Introduction

> Let me lay my cards on the table. If I were to give an award for the single best idea anyone has ever had, I'd give it to Darwin, ahead of Newton and Einstein and everyone else.
>
> (Dennett 1995, p. 21)

Listen to Your Mother

In later life the eminent physiologist Sir Charles Sherrington recalled that, as a young man in 1873, as he was departing his home for a summer holiday, his mother persuaded him to take along a copy of the *Origin of Species*, saying "It sets the door of the universe ajar!" (quoted in Young 1992, p. 138). Sherrington's mother was right. No other scientific theory has had such a tremendous impact on our understanding of the world and of ourselves as has the theory Charles Darwin presented in that book.

This claim will undoubtedly sound absurd to some familiar with the history of science. Surely the achievements of Copernicus, Galileo, Newton, Einstein, Bohr, and other scientists who developed revolutionary views of the world are of at least equal, if not greater, significance. Aren't they? Not really. Although it is true that such scientific luminaries made fundamentally important contributions to our understanding of the physical structure of the world, in the final analysis their theories are about *that* world, whether or not it includes life, sentience, and consciousness. Darwin's theory, by contrast, although it encompasses the entire world of living things, the vast majority of which are not human, has always been understood to have deep implications for our understanding of *ourselves*. Look at it this way: Part of what makes human beings distinct from other

living things is our impressive cognitive abilities. Unlike other species that simply manage to make a living in the world, we strive – and sometimes succeed – in *understanding* the world as well. It is partly in virtue of our ability to understand key aspects of the world that we have been so successful as a species. Our best means of understanding the natural world in a genuinely deep sense is through the scientific theories we create. But note: These scientific theories are the products of brains, which are themselves the products of natural processes. Darwin's theory provided the framework for the first credible naturalistic explanation for human existence, including the origin, function, and nature of those capacities that enable us to ponder why we have the characteristics we do. In other words, there is an important *asymmetry* between Darwin's and all other scientific theories. No other scientific theory purports to explain the capacities that permit us to devise and contemplate scientific theories, but Darwin's theory – precisely because the correct explanation for the evolution of human cognitive abilities lies within its domain – provides just such a framework. There is simply no other scientific theory that even comes close to playing this central role in our quest for self-understanding. The importance of understanding Darwin's theory cannot be overestimated.

"How Extremely Stupid Not to Have Thought of That!"

> If superior creatures from space ever visit earth, the first question they will ask, in order to assess the level of our civilization, is: 'Have they discovered evolution yet?'
>
> (Dawkins 1989a, p. 1)

In one sense, of course, Darwin's theory of evolution by natural selection is among the simplest scientific theories ever advanced. Living things vary among themselves. These variations arise randomly, that is, without regard to whether a given variation would be beneficial or not. Those living things with advantageous variations tend to stick around a bit longer than others, and give rise to more like themselves. Hence their numbers increase. That's the essence of Darwin's theory. What could be simpler? As Darwin's friend and scientific advocate Thomas Henry Huxley (1825–95) is reported to have exclaimed after first encountering the idea of natural selection, "How extremely stupid of me not to have thought of that!"

Alas, the apparent simplicity of Darwin's theory is deceptive. From the very beginning Darwin's great idea has been subject to differing interpretations, and even now professional opinion is sharply divided on a range

of fundamental issues. These are not challenges to Darwinism from without (such as "Scientific Creationism") that question the entire project of giving naturalistic explanations of living things but, rather, debates *within* Darwinism about the most basic causes, processes, and expected outcomes of natural selection. Central among these are debates about the nature and operation of natural selection, the scope and limits of adaptation, and the question of evolutionary progress.

Selection, Perfection, Direction

> As natural selection works solely by and for the good of each being, all corporeal and mental endowments will tend to progress towards perfection.
>
> (Darwin 1859, p. 489; 1959, p. 758)

So wrote Charles Darwin in all six editions of the *Origin of Species*.[1] What he meant by this claim, how later biologists have treated the issues it addresses, and whether (or in what sense) this claim might be true, are the subjects of this book.

