FOREWORD

MASSIMO PIGLIUCCI
GERD B. MÜLLER

JULIAN HUXLEY was one of the intellectual giants of the twentieth century. His academic career lasted only from 1910, when he was appointed Demonstrator in the Department of Zoology at Oxford, until 1927, when he resigned from his post at King's College in London to cowrite a popular book on biology with H. G. Wells. During and after this period, however, Huxley influenced the field of evolutionary studies by mentoring some of the greatest biologists of the first part of the twentieth century, including E. B. Ford, Gavin de Beer, Charles Elton, and Konrad Lorenz; he coined terms that are still in use today in biological practice, such as *cline* and *clade*; and of course he published this book, which introduced the Modern Synthesis, the conceptual structure underlying all of evolutionary biology for most of the twentieth century.

This would have been more than enough to ensure his fame, and yet Huxley was also the first director of UNESCO, the United Nations Educational Scientific and Cultural Organization, as well as founder of the World Wildlife Fund. He wrote extensively about science, humanism, and conservation, and his 1934 documentary film *The Private Life of the Gannets*, the world's first on natural history, won an Oscar. Although he flirted with eugenics (not an uncommon attitude among liberal intellectuals of the time), he famously wrote that race was a meaningless concept in biology, was a staunch critic of Stalinism, and was concerned with the human environmental impact on the world. He predicted that our population would reach six billion by 2000; he was wrong by less than two months: the actual date turned out to be October 12, 1999. All of this despite suffering on and off from bipolar disorder, not to mention a severe mental breakdown that consumed him for a whole year when he was 55. There are several other people's lifetimes packed into what Julian Huxley was able to do in his 87 years of existence.

It is particularly appropriate to re-release *Evolution: The Modern Synthesis* around the 150th anniversary of the publication of Darwin's *Origin of Species* (Darwin, 1859). Huxley's grandfather was Thomas Henry Huxley, otherwise known as "Darwin's bulldog," and it was from his grandfather that Julian initially got his interest in biology, and in particular in ornithology. Thomas brought Julian to the Kew Botanical Gardens to visit Joseph Dalton Hooker, one of Darwin's closest allies in the battle for the acceptance of the original evolutionary theory. It is hard to underestimate the vibrancy of the intellectual environment that characterized the Huxley family, which also included Julian's father, Leonard, who was an editor and writer; his maternal grandfather, Tom Arnold, another academic; and his brothers Aldous, the writer, and Andrew, a biologist who won the Nobel Prize, to mention just a few. Julian graduated from Oxford—with first class honors—in 1909, the same year that marked the 50th anniversary of the publication of *Origin*. Just shy of fifty years later, around the 100th anniversary of the book, Julian Huxley was knighted and won the prestigious Darwin-Wallace medal from the Linnean Society, the scientific organization that had published Darwin's and Alfred Russel Wallace's joint papers on the new theory of evolution by natural selection (Darwin and Wallace, 1858).

Julian Huxley was well known and appreciated as a science popularizer, but he was a first rate scholar in his own right. That is perhaps why it is rather difficult to classify the book you are about to read. Typically, *Evolution: The Modern Synthesis* is considered a popularization of the ideas then in ferment in the field of evolutionary biology, ideas whose scientific elaboration is usually attributed to books by Ronald Fisher (1930), Theodosius Dobzhansky (1937), Ernst Mayr (1942), George Gaylord Simpson (1944), and Ledyard Stebbins (1950)—although fundamental contributions to the synthesis were also made by population geneticists J. B. S. Haldane (1932), Sewall Wright (1932), and Bernhard Rensch (1959), among others.

And yet, *Evolution: The Modern Synthesis* is more appropriately described as a hybrid between a popular and a scientific book, written with academic rigor and scholarship but accessible to the general educated public, in the proud tradition of Darwin and Thomas Henry Huxley. The prestigious *American Naturalist* wrote of it: "The outstanding evolutionary treatise of the decade, perhaps of the century" (Hubbs, 1943). Indeed, in it Julian Huxley provides his readers with a breathtaking panoramic view of the many fields of inquiry that constitute evolutionary biology, from the theory of natural selection to the genetic basis of heredity, from speciation to adaptation, and from ecology to paleontological trends.

