Introduction

Contemporary analytic philosophy of biology was forged in the 1960s. It began a little more than 50 years ago with Morton Beckner's *The Biological Way of Thought* (1959). Building on this seminal contribution, in articles and books, Thomas Goudge (*The Ascent of Life*, 1961), Marjorie Green (*Approaches to a Philosophical Biology*, 1968), David Hull (*Philosophy of Biological Science*, 1974), and Michael Ruse (*The Philosophy of Biology*, 1973) laid the foundation for modern philosophy of biology.[1] These founders of the field articulated and staked out positions on nearly all the important logical and conceptual underpinnings of evolutionary biology, as well as the social implications of its theories and empirical discoveries.

Michael Ruse's 1973 *Philosophy of Biology* consolidated the field by providing a rigorous analysis and comprehensive treatment of nearly all the critical conceptual issues, including those that have remained contentious; it still stands as a *tour de force*. In 1979, *The Darwinian Revolution: Science Red in Tooth and Claw* was published. It remains an exemplar of the integration of philosophy of science and history of science. Since that time, he has:

- founded, in 1986, the leading journal in philosophy of biology, *Biology and Philosophy* (and nurtured it into being one of the top four journals in philosophy of science);
- founded, in 1995, and edited, from 1995 to 2011, the *Cambridge Studies in Philosophy and Biology* series, which during that period published 80 of the most important books in the field;

[1] A few biologists – J. H. Woodger, C. H. Waddington, and Bernhard Rentch, for example – and physicists – Erwin Schrödinger, for instance – had tackled philosophical aspects of biology but philosophical interest in biology by philosophers of science dates from the work of this group. Earlier philosophical work such as Henri Bergson's *Creative Evolution* and the use by philosophers of Darwinian fitness and Lamarckian inheritance, such as by Herbert Spencer, are very different from contemporary analytic philosophy of biology.

- written more than 20 books (almost all of which have been translated into other languages);
- edited more than a dozen books;
- contributed more than 100 journal articles;
- been a leader in championing evolution in the broader society and in promoting science education.

Moreover, his impact on philosophy of biology includes mentoring several generations of researchers and scholars who have achieved international reputations in their own right. He has received numerous prestigious research awards, including the John Simon Guggenheim Fellowship and Isaak Walton Killam Fellowship. He was elected Fellow of the Royal Society of Canada and Fellow of the American Association for the Advancement of Science, and has received honorary degrees from the University of Bergen, McMaster University, and the University of New Brunswick.

Given his formative role in the development of philosophy of biology, his contributions to research and scholarship, his broader social contributions, his mentoring of generations of scholars and researchers, and his impressive publication record and influence, it is fitting that this volume of original articles by internationally renowned philosophers of biology should be dedicated to him. Although some of the contributors to this volume disagree with some of his positions and arguments, all recognize his importance and the profound impact he has had on the field; many make direct reference to his work. As Michael has told so many of us over the last 50-plus years, "criticize me; just don't ignore me." He has certainly not been ignored and there is no shortage of criticism.

This volume continues the exploration of evolutionary biology that he initiated. Today evolution – both the fact that it occurred and the theory, descended from Darwin, describing the mechanisms by which it occurred – is an intrinsic and central component in modern biology. Theodosius Dobzhansky captures this well in the oft-quoted title of one of his 1973 papers,[2] "Nothing in biology makes sense except in the light of evolution." The correctness of this assertion is even more obvious today than in 1973. Philosophers of biology, historians of biology, and biologists agree that the fact of evolution is undeniable, and that the theory of evolution provides unity to evolutionary biology as a whole, is conceptually rich, and has far-reaching social implications. Like all scientific theories,

[2] Dobzhansky 1973.

however, there are some conceptual and epistemological underpinnings on which there is no settled opinion. Also, like all sciences, there are implications of evolutionary biology that engender intense public controversy.

Notwithstanding the central place of evolutionary theory in biology, there are a number of conceptual and epistemological underpinnings on which there is no settled opinion. These include: the relationship of organisms and their molecular components, the nature of species, the nature of adaptation, the formal (logical/mathematical) structure of evolutionary theory, and the nature and role of development. Each of these poses deep philosophical challenges. The chapters in this volume continue and advance the discussion of them.

