and broader biological principles eventually emerge. The actual methods of Darwin, Ayala contends, were far different from this depiction, falling instead squarely within a hypothetico-deductive framework. The latter scientific method has 2 steps: the formulation of one or more conjectures or hypotheses about the natural world and the design and implementation of critical empirical tests of whether deductions derived from each hypothesis are consistent with real-world observations. In support of his contention that Darwin consistently used the hypothetico-deductive method, Ayala cites examples from Darwin's work and even uses some of Darwin's own words, such as "How odd it is that anyone should not see that all observation must be for or against some view if it is to be of any service." Ayala speculates on why Darwin sometimes pretended to be a Baconian inductivist when in fact he mostly practiced what today would be considered modern hypothesis-driven deductive science.

In considering Darwin's legacy from the current vantage, Ruse (30) asks 3 related questions: Was there a Darwinian *revolution*? Was there a *Darwinian* revolution? And was there a *Darwinian revolution*? Ruse's answers to these questions are two resounding yesses and a qualified yes, respectively. The first resounding yes comes from the fact that after Darwin, rational observers could no longer accept the old picture of humans as somehow the miraculous products of special creation. In other words, the *revolution* challenged us to rethink dramatically—both emotionally and intellectually—what it means to be human. The second resounding yes comes from the evidence that it was Darwin, rather that his predecessors or contemporaries, who was primarily responsible for the scientific and the metaphysical shifts that society entailed in coming to terms with natural selection's role in the evolutionary process. The qualified yes comes from the realization that the third question is somewhat philosophical; the answer depends in part on whether to interpret major transformations of thought as continuous and gradual, or discontinuous and abrupt. Ruse discusses philosophical nuances of his own position on these issues.

Natural selection is the key Darwinian concept, and the evolutionary force given top billing in *The Origin*. However, common ancestry is a key concept too, a costar (albeit not originating strictly with Darwin) of the evolutionary theatre. Sober (31) considers how natural selection and common ancestry are related under Darwin's worldview, and he argues that the latter has a sort of logical (as well as historical) priority over the former. This is because, under Darwinian logic, arguments about natu-

**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" (35). 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 have often 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, and 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, such as 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 will be to promote the evolutionary sciences through state-of-the-art colloquia and their published proceedings. Each installment will explore 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, address some of the most intellectually engaging and pragmatically important societal issues of our times, and foster a greater appreciation of evolutionary biology as a consolidating foundation for the life sciences.

ral selection often require the supposition or backdrop of common ancestry (i.e., genealogy and heredity), whereas the logical defense of common ancestry does not require natural selection. In this epistemological sense, Darwin ordered things backwards, Sober argues, when he presented natural selection, rather than common ancestry, first and foremost in *The Origin*. Rather than "evolution by natural selection," Darwin's theory might better be described as "common ancestry plus natural selection."

Richards (32) presents a revisionary argument that seems likely to be highly controversial. Using excerpts from Darwin's writings, Richards makes a case that "Darwin's theory originally reinfused nature with moral purpose and used teleological means of doing so," and that "Darwinian evolution had the goal of reaching a fixed end, namely man as a moral creature." These conclusions fly in the face of conventional wisdom, which holds that Darwin's elucidation of natural selection was philosophically and scientifically revolutionary precisely because it banished the necessity for invoking ultimate purpose or goal-directedness in biological evolution. Nevertheless, Richards contends that many of Darwin's writings are infused with teleological statements, and that to dismiss these, or to rationalize them as rhetorical devices (for example, whether Darwin was trying to assuage Victorian readers) is unwarranted. Richards bolsters this argument by tracing various of Darwin's ideas to his early life, and how these concepts eventually played into the construction of Darwin's theory. Thus, Richards interprets many of Darwin's writings as consistent with notions of evolutionary purpose and biological progress. It will be interesting to monitor the responses of other evolutionary historians to this provocative suggestion.

The title of Dennett's essay (33)—"Darwin's strange inversion of reasoning"—refers to a quote from one of Darwin's critics who in 1868 wrote that Darwin, "by a strange inversion of reasoning, seems to think Absolute Ignorance [natural selection; editors' addition] fully qualified to take the place of Absolute Wisdom [God] in all of the achievements of creative skill." Dennett likens Darwin's strange inversion of reasoning to another such profound inversion of reasoning, this time by Alan Turing in the physical sciences. In the 1930s, Turing argued that it would be possible to design exquisite calculating machines [such as modern computers] that were absolutely ignorant yet fully capable of performing highly complex mathematical tasks. Whereas the truth of Turing's strange inversion in physics is universally acknowledged today, many people (namely, creationists) still cannot abide Darwin's strange inversion in biology. Dennett explores the philosophical ramifications for Darwin's inversion of reasoning, and finds them to be truly profound.

A recent article in the *New York Times* (July 15, 2008) was entitled "Let's get rid of Darwinism." It was written by Olivia Judson, an evolutionary biologist and the author of a best-selling evolutionary book (34). In that article, Judson wrote, "I'd like to abolish the insidious terms Darwinism, Darwinist, and Darwinian. They suggest a false narrowness to the field of modern evolutionary biology, as although it was the brainchild of a single person 150 years ago, rather than a vast, complex and evolving subject to which many other great figures have contributed. . . . Obsessively focusing on Darwin, perpetually asking whether he was right about this or that, implies that the discovery of something he did not think of or know about somehow undermines or threatens the whole enterprise of evolutionary biology today." The term Darwinism also "suggests that Darwin was the beginning and the end, the alpha and the omega, of evolutionary biology, and that the subject has not changed much in the 150 years since the publication of the Origin." Judson went on to suggest that constantly, using terms such as Darwinism and Darwinian is rather like calling all of modern aeronautical engineering "Wrightism" after the Wright brothers, or referring to all fixed-wing aircraft as "Wrightian" planes. Similar sentiments were expressed by another well-known biologist, Carl Safina, in a N.Y. Times article (Feb. 10, 2009), entitled "Darwinism must die so that evolution may live."

Our intent in this Sackler Colloquium has not been to idolize Charles Darwin, but rather to celebrate the field of evolutionary biology that he played such an important role in developing nearly 2 centuries ago. We submit that if Darwin were alive today, he would be satisfied with his own pioneering efforts, but also completely astonished at the breadth, depth, and vibrancy of the modern field.

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