Part I focuses on natural selection, the central theoretical principle of Darwinism. Selection explains why living things display complex adaptations, giving them the appearance of having been intelligently designed. But life exists on many "levels," with biological systems organized hierarchically from genes and cells up through species and ecosystems. Selection is usually thought of as acting upon organisms. But does selection act at other levels as well? How did Darwin think about the level(s) at which selection operates and forges adaptations (Chapter 1)? Does selection operate at levels "above" individual organisms, e.g., at the level of groups (Chapter 2)? What has led biologists to argue about the correct "unit of selection," and how are such disputes best resolved (Chapter 3)?

Part II examines the issue of biological "perfection." The two most striking general facts about the living world that require explanation are the sheer diversity of forms of life, and the incredible adaptive fit between living things and their environments. It has sometimes even been claimed that organisms are *perfectly* adapted to their ways of life. But is the idea of perfect adaptation even coherent? How did Darwin view the issue of biological perfection (Chapter 4)? How have biologists after Darwin understood the relationship between natural selection and adaptation (Chapter 5)? What degree of biological perfection does the theory of natural selection predict, and what factors prevent living things from achieving perfect adaptation (Chapter 6)?

Part III examines the controversial issue of "evolutionary progress." It has seemed obvious to many biologists that there has been an overall direction in the evolution of life toward more complex, sophisticated organisms. Once there were only the simplest sorts of living things – replicating molecules, perhaps. Now the world burgeons with innumerable species displaying amazing adaptations fitting them for every conceivable niche in the economy of nature. How could anyone who accepts an evolutionary view of life deny that progress has occurred? Yet perhaps no other issue in evolutionary biology has inspired such passionate controversy. How did Darwin approach the issue of evolutionary progress (Chapter 7; additional discussion of this highly contested issue appears in the Appendix)? How have later biologists addressed this issue (Chapter 8)? Does talk of "higher" and "lower" organisms make sense? Are some organisms more "advanced" than others? Is there an overall direction to evolution? In the final analysis, does it make any sense at all to describe evolution as "progressive" (Chapter 9)?

Although different parts of the book focus on each of the three issues of "selection," "perfection" (adaptedness), and "direction" (progress), they are closely related to one another, and the interconnections between them are as interesting as the details of each one taken separately. As noted above, Darwinism is uniquely important as a scientific theory in large part because it bears directly on the origin, nature, and destiny of the human species, including explanations for both our "corporeal and mental endowments," as Darwin called them. The final chapter explores these issues as they relate to our self-understanding as a species. Can selection account for the most distinctive human characteristics? How well adapted, in body and mind, are human beings? Was there anything inevitable about the evolution of *Homo sapiens*? Finally, given our best current understanding of evolution, what sort of fate might our species anticipate? Such questions are addressed by reviewing the results of earlier chapters with an eye to understanding their significance for human evolution. They form the bulk of Chapter 10.

Science and Religion

> [W]e are not here concerned with our hopes or fears, only with the truth as far as our reason allows us to discover it.
>
> (Darwin 1871, vol. 2, p. 405)

Having said this, one might naturally expect to find an extended discussion of the implications of evolutionary ideas for traditional religious

conceptions of humankind. After all, for many nonbiologists (and even for some biologists), "Darwinism" is inextricably linked to theological issues.[2] This is understandable. In the public mind, Darwinism and "creationism" are often seen as locked in a battle for the hearts and minds (and souls) of men. From the very beginning, friends and foes alike have seen in Darwin's theory profound implications for religious beliefs about the origin, nature, and destiny of human beings. Are we the special creations of a loving Deity, made in His image, or the accidental by-products of a blind, purposeless process which never had us (or anything, for that matter) in mind in the first place? Do we have immaterial souls which distinguish us from all other living things, making possible self-consciousness, a conscience attuned to the dictates of morality, and the hope for immortality, or are we simply bipedal primates whose peculiar adaptation consists in a hypertrophied neocortex, enabling us to ponder questions whose answers lie forever beyond the range of our impressive (but bounded) cognitive abilities? Do each of us as individuals have a glorious (or hellific) future to anticipate, or will each of us at the moment of death simply cease to exist, the personal analog of the extinction that has determined the destiny of 99.99 percent of all species that have ever existed?