The contributors to this volume are philosophers and biologists who have been at the forefront of seeking resolutions to these pivotal conceptual and societal issues. With the exception of the tension between evolution and certain religious sects, there has been considerable convergence, over the last 50 years, with respect to all these issues. Sometimes the convergence has moved debate closer to resolution; sometimes it has led to an identification of remaining impediments. In the case of the tension between evolution and literalist fundamentalist Christianity and Islam, the nature of the tensions and the critical importance of resolving them have been brought into sharper focus. The goal of the volume is to provide readers with a window on the current thinking of those who have shaped the discourse on these contentious issues over several decades.

The collection begins with a contribution from the eminent evolutionary biologist Francisco Ayala. Professor Ayala has a longstanding history of collaboration with Michael Ruse, and his chapter demonstrates the rich potential to be found in the cross-pollination between philosophy and evolutionary biology that Ruse has done so much to foster. Ayala takes up themes broached in Ruse's most recent book, *The Philosophy of Human Evolution* (2012). Specifically, Ayala addresses the evolution of ethical behavior in the transition from ape to human. Ethical behavior has clearly evolved, but quite how it might have done so has been a challenge to evolutionists. There are two principal problems for any evolutionary ethics. The first is that the standard strategy deployed in explaining the evolution of some structure or ability appears to break down in the case of the human capacity for moral judgment and action. Typically, to explain the conditions under which some feature has evolved, one simply articulates the fitness benefit that feature confers on its bearers. The vexed problem for evolutionary ethics is that moral imperatives and fitness imperatives don't obviously coincide. The second problem is what Ayala calls the

"naturalistic fallacy." Those who seek to ground ethical behavior in evolution run the risk of negating it. If ethical behavior consists in acting ultimately on fitness imperatives, then we have merely been duped by our genes into thinking we are acting under the guise of the moral good.

Ayala's chapter seeks to finesse these two problems simultaneously. He distinguishes between two questions that are often conflated: (1) whether our capacity for moral deliberation and behavior is an evolutionary endowment, and (2) whether the specific moral norms that guide our actions are an evolutionary endowment. Ayala delivers a positive verdict on the first question: "Humans evaluate their behavior as either right or wrong, moral or immoral, as a consequence of their eminent intellectual capacities, which include self-awareness and abstract thinking. These intellectual capacities are products of the evolutionary process, but they are distinctively human" (p. 18). But, in opposition to much of sociobiology and mainstream evolutionary ethics, he insists upon a negative answer to the second: "moral norms according to which we evaluate particular actions as morally either good or bad … are products of cultural evolution, not of biological evolution. The norms of morality belong, in this respect, to the same category of phenomena as the languages spoken by different peoples, their political and religious institutions, and the arts, sciences, and technology" (p. 18).

The capacity for ethical behavior, Ayala argues, is conferred on us by three distinctively human cognitive abilities: the ability to anticipate consequences, the ability to make value judgments, and the ability to choose between available courses of action. While these abilities are jointly constitutive of the capacity for ethical behavior, they are not exclusively moral faculties. They grow out of the facility that our hominin ancestors developed for the use and production of tools, means–end reasoning, the planning and assessment of other forms of action. Ayala sees "no evidence that ethical behavior developed because it was adaptive in itself … It seems rather that the likely target of natural selection was the development of advanced intellectual capacities" (p. 22).

After Francisco Ayala's tour through the challenges facing the study of human evolution, Part I of this collection turns to an area of dispute in which Michael Ruse has become particularly prominent in recent years: the compatibility of evolutionary biology with religious thought. Ruse has been perhaps the pre-eminent exponent of conciliation between the power of evolutionary biology to reveal the mysteries of life, and the draw many feel toward devotional religious belief. Ruse has consistently valued irenics over histrionics on these matters; his has been the voice of

moderation heard over the stentorian tones emanating from both secular and religious extremes. His *Evolution and Religion: A Dialogue* (2008) captures all these tones with a keen composer's ear. This section features two eminent philosophers of science, Elliott Sober and Philip Kitcher. Each in his way comes out strongly in support of both Ruse's placatory tone, and his compatibilist message.

