1959: THE APOTHEOSIS OF THE MODERN SYNTHESIS

Almost exactly fifty years before the Notre Dame conference, the world’s largest centenary commemoration of Darwin’s legacy was held at nearby University of Chicago. This event, organized by a committee spearheaded by University of Chicago anthropologist Sol Tax, drew nearly 2,500 registrants. In attendance were the primary leaders of evolutionary biology, paleontology, anthropology, and genetics, with a representation of sociologists, philosophers, and theologians (Smocovitis 1999). Two hundred and fifty delegates from universities and professional societies representing fourteen countries added an unusually high level of general academic prestige to the event as well.

Although other conferences were held in 1959, coordinated by an international super-committee formed in the mid-fifties—the Darwin Anniversary Committee—none equaled the University of Chicago symposium either in scope or in the assemblage of intellectual accomplishment. Accompanied by civic events, a grand procession to Rockefeller Chapel, and even an operetta written for the occasion, the Chicago celebration is an archetypal example of how scientific commemorations create, as well as celebrate, a major scientific consensus,
in this case the theoretical framework of neo-Darwinism, often termed since a classic statement of Julian Huxley (Huxley 1942), as the “Modern Synthesis” or simply “Synthesis.”

The character of this neo-Darwinian theoretical framework, as it was highlighted at Chicago, was the outcome of a four-decade process of theoretical unification of two conflicting strands emerging from Darwin’s original work, both of which could receive justification from the texts of Darwin and the arguments of his early interpreters. One was a theory of descent from common ancestors by means of natural selection, in which, as Darwin himself eventually came to explain the process (Darwin 1876), modifiable traits are transmitted from generation to generation by physical atomistic units—“gemmules” in Darwin’s original formulation. These were subsequently named “pan-genes” by Hugo DeVries in 1889, with the designator later shortened to “genes” by Wilhelm Johannsen in 1909. As it entered biological discourse, this “gene” concept was combined after 1900 with Mendelism, particularly as interpreted after 1900 by Hugo DeVries and William Bateson. From this point it was combined with the chromosome theory by Thomas Hunt Morgan and his students through their landmark work on the fruit fly Drosophila (Schwartz 2008; Beurton, Falk, and Rheinberger 2000; Keller 2000).

The initial implication drawn by many from this theory of genetic inheritance for evolutionary change was that such change must be discontinuous, that normal genetic assortment processes in accord with Mendelian principles could only lead to recombinatorial novelty, and that only by means of discontinuous “mutations” of atomistic genes could genuinely new properties relevant to the evolution of species be introduced into a population. This strand deemphasized the role of natural selection in the genesis of new species. Into the 1930s, this theory, in modified form, had prominent supporters, even receiving endorsement in such influential works as Erwin Schrödinger’s 1944 What is Life? lectures (Bowler 1983, chap. 8; Schrödinger 1974, chap. 3).

The other strand emphasized evolutionary change as a continuous and gradualistic process, in which species are conceived as ephemeral entities that evolve slowly under the action of natural selection, often seen as a force operating directly on organisms. In conjunction with a sophisticated mathematical interpretation by the creators of modern
statistics, most notably Karl Pearson, this interpretation placed itself in open opposition to the new Mendelism in the 1910s and ’20s, resulting in one of the great theoretical controversies within modern biology (Pence 2011; Gayon 1998; Olby 1987; Depew and Weber 1995, chaps. 8–9; Provine 1971). Genetical determinism or statistical population analysis; saltational stepwise change or evolutionary gradualism; discontinuous mutations or the gradual accumulation of slight morphological changes in response to external selective pressure exerted by the environment—these were the oppositions that the Synthesis sought to reconcile.

Through the complex mathematical analysis of population genetics developed in papers of the 1910s and ’20s, and in detail in his major work of 1930, *The Genetical Theory of Natural Selection*, Ronald A. Fisher was able to deal with both sides of this controversy and successfully combine the statistical mathematics of large number populations with a theory of atomistic genes subject to micromutational modifications (Okasha 2012; Depew and Weber 1995, Provine 1971). Such small mutations, preserved within the population by Hardy-Weinberg equilibrium, could now form the raw material upon which natural selection operated. Natural selection was conceptualized as a deforming pressure analogous to a Newtonian force acting upon genes in populations rather than as an external selection process operating primarily on whole organisms in nature. The result of this mathematical theory of natural selection was a reworking of the traditional Darwinian theory of natural selection. It enabled one to maintain both a gradualistic theory of species change over time and the particulate theory of inheritance operating according to Mendelian principles. Random micromutations of discrete and atomistic genes formed the foundation of evolutionary novelty. Operating over sufficiently expansive time scales, this was deemed competent both to explain the microevolution of species accessible to field and laboratory observation, and also the longer-term macroevolution of major groups in geological time. The theoretical resolution of several of these issues that emerged in the 1930s and ’40s, associated with the names of Ronald A. Fisher, Julian Huxley, J. B. S. Haldane, Ernst Mayr, G. Ledyard Stebbins, Theodosius Dobzhansky, George Gaylord Simpson, and Sewall Wright, constituted “the Modern Synthesis.” The assumption that such a
theoretical synthesis had been achieved, in which had been resolved the main historic issues surrounding Darwin’s theory of evolution by natural selection, formed the implicit framework of the proceedings of the 1959 Chicago symposium.

