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In the light of evolution I: Adaptation and complex design

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Darwin's elucidation of natural selection as a creative evolutionary force was one of the monumental intellectual achievements in the history of science, not only revolutionizing thought across the biological sciences but also fundamentally impacting much discourse in the social sciences, philosophy, and religion. No longer were explanations for the origin and marvelous adaptations of organisms necessarily to be sought solely in the context of supernatural causation. Instead, biological outcomes could now be interpreted within the critical scientific framework of natural processes governed by natural processes and laws.

As a young man, Charles Darwin (like most biologists of his era and before) was a natural theologian steeped in the notion that an attentive study of organisms in nature would ineluctably serve to document and further glorify the infinite creative powers of the Almighty. Darwin read and greatly admired William Paley's 1802 *Natural Theology*, which eloquently developed the "argument from design" that biological complexity was *prima facie* evidence for an intelligent engineer. This age-old idea had an illustrious intellectual pedigree. For example, it had been one of the "Five Ways" that St. Thomas Aquinas (an influential Dominican scholar of the 13th century) purported to prove God's existence. In 1779, the Scottish philosopher David Hume again encapsulated conventional wisdom when he wrote

the curious adapting of means to ends, throughout all of nature, resembles exactly, although it much exceeds, the productions of human contrivance, of human design, thought, wisdom, and intelligence. . . . By this argument *a posteriori*, and by this argument alone, do we perceive at once the existence of a Deity, and his similarity to human mind and intelligence.

Dialogues Concerning Natural Religion

The link between adaptation, biological complexity, and omnipotent design was apparent not only to philosophers and theologians. As phrased in the 1600s by the Christian scholar and scientist John Ray,

You may hear illiterate persons of the lowest Rank of the Commonality affirming, that they need no Proof of the being of God, for that every Pile of Grass, or Ear of Corn, sufficiently

proves that. . . . To tell them that it made it self, or sprung up by chance, would be as ridiculous as to tell the greatest Philosopher so.

The Wisdom of God Manifested in the Works of Creation

When Darwin boarded the HMS Beagle in 1831, he had no inkling that his voyage of discovery would eventually lead him to a revolutionary concept: that a purely natural process—natural selection—can yield biological outcomes that otherwise seem to have the earmarks of intelligent craftsmanship. Natural selection is an inevitable process of nature whenever organisms show heritable variation in their capacity to survive and reproduce in particular environments, but the operation has no more consciousness or intelligence than do natural physical forces such as gravity or weather. Thus, Darwin's key legacy is not the mere demonstration that evolution occurs (several of Darwin's predecessors were aware that species evolve), but rather the stunning revelation that a natural rather than a supernatural directive agent can orchestrate the evolutionary emergence of biological adaptations.

Nevertheless, 150 years after Darwin the challenge of understanding nature's complexity remains in many regards in its infancy. Only recently has science developed the necessary laboratory tools for delving deep within the molecular structure and function of genes that underlie particular complex adaptations (such as the eye or the body plans of vertebrate animals). Only recently has it become possible to conduct genomic analyses in ways that permit the discovery of heretofore unspecified structural and regulatory genes that contribute to the molecular assembly of complex organismal phenotypes. Only recently have phylogenetic methods progressed to the point where the histories of complex phenotypes can be reliably elucidated. Scientific progress is occurring on many related fronts as well. For example, recent developments in evolutionary genetic theory have opened exciting new avenues for exploring the geneses and maintenance of biological complexity at the levels of genetic and metabolic pathways. The articles in this Colloquium illustrate a wide variety of current scientific perspectives and methodological approaches directed toward understanding the origin and maintenance of complex biological adaptations.

In the first article of this Colloquium, Francisco Ayala (1) develops the thesis that the Darwinian revolution in effect completed the Copernican revolution by extending from physics to biology a notion that the universe operates by natural laws that fall within the purview of rational scientific inquiry. In 1543, Nicolaus Copernicus published *De revolutionibus orbium coelestium* (*On the Revolutions of the Celestial Spheres*), which introduced the idea that the earth is not at the center of Creation and that natural laws govern the motion of structures in the physical universe. This thesis was bolstered and elaborated by the scientific discoveries of Galileo, Kepler, Newton, and others during the 16th and 17th centuries, but it was left to Darwin in the 19th century to discover that natural laws and processes also govern the emergence of apparent design in biological systems.

Most of the remaining articles in the Colloquium fall under three themes: *Epistemological Approaches to Biocomplexity Assessment*, *From Ontogeny to Symbiosis* (*A Hierarchy of Complexity*), and *Dissecting Complex Phenotypes* (*Case Studies*).