It would be tempting to try to draw definitive conclusions about such matters from a survey of Darwinian ideas. Many have succumbed to this temptation, often cloaking deeply entrenched personal opinions in the thinnest of scientific attire (e.g., Provine 1988). Matters are rarely so simple, and the implications of Darwinism for perennial questions such as "the meaning of life" are not straightforward (Miller 1999; Ruse 2000; Stenmark 2001). The reader will look in vain for such a discussion in the present book, which focuses on Darwinism *per se*, rather than on its relationship to other (nonscientific) issues. I want to leave entirely open the question of whether a Darwinian view of life is compatible with a religious view of life. (This is, incidentally, the very same approach that Darwin took in the *Origin of Species*.) The reasons for this exclusion are both practical and philosophical. Practically, this would be a much different, and much longer, book were it to address such issues. Philosophically, the relationship between evolutionary ideas and religious beliefs is far more subtle and complex than is often supposed. Besides, any *serious* discussion of the relationship between Darwinism and religious belief presupposes an historically informed and philosophically critical understanding of evolution – just what this book attempts to provide. Readers are invited to follow out the implications for religious belief of the various evolutionary

ideas discussed in this book, if they wish, but they will receive no direct assistance from this book itself. Its central concerns lie elsewhere.

Methodological Confessions

> [One] does not know a science completely as long as one does not know its history.
>
> (Auguste Comte; quoted in Kragh 1987, p. 12)

Like life itself, scientific theories are historical entities whose present forms are products of the past, and are thus fully comprehensible only when understood against this background. This is perhaps especially true for ideas concerning evolution, since controversy has accompanied evolutionary thought from the very beginning. Consequently, the discussions that follow approach each of the main topics of the book (selection, adaptation, progress) historically by looking first at early views (especially those of Darwin), then moving forward as the ideas were further developed and modified in the twentieth century, and finally ending with contemporary views and debates. There is plenty of history in the pages that follow. Nonetheless, one thing the reader will not find in this book is history for history's sake. I have enormous respect for historians and for the work they do. The fruits of their researches inform many of the discussions that follow. But the history presented here always has one eye on the present, in the sense that contemporary debates determine which aspects of the history of evolutionary thought merit detailed discussion. In this sense the history discussed here is "presentist" – a serious sin from the perspective of some historians, but one which is necessary to accomplish the task at hand.[3]

The historical treatments that follow are therefore necessarily selective. When a cartographer surveys a tract of land, certain features stand out as peaks and high points, while others drop below the line of sight. Both are important, but every feature of the landscape cannot be included in the final map. Likewise, in surveying the scientific landscape of the development of evolutionary biology, certain episodes stand out as deserving of special treatment. This study is organized around these high points.[4]

Darwin's Long Shadow

> No other field of science is as burdened by its past as is evolutionary biology. . . . The discipline of evolutionary biology can be defined to a large degree as the ongoing attempt of Darwin's intellectual descendants to come to terms with his overwhelming influence.
>
> (Horgan 1996, p. 114)

Our examination of the three major topics of this book – selection, perfection, and direction – begins with an examination of Darwin's views on each of these topics. Understanding Darwin's views is fundamental. Darwinism begins with Darwin, and if we wish to understand how Darwinism has changed – the "evolution of Darwinism" – then we will need to know what Darwinism was in its original formulation(s). Such understanding can then serve to anchor our examinations of later developments. Getting clear about Darwin's own view is important for an additional reason. More than any other figure, Darwin continues to function as the patron saint of evolutionary biology. Showing that one's own view is the same as Darwin's can serve as a powerful rhetorical device in legitimating one's view. It therefore becomes important to have an accurate account of Darwin's views on these topics.