Elliott Sober argues that evolutionary theory is logically consistent with the conception of a god familiar to Abrahamic religions, who intervenes in the processes of the world. Sober explains that evolutionary theory is fundamentally probabilistic. The theory yields probabilities of certain outcomes – for instance the increase of one trait type over another – given certain conditions. As Sober points out, probabilistic theories can be true, inductively generalizable, testable, and informative, even if they are not causally complete. There is room then, for "hidden variables," causes of evolutionary phenomena that are not articulated by the theory. It is *logically* consistent, then, with evolutionary theory that these unarticulated causes may be supernatural in origin. Nothing in evolutionary theory proscribes this. It is commonly thought that if there is divine involvement in the processes of evolution, it should be manifested in the pattern of evolutionary novelties. A providential god should or would bring about novelties that are beneficial to those organisms in which they arise. Biologists know, however, that evolutionary novelties arise through mutations, and that mutations are random – in the sense of unguided. But the unguidedness of mutations is in no way incompatible with the thesis that they are divinely caused: "[W]hat biologists mean, or ought to mean, when they say that mutations are unguided says nothing about whether God ever causes a mutation to occur" (p. 32). Invoking Pierre Duhem, Sober reminds us that the application of a scientific theory to the world requires auxiliary assumptions. Evolutionary theory could only have implications about the existence of a deity if it were supplemented by certain auxiliary assumptions. But these auxiliary assumptions are all philosophical, and not biological, in nature. They are not licensed by evolutionary theory alone. Striking a note strongly concordant with Ruse's own message, Sober concludes: "Atheists who think that evolutionary theory provides the beginning of an argument for disbelieving in God should make clear that their arguments depend on additional premises that are not vouchsafed by scientific theory or data" (p. 43).

Philip Kitcher in his chapter addresses the delicate issue of reconciling the role of religion with the atheist's conviction that religious beliefs are false. Kitcher aligns himself with Ruse here, against a phalanx of

outspoken contemporary atheists, particularly the self-anointed "four Horsemen." "Although we agree with the Horsemen that there is a sense in which all religious doctrines are false, we don't take this to be the end of the proper discussion of religion" (p. 46). Kitcher draws upon the pragmatist insight that the world we inhabit is to a significant degree one of our own making, structured by "our psychological faculties and our purposes" (p. 48). As scientists we pursue the process of comprehending, predicting, and intervening on the world. And we have generated ways of thinking appropriate to those purposes. "But these are not our only purposes," Kitcher reminds us (p. 49). "We devise ways of thinking and forms of language directed toward different ends – in play, in literature and arts, in ethics, and in religion" (p. 49). Kitcher introduces us to the idea that truth in general applies to sentences that are employed in the pursuit of a human project. As such there exist a range of species of truth. Kitcher outlines his conception of religious truth. *S* is weakly religiously true (roughly) just when there is an established religious practice that affirms *S*. *S* is strongly religiously true (again, roughly) just when any progressive modification of said practice would continue to affirm *S*. There are weakly religious truths. Kitcher speculates that there may be no strongly religious truths (except, perhaps, for strong ethical truths). He doubts "whether any particular fiction, even the myths of the axial age, is so deep and fundamental that it delivers strong religious truths" (p. 60). That said, religious practice will rightly continue to form a part of the human project of responding to the challenges of "forging identities" and "achieving communities". These projects are in no way incompatible with the scientific project of comprehending, predicting and intervening on the world.

Part II focuses on taxonomy and systematics, another topic on which Ruse has made many important contributions. The concept "species" is central to taxonomy and has been a thorny concept since before the publication of the *Origin*. Darwin spends much of the first three chapters of the *Origin* arguing for, essentially, a nominalist conception; that is, species are not real, they are a human artifact that is useful – perhaps essential – to biology but not part of the nature of things. Contemporary evolutionary biologists recognize a number of different – and not necessarily compatible – definitions of "species." The most commonly known is the biological species concept; members of the same species can interbreed without sterility. This has proved a useful definition in a number of contexts but does not apply to non-sexually reproducing organisms, and they comprise most of the living world. Moreover, it doesn't even apply in many cases of

sexually reproducing organisms. The classic exception is ring species and there are numerous instances of ring species.