Epistemological Approaches to Biocomplexity Assessment

The sphere of biological phenomena interpretable in the light of evolution is vast, so perhaps it is not surprising that researchers from many different scientific backgrounds and orientations have weighed in on how best to approach the study of complex adaptations. The articles under this heading will illustrate some of this diversity.

Robert Hazen *et al.* (2) raise two important related questions: What actually is meant by biological "complexity" and how might complexity be quantified?

This paper serves as an introduction to this PNAS supplement, which resulted from the Arthur M. Sackler Colloquium of the National Academy of Sciences, "In the Light of Evolution I: Adaptation and Complex Design," held December 1–2, 2006, at the Arnold and Mabel Beckman Center of the National Academies of Sciences and Engineering in Irvine, CA. It is the first in a planned series of colloquia under the umbrella title "In the Light of Evolution" (see Box 1). The complete program is available on the NAS web site at www.nasonline.org/adaptation.and.complex.design.

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The authors suggest that a hallmark of any complex system (physical or biological) is its potential to perform a quantifiable operation. Starting with that premise, they formally define a metric—functional information—that basically describes the fraction of all possible configurations of the system that possess a specified degree of function. Although this metric may be difficult to apply in the real world (because it requires knowledge of all possible configurations and the degree of function of each), it nonetheless may have heuristic merit for studying the properties of complex systems. The authors illustrate this approach using a virtual world of computer programs that self-replicate, mutate, and adapt by natural selection.

In 1975, Mary-Claire King and Allan Wilson (3) popularized an earlier idea by Roy Britten and Eric Davidson (4) that evolutionary changes in gene regulation, rather than DNA sequence mutations in protein-coding exons *per se*, were largely responsible for phenotypic evolution and the emergence of complex adaptations. This sentiment has since become mainstream, as reflected in several articles in this Colloquium. John Gerhart and Marc Kirschner (5) accept the notion that regulatory changes are of central importance, and indeed they argue that most key phenotypic evolution over the past 600 million years has resulted from altered usage patterns in a large set of otherwise conserved core genetic components that direct organismal development and physiology. In the “theory of facilitated variation” formulated by Gerhart and Kirschner (5), several regulatory features of the genome collude to foster more phenotypic evolution with less genetic change than would otherwise have been possible.

Adam Wilkins (6) then examines the converse of evolutionary plasticity: phenotypic constraint. It has long been evident that phylogenetic legacies and developmental contingencies restrict (albeit to a debatable degree) the suite of evolutionary pathways potentially available to any species. Wilkins proposes that, in addition to these conventionally recognized inhibitors of phenotypic evolution, inherent constraints also operate at the levels of interacting genes and complex genetic networks. If molecular biologists can illuminate the genetic biases that constrain as well as promote the evolution of particular phenotypes, it might become possible, Wilkins argues, to specify the relative probabilities of alternative evolutionary trajectories (at least over the short term) for particular lineages. Traditionally, this kind of predictability about evolutionary futures had been regarded as essentially impossible.

Michael Lynch (7) reminds us that mechanistic explanations of phenotypic evolution that emerge from the fields of developmental biology and molecular genetics cannot violate the fundamental dynamics of the evolutionary process as elucidated by a century of work in theoretical population genetics. Regardless of which genes underlie complex or other phenotypes, their microevolutionary dynamics remain governed by the forces of mutation, gene flow, natural selection, recombination, and random genetic drift. The point, however, is not to claim priority for one discipline over another, but rather to emphasize that any evolutionary model that disregards population genetic reality does so at its peril. To illustrate his argument, Lynch examines the ineluctable consequences of genetic drift, especially in small populations, and he highlights a wide assortment of genic and genomic phenomena that make sense only after accounting for variation among taxa in the relative power of nonadaptive evolutionary forces.

From Ontogeny to Symbiosis (A Hierarchy of Complexity)

Biological complexity is displayed at many hierarchical levels, from molecular

and cellular operations within an organism to species’ interactions in ecological communities. At any level, biological entities are enmeshed in interactive networks that typically involve potential conflicts as well as collaborations. For example, a multicellular organism can be viewed as a social collective of cells whose genes must not only collaborate to generate a viable individual but also compete for inclusion in gametes that will form the next generation. Articles in this section deal with some of the complex interactions that characterize biological systems at the levels of ontogeny, multicellularity, eusociality, and symbiosis.