The book will be somewhat surprising to the contemporary reader for a variety of reasons. To begin with, it is fascinating to experience how modern Huxley's thinking already was at the beginning of the 1940s, a time at which we had yet to discover the structure of DNA, and when "Mendelism" was still a relatively new idea. Moreover, Huxley gives ample space to a few scientists whose fame has waned since then, not necessarily for good reasons. Chief among these is the German geneticist Richard Goldschmidt, whose work *The Material Basis of Evolution* (1940) was then considered an important part of the ongoing discussion on evolutionary theory, but is rather unfortunately dismissed today for his suggestion that evolution sometimes produces "hopeful monsters." These were organisms characterized by substantial differences from their close relatives, which Goldschmidt thought would from time to time inject some radical new variation into the evolutionary process. Goldschmidt's book is full of fascinating biology and raises still relevant questions, such as the origin of evolutionary novelties. His infamous monsters appear only at the end of the large volume. Today we know that Goldschmidt's imagined mechanism for the appearance of monsters was wrong: genetic "revolutions," that is, radical rearrangements of the genome, do not occur. But we also have several examples of the actual rapid evolution of new forms, especially among plants, and the most current debates in evolutionary biology once again focus on a variety of possible mechanisms that may quicken the evolutionary pace (e.g., Müller and Newman, 2005; West-Eberhard, 2005; Budd, 2006; Hong, Hendrix, and Levine, 2008).

A similar observation can be made about Huxley's remarkably pluralistic treatment of species concepts and speciation processes. The (far from being universally accepted) orthodoxy today is that Mayr's definition of species in terms of reproductive isolation applies to everything but a few exceptions, and that allopatric speciation is the prevalent, if not the only, mode of speciation (Coyne and Orr, 2004). In reality, the "exceptions" in question conservatively include hundreds of thousands of species (many plants and fungi, all bacteria, etc.), and the direct empirical evidence for allopatric speciation is as good (or bad) as the evidence for other "mechanisms," allopatry carrying the day only if one accepts it as the default null hypothesis, which arbitrarily shifts the burden of proof. It is refreshing to see, then, that Huxley clearly referred to the "biological" species concept as too narrow, instead discussing a variety of types of species in nature and then proceeding to present his readers with a rich taxonomy of modes of speciation, types of isolation, and speed of phenotypic and genetic differentiation.

Due to Huxley's emphasis on the powers of natural selection, on population level change, and on speciation, it is generally overlooked how acutely aware he was of the fact that this does not cover all aspects of organismal evolution. In a thought-provoking chapter on trends, he addresses the peculiarities of phenotypic change. Carefully, so not to be mistaken as advocating any kind of goal-directed, Lamarckian, or anti-mechanistic factors of adaptation, Huxley discusses the problems of phenotypic trends and the question of whether these are always adaptive. He chastises orthogenesis, the term of the period for what might today be called internal dynamics, but at the same time he allows for restrictions on the amount of possible variation and recognizes both mutational and historically acquired biases that limit variation, or even make it impossible. In this context he develops a genuine concept of "consequential evolution," which essentially is an attempt to account for the directional effects of ontogenetic development. Huxley treats development mostly in terms of allometric growth and heterochrony, and puts forth a visionary speculation about the role of rate genes that act through affecting the timing of development. He sees certain types of trends as consequences of the restrictions imposed by gene-development interactions, invoking the works of Haldane, Goldschmidt, Waddington, de Beer, and others, and reaches the firm conclusion that the course of Darwinian evolution is not merely determined by mutation, natural selection, and the history of the species but also, as he emphasizes forcefully, "by the nature of the developmental effects of genes and of the ontogenetic process in general" (chap. 9, p. 555). Although Huxley points to the originality and importance of this thought even in the preface, it took nearly half a century until it was taken seriously by the research program of Evo-Devo.