Marc Ereshefsky responds directly to Michael Ruse's work on the species concept. He identifies two philosophical issues that Ruse has addressed. One is the ontological status of species: are species natural kinds akin to elements on the periodic table or are species individuals akin to particular organisms? The other concerns whether "species" refers to a real category in nature or whether the species category is merely an artifact of our theorizing. On both issues, he contends that Ruse made major and important contributions. Nonetheless, although Ruse's arguments concerning species are cogent and innovative, Ereshefsky contends that they are flawed. He mounts a case for considering species as historical entities, something to which, he contends, Ruse pays too little attention. On the question whether "species" refers to a real category in nature, he offers a pragmatic form of species anti-realism.

David Castle explores the nature and role of DNA barcoding in taxonomic practice. Barcoding is relatively new in taxonomy. As the term suggests, DNA barcoding is similar to merchandise barcoding except the "bars" are short segments of DNA rather than lines of different lengths, thicknesses, and spacing. Hence, barcoding provides a method by which groups of organisms can be differentiated by comparing short, standardized regions of DNA. Castle examines the how the taxonomic community has responded to DNA barcoding; to state that this technique is still controversial is to understate the polarization it has created. A pluralist perspective seems appropriate – that is, traditional taxonomic practice and barcoding informing each other – but that has yet to be achieved. Castle opens his chapter with a very useful introduction to barcoding, its aims and methods. He then examines three main objections to barcoding. His position centers on barcoding as an evolving method and he sees the objections to it as, in significant part, being motivated by protection of past practices; barcoding, "exemplifies to traditional taxonomists many perceived threats they most fear." The outcome of his analysis should lay the groundwork for a pluralistic approach and allay the fear of traditional taxonomists.

Part III focuses on the structure of evolutionary theory. Two views on the structure of evolutionary theory dominated philosophical discussion in the 1960s. One, strongly influenced by logical empiricism, maintained that the logical structure of theories in biology was the same as physics; both sought axiomatic-deductive systems of laws, which explained and predicted phenomena by deducing them using the laws of the theory and

relevant conditions. This is the view Ruse championed in his 1973 book. He provided a sketch of the axiomatic and deductive nature of evolutionary theory and gave examples of explanatory deductions. The other view maintained that evolutionary theory was different from theories in physics. The nature of those differences varied. Thomas Goudge's "narrative explanation" is an example of a non-deductive explanatory pattern. Ruse contended that narrative explanations were enthymemes and when complete were in fact deductive. Paul Thompson and Jean Gayon essentially agree with Ruse that theories and explanations in biology and in physics are for the most part the same. They, however, are not committed to a logical empiricist conception of either physics or biology. They also recognize that in physics and biology there are numerous metaphors and analogies that motivate and interpret concepts, as Jean Gayon's chapter underscores. And they hold that mathematics provides the language and structure for theories, as Paul Thompson's chapter emphasizes. Thompson's and Gayon's chapters are focused on the genetical theory of evolution, but, in the last 30 years, it has become apparent that a complete causal account of evolution must embrace development. Just how that should be done and what the resulting causal structure of evolutionary theory will look like is emerging, as Jane Maienschein and Manfred Laubichler's chapter makes clear.

In his chapter, Thompson develops a response to an obvious, and frequently voiced, criticism regarding his claim that mathematics is the language of scientific theories. In *The Origin of Species*, Darwin employs no mathematics, and yet he formulated a theory that is central to modern biology; this is beyond doubt. Thompson claims that Darwin provided a brilliant "informal" theory along with a wealth of evidence. It was not, however, until a mathematical "formal" account was given in the late 1920s that the internal structure of the theory and its empirical implications were clearly understood. The debates, in the 50 years after the publication of *The Origin*, about whether selection acting on small individual variations could lead to evolutionary change, whether selection decreased variation, whether selection and Mendelian heredity are compatible – or not, as Bateson claimed – and the like were only resolved when a mathematical formalization was provided that integrated Darwinian theory, Mendel's theory, and biometry into a single theory.