During ontogeny, suites of genes (and the RNA and protein molecules they encode) direct the molecular dances of development that produce a functional multicellular organism. The ontogenetic choreographies themselves evolve, as evidenced by the great diversity of body plans and other phenotypes in different organismal lineages. What kinds of genetic mechanisms underlie ontogenetic shifts and the emergence of novel morphologies? Most researchers suspect that evolutionary changes in gene regulation are especially important and that such alterations often involve the cooption of

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” (24). 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 purposely 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, such as education, medicine, sociology, and other applied fields including agricul-

ture, 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 as well as pragmatically important societal issues of our times, and foster a greater appreciation of evolutionary biology as a consolidating foundation for the life sciences.

The organizers and founding editors of this effort (J.C.A. and F.J.A.) are the academic grandson and son, respectively, of Theodosius Dobzhansky, to whose fond memory this *In the Light of Evolution* series is dedicated. May Dobzhansky’s words and insights continue to inspire rational scientific inquiry into nature’s marvelous operations.

preexisting genes and proteins into new functions. Benjamin Prud'homme *et al.* (8) illustrate how such cooptions can occur via shifts in the deployment of cis-regulatory elements and their associated transcription factors. They argue that this specific kind of architectural change in regulatory networks offers a key to understanding how morphological evolution is linked to molecular ontogenetic processes.

Multicellularity itself is a complex trait, yet the phenomenon has arisen independently on numerous occasions. Each evolutionary transition from unicellularity to multicellularity likely proceeds through a succession of stages: initial aggregation of cells, increased cooperation within the group, the evolution of policing mechanisms against cheater cells, increases in group size, and the spatial and functional specialization of cell types. The process is remarkable because it entails, in effect, the emergence of reproductive altruism, wherein most cells forego personal reproduction in favor of working on the colony's behalf, a situation that undoubtedly necessitates high within-colony kinship (9). Rick Michod (10) discusses these topics with special reference to living volvocine green algae, which collectively display several stages along the unicellularity to multicellularity continuum. Michod contends that multicellularity is not "irreducibly complex" in an evolutionary sense, but rather can be understood in terms of evolutionary tradeoffs and fitness advantages that can attend various intermediate stages in the evolutionary transitions between one kind of individual and another.

Eusociality is perhaps the epitome of complex social behavior and apparent reproductive selflessness. In eusocial colonies, such as those of many hymenopteran insects, individuals show striking reproductive divisions of labor, with sterile workers striving to maintain and defend a colony whose offspring are produced by the reproductive elites. Eusociality has long intrigued biologists. A key insight came from William Hamilton (11), who proposed that the evolution of extreme reproductive altruism by workers was facilitated by the altered genetic relationships among various colony members stemming from haplodiploid sex determination. Joan Strassman and David Queller (12) review current thought about the evolution of eusociality, including the important point that kin selection predicts a degree of cross-purpose and conflict (as well as extensive cooperation and common purpose) in eusocial insect colonies. They conclude that kin-selection theory, by making specific testable predictions about

behavioral phenomena in eusocial colonies, nicely exemplifies the power of scientific explanation for complex biological phenomena.

Genomic evolution was traditionally thought to proceed independently in different lineages, but a growing body of literature has revealed numerous exceptions. For example, horizontal gene transfer events have proved to be rather common in various prokaryotic groups, sometimes affording the recipient with novel metabolic capabilities. Another evolutionary route by which lineages may acquire functional innovations involves the establishment of stable (and sometimes heritable) symbiotic associations. Nancy Moran (13) interprets various symbioses among microorganisms, and between microorganisms and their multicellular hosts, as important (and previously underappreciated) evolutionary sources of phenotypic novelty. Using compelling examples from insects and other organisms, Moran shows how obligate symbiosis can yield complex evolutionary outcomes, ranging from the emergence of specialized cell types and organs to various developmental mechanisms that regulate the intergenerational continuance of the symbiotic association.

Dissecting Complex Phenotypes (Case Studies)

The articles under this heading provide examples of how scientists are tackling the empirical challenge of dissecting complex phenotypes. In *The Origin of Species* (14), Darwin deemed the eye to be an organ of "extreme perfection and complication." He also wrote, "To suppose that the eye with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest degree." Nonetheless, "reason tells me, that if numerous gradations from a simple and imperfect eye to one complex and perfect can be shown to exist, each grade being useful to its possessor, . . . then the difficulty of believing that a perfect and complex eye could be formed by natural selection, although insuperable to our imagination, should not be considered subversive of the theory." Ayala's opening article of this Colloquium (1) addresses how light-sensing organs in mollusks vary from the simple to the highly complex, each type nonetheless of utility to its bearers. Francesca Frentiu *et al.* (15) delve deeper into the molecular basis of vision by discussing the comparative evolution of genes and proteins underlying color-vision phenotypes in

primates and butterflies. The research summarized by these authors demonstrates some remarkable parallels in how particular amino acid sites in photopigments can be involved in color perception in both insects and mammals.