Given the number of years that have passed between the publication of Darwin's works and the present, it would be natural to suppose that all is now well understood about how he conceived of the fundamental nature of the evolutionary process. But this would be mistaken. Although he generally wrote with admirable clarity, the exact nature of Darwin's views on a number of basic issues remains a matter of scholarly dispute. Understanding precisely what he had in mind raises difficult interpretive problems which, given his critical historical role in the development of evolutionary biology, are worth examining and attempting to resolve.

The title of this book reflects the *dual* goals it aims to achieve: First, to convey an understanding of the *sort of evolution* that forms the basis for contemporary Darwinism (i.e., evolution and its products as understood from a Darwinian perspective); second, to understand how *Darwinism itself* has evolved (i.e., developed historically) in its understanding of the living world. Accomplishing both of these aims requires tackling a range of difficult historical, scientific, and philosophical issues. Let's get to it.

PART I

SELECTION

1

Darwin and Natural Selection

> Natural Selection, as we shall hereafter see, is a power incessantly ready for action, and is as immeasurably superior to man's feeble efforts, as the works of Nature are to those of Art.
>
> (Darwin 1859, p. 61)

Introduction

"After having been twice driven back by heavy south-western gales, Her Majesty's ship *Beagle*, a ten-gun brig, under the command of Captain Fitz Roy, R. N., sailed from Devonport on the 27th of December, 1831" (Darwin 1839, p. 1). So begins Darwin's travel journal, *The Voyage of the Beagle*, published in 1839. The purpose of the expedition was to survey the South American coast and to make chronometrical measurements. The twenty-two-year-old Darwin had signed on as (unofficial) ship naturalist and (official) "gentleman dining companion" for the captain. The expedition was planned as a two-year voyage. In fact, it would be nearly five years before the *Beagle* returned to England (29 October 1836). Its voyage proved to be the seminal experience in Darwin's life.

A Theory by Which to Work

The story of Darwin's discovery of "evolution by means of natural selection" has been told many times (e.g., Bowler; 1989; Young 1992). Although scholars continue to debate the relative importance of one or another element in this story, there is nonetheless widespread agreement on the basic factors that led Darwin to his theory. Prior to his voyage on the *Beagle*, Darwin had spent three years at Cambridge University, training

to be a country parson, and before that had studied medicine at the University of Edinburgh. Having discovered that he was more interested in beetle collecting and "geologizing" than either medicine or theology, Darwin abandoned his course of studies and eagerly sought and (with the help of some well-placed connections) secured a place aboard the H.M.S. *Beagle* for its voyage around the world. At each place the ship docked, Darwin made arduous trips inland to collect plants, animals, fossils, and rocks. Despite being seasick for much of the voyage, he took extensive notes on the geology and biology of each area. On his return to England in October 1836, thanks to the correspondence he maintained with scientists at home, Darwin was welcomed as a respected and accomplished naturalist. He immediately set to work sorting out the material and observations he had collected on the voyage.

Darwin opened his first private notebook recording his evolutionary speculations in July 1837.[1] In it he considered how the "transmutation" of one species into another could account for some of the observations made during his voyage. For example, finches on the Galapagos Archipelago (six hundred miles due west of Ecuador) differed dramatically from one island to another, yet all resembled finches on the South American mainland in their basic structure, despite the fact that the volcanic islands represented a quite different environment. The resemblance could be explained, Darwin realized, by supposing that a few individuals from the mainland were carried by storms out to the islands, where their descendants then became modified to each different island environment. Over sufficient time, each form had evolved into a new species. Darwin also realized that this explanation could be generalized. In a world characterized by environmental change, some individuals will vary in a way that better fits them to the new circumstances. With sufficient change, the descendants of these individuals will form new species. Others will fail to adapt and will go extinct, leaving gaps between those forms remaining. This would account for the large differences between some species but not between others. Darwin became convinced that this account was true, and by the end of 1837 was in search of a cause of this species formation.

Famously, it was Darwin's reading ("for amusement") of the Reverend Thomas Malthus's *Essay on the Principle of Population* (1798) in September 1838 that, he said, provided the crucial insight he needed (Darwin 1958, pp. 119–20). Malthus had noted that populations tend to increase faster than their food supply, leading to a struggle for existence amongst their members. Darwin realized that any variations among individuals