The 1959 Chicago commemoration provided a forum for all the main strands of development within the tacit consensus as it had coalesced to that point, with major papers by most of those typically identified as architects of the Synthesis: Ernst Mayr, George Gaylord Simpson, E. B. Ford, Alfred Emerson, G. Ledyard Stebbins, Sewall Wright, and Theodosius Dobzhansky. At the same time, there were indications of some of the tensions within the theoretical structure of neo-Darwinian theory that have emerged to greater prominence in the past half-century. These bear on the shape evolutionary theory may take in the next decades.

TENSIONS WITHIN THE SYNTHESIS

Two groups of scientists—paleontologists and developmental biologists—had often not been comfortable with the solutions to issues claimed by the architects of the Synthesis, with the notable exception of paleontologist George Gaylord Simpson, who continued to argue in his Chicago presentation for the smooth theoretical coherence of paleontology and neo-selectionist Darwinism that he had advocated in the 1940s (Simpson 1944, 1960; Amundson 2007, chaps. 8–10). In spite of Simpson’s defense, however, concerns from the side of paleontology were raised by the presentation at the conference by University of Chicago paleontologist Everett C. Olson, who saw the need for new and radical thinking to deal with the nagging issue of major steps in evolutionary history: “Just what directions these [new reflections] might take is uncertain, but it will require persons able to think in radical terms, outside the current framework, to undertake the early steps” in a theoretical reform (Olson 1960, 543).

Edinburgh developmental biologist Conrad Hal Waddington, who had long been concerned with issues beyond simple gene inheritance, for which he had coined the term “epigenetics” (Waddington...
1942), also posed some objections. Waddington’s contribution, devoted to adaptation within the evolutionary process, is notable for its surprising willingness to consider presumably discarded “Lamarckian” issues surrounding the interplay of environment, genome, and heritable evolutionary change. In his view, a new role needed to be given to external causes of changes in the genetic structure through the effects of ionizing radiation, chemical factors, and even variations in normal environmental conditions. Waddington was also one of the few speakers to make reference to the possible importance of external effects on the underlying DNA as a source of evolutionary novelty, a discovery that was only slowly being assimilated into biological communities outside of biochemistry and microbiology by that date (Olby 2003; Strasser 2003; Gingras 2011, Sloan 2014). In his contribution, Waddington displayed considerable interest in finding theoretical explanations for the phenomenon of coordinated morphological change in evolutionary history (Waddington 1960). Organisms were not, in Waddington’s view, simply loose assemblages of parts and functions governed by atomistic genes, and the coordination of morphology and development displayed by real organisms seemed little explained by the reigning population genetical interpretation of natural selection (Amundson 2007, chap. 9).

A review of the scientific developments in evolutionary theory since the Chicago commemoration highlights the importance of these complaints from paleontologists and developmental biologists, complicating the understanding of the history of evolutionary theory since 1959 (Depew and Weber 1995; Gilbert, Opitz, and Raff 1996). In retrospect, the reservations of paleontologists and embryologists a half century ago now seem prescient of the subsequent theoretical developments considered in this volume. What has occurred most prominently in the interim has been a new awareness of complications introduced into the understanding of evolution by paleontology, molecular genetics, and developmental biology. Whether these complications constitute a fundamental alteration in evolutionary theory, warranting the language of a “paradigm shift” as claimed by some, or if they are only a cause for minor adjustments within the theoretical structure of the Synthesis, is an issue that is currently under debate and can only be
assessed by future history (Gilbert, Newman, and Gayon chaps. in this volume; Leland et al. 2014; Bateson and Gluckman 2011; Pigliucci and Müller 2010, esp. chaps. 1, 16, 17),