In his chapter, Gayon explores R. A. Fisher's analogical use of economic theory in both his population genetics work and his eugenics. Gayon provides numerous examples and weaves a compelling argument that economic analogies connect these two strands of his work and, moreover,

that his eugenic ideas motivated the way he defined and explicated natural selection in his *Genetical Theory of Natural Selection*. Gayon examines in detail the analogy between growth of a population (Fisher's Malthusian parameter) and growth of capital, thereby demonstrating that "Fisher's demographic approach to natural selection relied upon an explicit economic analogy: making children is interpreted in terms of investment, cost, benefit, and repayment." The same dependence on an economic analogy is found in his eugenics writings. The core insight of this chapter is that "Fisher's economic interpretation of the Malthusian parameter was motivated, or at least inspired, not by abstract considerations about natural selection, but by his eugenic way of thinking" (p. 143).

Jane Maienschein and Manfred Laubichler discuss the philosophical and theoretical implications of one of the most exciting and expansive areas of biology to emerge in the last quarter-century – evolutionary developmental biology. Rightly or wrongly, Modern Synthesis lore has it that organismal development was left out of the synthesis. This may not be wholly historically accurate, but it seems fair to say that a proper understanding of the importance of development for evolution has only recently emerged. But quite where this significant expansion of our understanding leaves evolutionary theory is a matter of some debate. Some authors see the assimilation of development into evolution (evo-devo) as wholly complementary to accepted evolutionary theory, as a completion of the project of synthesizing biology's various sub-disciplines embarked on so boldly in the 1930s. "Within evo-devo, the logical place of development within evolutionary theory was in explaining the details of the genotype-phenotype map without changing the explanatory structure of evolutionary biology, which, at its core, was still based on population dynamics" (p. 162). But there is another interpretation; developmental evolutionary biology ('devo-evo') sees tensions. Developmental evolutionary biology promotes a more radical reorientation of evolutionary theory: "[I]n the context of developmental evolution the causal structure of evolutionary explanation has shifted from a primacy of population-level dynamics to the primacy of developmental mechanisms and that explaining the origin of variation rather than the fate of variants within populations is the first and most important problem for all theories of phenotypic evolution" (p. 168).

Adaptation, teleology, and design were at the heart of the *Origin* and are still contentious concepts in evolutionary theory. Part IV explores why living things are the only non-artifacts about which talk of design and purpose seems appropriate – even perhaps indispensable. Organisms are adapted to their conditions of existence – sometimes extravagantly

so – and this alone sets them apart from the rest of the natural world. Indeed reconciling the place of organisms as products of blind, natural processes with their evident exquisite adaptations is a central challenge to evolutionary biology and its philosophy. It was a central objective of Darwin's theory, and it continues to challenge and perplex. Evolution, we are told, is fundamentally chancy, and yet the very concepts of *design and purpose* are in diametrical opposition. In this section three philosophers of biology explore the chance/purpose tension.

John Beatty discusses the metaphor of selection as an architect, found repeatedly throughout Darwin's writing. There are two components to building a construction: materials and a design. Darwin likens variation to the former and natural selection to the latter. But the analogy is multiple and ambiguous and, as beautifully documented by Beatty, is used in a variety of ways by Darwin himself. The ambiguities point to a long-standing question in both the interpretation of Darwin and in modern evolutionary biology concerning the relative importance of variation over selection in the explanation of form. On a strong – nowadays called 'adaptationist' – reading the sources of variation may be explanatorily negligible in comparison to selection. Beatty says: "If the causes of variation do not bias it toward (or away) from the direction of selection, then the direction of evolution by natural selection would seem to be unaided (and unimpeded) by the course of variation, and thus natural selection would seem to be solely responsible for the outcome" (p. 179). But the architect analogy does not support the primacy of selection over the sources of variation univocally. "Whether … the architect analogy demonstrates the major importance of natural selection, and the minor importance of the production of variation, depends on how the analogy is interpreted" (p. 188). Like Darwin's theory itself, nothing about his recurrent architect metaphor commends the primacy of natural selection over chance variation in the explanation of adaptive form.

Denis Walsh discusses the alleged reduction of teleological concepts like function and purpose in evolutionary biology. Evolutionary biology, as Michel Ruse has often pointed out, is peppered with teleological-sounding talk of functions and purposes. Most commentators believe that the status of evolutionary biology as a science depends upon explaining this teleology away – ersatz teleology is acceptable, real teleology is taboo. The standard way of de-teleologizing biological talk is to interpret all teleological locutions as instances of a particular kind of historical explanation that adverts to the effects of natural selection in the past. This is the Etiological Theory of Function, first introduced and promoted by Michael