Huxley, of course, is far from getting everything right. He is a scientist, after all, not a magician. His discussion of natural selection often sounds too "adaptationist" (Gould and Lewontin, 1979) for readers familiar with the modern concepts of genetic and developmental constraints, and his lengthy critique of notions like Lamarckism and orthogenesis are a reflection of what was then still an open intellectual debate about modes of inheritance and mechanisms of macroevolution—neither of which have survived much past the Modern Synthesis. Huxley devotes his last chapter to a discussion of the idea of progress in evolution, touching on a topic that few biologists would seriously entertain today (not necessarily a satisfactory state of affairs). For Huxley, evolution makes progress without having a goal—with progress defined as "a raising of the upper level of biological efficiency, this being defined as increased control over and independence of the environment" (chap. 10, pp. 564–565). In other words, for Huxley progress in biology has nothing to do with Aristotelian notions of teleology, nor does it imply a "Scala Naturae" with human beings at the top, as the pinnacle of creation. Nonetheless, for Huxley and for some contemporary biologists there is still something to be explained, something that deals both with the undeniable increase in complexity of biological organisms over geological time (see Gould, 1996 for a non-teleological account) and with the idea that the degree of adaptness of lineages to their environment ought logically to increase over time as a result of natural selection (except that it apparently does not: see Van Valen, 1973).

Huxley's seminal 1942 volume became one of the most successful books in the history of biology. It has seen five reprintings as well as a second (1963) and a third (1974) edition. Both subsequent editions contained new introductory chapters that brought the volume up to date with the current knowledge of the period. The 1963 introduction, by Huxley himself, covered all new discoveries, ideas, and lines of study, both theoretical and experimental, demonstrating his commanding oversight of the ongoing developments in evolutionary biology. His conclusion was that the basic edifice of the Modern Synthesis had been strengthened, and new details added, but that the new results, including the discovery of the structure of DNA, had not fundamentally altered evolutionary theory or our understanding of the course of evolution. The introduction to the 1974 edition was coauthored by nine experts from different fields of evolutionary biology, most of them close associates of Huxley, providing authoritative overviews of the massive progress in the diversified fields of study and adding a host of new data obtained with the greatly expanded toolkit of biological research. Yet again, no significant conceptual change of the Synthesis framework had been perceived. Both these substantial introductions, as well as their attendant bibliographies, are included in the present edition, and together with Huxley's text provide a complete overview of the field as it was understood at that time.

Since 1974, the field of evolutionary biology has not only grown exponentially and diversified in an even greater fashion, including an avalanche of new data resulting from the technologies of the molecular era, but a number of theoretical modifications and conceptual innovations have also taken place that have expanded the core theoretical framework and the explanatory capacity of the Modern Synthesis. No new introductory chapter could have done justice to these conceptual developments, which is why the present reprinting of *Evolution: The Modern Synthesis* has a companion volume edited by the authors of this foreword, entitled *Evolution—the Extended Synthesis* (Pigliucci and Müller, 2010).

The idea of a new, extended evolutionary synthesis that we advocate in the companion volume is as controversial today as the idea of the Modern Synthesis was in Huxley's time. Just as he had to clear the air of Lamarckism and orthogenesis, we are in the process of cutting down to size the gene-centrism that has dominated biology since the molecular revolution of the latter part of the 20th century. In the same way that Huxley wrote from a pluralist perspective about species concepts and mechanisms of speciation, we are pushing a complex view that includes the legitimacy of multiple levels of selection (from gene to species) as well as the existence of mechanisms that create self-organized complexity in addition to natural selection. In due course we also expect some of the new ideas to be discarded or significantly modified, analogous to what happened to many proposals discussed in Huxley's landmark volume.

This continuing revision of the edifice whose foundations were laid out by Charles Darwin in the middle of the nineteenth century should not give comfort to creationists, intelligent design proponents, and other anti-science advocates. On the contrary, reexamination of old ideas, proposal of new ones, and synthesis of the best of what is available is precisely how science works, and how biologists have slowly built a solid set of explanations for what Darwin called "the grandeur" of life.