The dramatic introduction in 1972 of the so-called “punctuated equilibrium” theory by the paleontologists Niles Eldredge and Stephen Jay Gould was the first in a series of programmatic statements to announce itself as offering a new framework for understanding evolutionary change (Eldredge and Gould 1972). As Eldredge and Gould presented their original arguments, the discontinuities displayed by the fossil record were not to be covered over by appeals to the traditional “imperfection of the geological record” argument employed by the Synthesis tradition. These gaps were instead taken as real, requiring additional explanations of evolutionary change beyond the reigning genetical theory of natural selection. Although some parties latched on to these arguments to defend supernaturalistic accounts or saltationist models of evolution, the concern of Eldredge and Gould was rather to suggest an alternative naturalistic explanation that better fit the empirical geological evidence than the gradualist assumptions of the genetical theory of natural selection. The explanatory structure of this new perspective drew heavily on developmental biology, as Stephen Gould attempted in his landmark *Ontogeny and Phylogeny* (Gould 1977).²

The development of complex regulatory genetics in the late 1950s, led by the French school associated with the names of François Jacob, André Lwoff, Élie Wollman, and Jacques Monod, raised further conceptual problems for the atomistic “gene” concept assumed as foundational in theoretical population genetics and the genetical natural selection theory built upon this (Gilbert 2000; Morange 2000; Moss 2003, chap. 5). The gene concept assumed in the mathematical models of population genetics proved difficult to reconcile with the description of the enormously complex biochemical pathways and feedback and repressor mechanisms of regulatory genetics. These processes linked the nucleotide base sequences in DNA to the production of proteins and structures and functions of real organisms in the process of development. The complex relationship between the concept of the “gene” employed in statistical-population genetics and that utilized in developmental biology and molecular genetics continues
to define an area of philosophical inquiry in life science (Falk 2000, Neumann-Held and Rehmann-Sutter 2006; Rheinberger 2010, chap. 8; Waters 2013).

In summary, the strong emergence of developmentalist and epigenetic perspectives in modern evolutionary biology in recent decades has reemphasized concerns that for various reasons, including practical ones, were not considered in the classic Synthesis. New attention is now given to factors in evolution typically ignored in the evolutionary theory of 1959, including such issues as the influence on evolutionary history created by the restrictions imposed by morphology and the coordination of form and function in organisms. It also has led to reconsideration of the active interactions of organisms with their environment, the importance of learned behavioral traits and their effect on the genome, and even the possibility that environmental factors can play a more significant causal role in evolutionary change than previously allowed, viewpoints long excluded as “Lamarckian” but now developed in more subtle ways by several biological theorists (Gissis and Jablonka 2011; Bateson and Gluckman 2011). The complexity of the “gene” concept introduced by developmental genetics and molecular biology has also challenged the hard determinism assumed between elements of a sequestered germ plasm and the phenotype (West-Eberhard 2003; Moss 2003, 2006). We now see experimental work that suggests the importance of a looser connection in the phenotype-genotype relationship, and how this may explain the rapidity of evolutionary change in some biological groups in paleontological history under new environmental conditions, such as the famous “Cambrian explosion.” With these developments, a new way of understanding “macro” evolution—the evolution of major new groups and body plans in history—has come into play (Müller and Newman 2003).

**IMPLICATIONS FOR AN INTERDISCIPLINARY DIALOGUE**

There are also additional reasons for drawing out the consequences of the new developmentalist, organismic, and systems perspectives that have emerged in recent biology for broader issues. These bear on their consequences for the anthropological and theological issues
raised by evolutionary theory that are explored in limited ways in this volume. One of the greatest sources of difficulty in developing a productive cross-disciplinary discussion, particularly between working scientists and theologians interested in evolution, has been a direct consequence of certain ground assumptions of the theory of natural selection imbedded in neo-Darwinian theory that have been elevated to metaphysical claims in the philosophy of nature. This particularly concerns two interrelated issues: One is the denial of some kind of natural teleology operative in nature and in organic life that flows from the high priority given within the classic Synthesis to purely chance-like events in evolutionary history. The second, and related, issue concerns the link of these interpretations to the well-worn “evolution and creation” debates. The need for greater clarity in the academic, as well as the public, discussion of these issues is urgent, and it is envisioned that the papers in this volume provide a contribution to a more illuminating cross-disciplinary conversation in the future.