Darwin was interested in the close parallels between natural selection and artificial selection, and in 1868 he published a book on the topic of phenotypes in domesticated plants and animals (16). Jeffrey Ross-Ibara *et al.* (17) illustrate modern genetic approaches to dissecting important phenotypes that have evolved under human influence, with special reference to domestic corn. They distinguish top-down genetic approaches (such as QTL mapping) from bottom-up approaches (such as candidate gene assays) and conclude that the latter method, despite some pitfalls, generally holds greater promise for revealing how key phenotypes in crop plants have evolved under domestication from their ancestral wild states.

Al Bennett and Richard Lenski (18) address a longstanding question: Is there a necessary cost to adaptation? In other words, does the evolution of a phenotype that is adaptive to a particular environment necessitate deterioration in other traits? If so, what natural selection can achieve via the adaptive process would inevitably be constrained by such fitness "tradeoffs." To examine this issue empirically, the authors monitored multigeneration selection responses of bacteria to altered temperature regimes. After 2,000 generations of thermal selection, most colonies that showed improved fitness at low temperatures also showed fitness declines at high temperatures, but this was not invariably the case. The fact that exceptions exist indicates that fitness tradeoffs are not an inevitable component of the adaptive evolutionary process.

Bacteria such as *Escherichia coli* are model experimental organisms because they have short generation lengths and are easy to manipulate, but they also have relatively simple phenotypes. Near the other end of the continuum is *Homo sapiens*, which has many complex phenotypes of special interest but is far less tractable to experimental manipulation. Cynthia Beall (19) describes the adaptations to high-altitude hypoxia (oxygen shortage) displayed by humans indigenous to the Andean and Tibetan Plateaus. Remarkably, the physiological and molecular adaptations to hypoxia differ dramatically between these two populations, suggesting different evolutionary pathways to the same functional outcome. Beall describes how scientists are currently dissecting the evolutionary genetic responses to oxygen deprivation

displayed by these two populations, and in so doing reveals some of the special challenges of working with a nonmodel experimental species.

Beetles (Coleoptera) have long intrigued biologists. The British geneticist and evolutionist J. B. S. Haldane famously remarked that the Creator must have had an inordinate fondness for beetles because he made so many species of them (at least half a million). A century earlier, Darwin had speculated that the oft-ornate horns that many beetles carry on their heads or thorax were favored by sexual selection as weapons, used in jousts between males over mating access to females (20). Darwin's fascination with beetles began in childhood and grew in his college years, as indicated in his autobiography: "no pursuit at Cambridge was followed with nearly so much eagerness or gave me so much

pleasure as collecting beetles" (21). Douglas Emlen *et al.* (22) describe modern research on the molecular genetics, ontogeny, and phylogenetics of beetle horns. These authors advance fascinating mechanistic scenarios for the evolutionary origins of these peculiar devices and for subsequent evolutionary alterations in horn shapes, allometries, body locations, and patterns of sexual dimorphism.

Overall, the collection of ideas and data in this Colloquium is highly eclectic but nonetheless broadly illustrative of modern scientific attempts to understand the evolution of complex adaptations. These scientific endeavors are coming at a time of resurgent societal interest in supernatural explanations for biological complexity. Especially in the United States, proponents of intelligent design (ID)—the latest reincarnation of religious creationism—argue that biotic

complexity can only be the product of a supreme intelligence (i.e., God). In the closing article of this Colloquium, Eugenie Scott and Nicholas Matzke (23) examine the history of the ID movement, and they conclude that although without scientific merit, the crusade itself is of consequence to broader society because it represents a serious assault on the integrity of science education.

Perhaps there is a middle ground for scientific and theological interpretations of complex biological design. In his 1973 commentary titled "Nothing in Biology Makes Sense Except in the Light of Evolution" (24), Theodosius Dobzhansky famously proclaimed "I am a creationist and an evolutionist. Evolution is God's, or Nature's method of creation." Regardless of what our personal philosophical persuasion may be, let us rejoice in biotic complexity and in the scientific efforts to understand its geneses.

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