The theoretical framework that lies behind this strong emphasis on stochastic and indeterminist principles in neo-Darwinian theory is a topic of considerable discussion in the philosophy of biology, with competing positions drawn that reach a high level of sophistication and involve the interpretations of the interactions of concepts of fitness and probability theory (Ramsey and Pence forthcoming; Pence and Ramsey 2013). As historical studies have shown, the elevation of the concept of “chance” in evolutionary theory to the importance it attained in the classic reconciliation of genetics and natural selection theory in the 1930s is the product of a conceptual development of the early twentieth century. It is not itself something we find emphasized in the texts of Darwin, who, writing before the “probabilistic revolution” of the nineteenth century, mainly referred to “unknown laws” that governed the causes of variation.3

In formulating the genetical theory of natural selection, R. A. Fisher was concerned to develop an interpretation of evolutionary theory modeled on statistical mechanics of Ludwig Boltzmann, Willard Gibbs, and James Clerk Maxwell (Depew and Weber 1995, chap. 10; Hodge 1992). This physical theory accounted for such phenomena as the macrobehavior of gases in accord with standard deterministic
laws of pressure and volume as mass-action effects underlain by the randomized behavior of component atoms that were themselves governed only by probabilistic laws in their individual behavior. By the explicit transposition of an analogy between the behavior of molecules in gases and the behavior of genes in populations acted upon by selective forces, it became possible to analyze evolutionary change with statistical models, utilizing the idealizations of parametric statistics, one of which is mathematical randomness. Interbreeding within populations was modeled as a random process; micromutation, as the fundamental source of evolutionary novelty, was envisioned as undirected, unpredictable, and likely caused by such events as randomized cosmic ray bombardment. As a consequence, evolutionary change was presumed to be governed in its theoretical foundations by undirected causal chains eventually reaching back to randomized mutations acted upon by natural selection.

The axiomatic status of this claim in common interpretations of neo-Darwinian theory has subsequently come to underlie the recurrent claim, encountered in the textbooks as well as the writings of popularizers, that evolution is governed by blind chance, and that it thereby destroys all traditional notions of natural teleology and, by implication, theology (Dawkins 2008, 1987; Monod 1971; Stamos 2001). In the words of geneticist Peter Medawar, “it is upon the notion of randomness that geneticists have based their case against a benevolent or malevolent deity and against their being any overall purpose or design in nature” (Medawar and Medawar 1977, 167). The predictable pushback against these claims from various constituencies has been the main generating source of the ongoing controversy over “creation science” and “intelligent design” that has spilled over into decisions of school boards, court trials, legislative decrees, and eventually electoral politics in the United States and even internationally.

Gaining greater clarity on these matters is urgently important, but the heated character of the public debate makes this difficult. It also requires clarity over the issues at stake in the debate. Are these issues of probability theory, of scientific realism, or of the fundamental metaphysics of nature? The deficiencies of the traditional conceptualization of this debate on philosophical grounds are addressed in limited ways
in this volume in the chapters by David Depew; Gennaro Auletta, Ivan Colagè, and Paolo D’Ambrosio; William Carroll; John O’Callaghan; and Józef Życiński; and deeper clarification hinges on developing a more accurate understanding of the meaning of “creation” in relation to “purpose” as it has functioned in the tradition of Abrahamic religions. But in addition to arguments that can be raised on a philosophical level, there are also conceptual developments emerging from within modern evolutionary biology itself that require some rethinking of the role of undirected natural events as a fundamental explanatory category in evolutionary theory. These developments open up new territory for conversation between evolutionary scientists with philosophers, ethicists, and theologians, which this volume will explore in a limited way.

The new concepts and perspectives that have accompanied the evolutionary-developmental and systems-theoretical perspectives of “evo-devo,” and the post–Human Genome Project concern with “epigenetics,” have forced back onto the table consideration of issues of form, structure, immanent teleological directedness, and the dynamic interaction of organisms and their environments (West-Eberhard 2003). These developments are taking place often through the introduction of a different conceptual vocabulary—concepts such as “robustness,” “system,” “plasticity,” “niche construction,” and “teleonomy” (Bateson and Gluckman 2011; Pigliucci and Müller 2010; Nijhout 2002)—and do much of the work that commentators in touch with a longer tradition of discourse might understand as being appeals to “formal” and even “immanent final” causes (Grene 1967). The fact that such conceptual translations can now be made, even if imperfectly, facilitated by developments emerging from within evolutionary science itself, opens up space for a new level of conversation between ethicists, theologians, philosophers, and scientists concerning such crucial issues as the place of the human being in an evolutionary cosmos, the possibility of a normative ethics with some connection to biology, and new ways of conceptualizing human transcendence—in-continuity. This can be conducted without entry into the controversies over “intelligent design,” which inevitably return us to the heritage of the Platonic-Stoic and British natural theology traditions that Darwin’s arguments discredited.