The Evolution of Darwinism

Selection, Adaptation, and Progress in Evolutionary Biology

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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.

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 providing an advantage over others would help those individuals to survive, and disadvantageous variations would tend to be eliminated from the population. If the beneficial variations were passed on to offspring, there would be a gradual change as successive individuals became better adapted to their environments. As Darwin later wrote: "Here, then, I had at last a theory by which to work" (Darwin 1958, p. 120). Having the theory in hand, he began collecting additional evidence to show that it would explain a wide range of otherwise puzzling phenomena.

The theory was sketched out briefly for the first time in an essay in 1842, and then enlarged further in an essay of 1844 (F. Darwin 1909). It is significant that in the latter work Darwin was putting his ideas on paper in the same year that a book espousing a very different account of the evolution of life appeared. Although it enjoyed a degree of popular success, *Vestiges of the Natural History of Creation* (1844), written by Robert Chambers but, wisely, published anonymously, was generally scorned by the scientific community as embodying the worst sort of unfounded evolutionary speculation. Chambers's suggestion, for example, that mammals had evolved from birds via platypuses as an intermediary, received the ridicule it deserved. Darwin had no intention of subjecting his own ideas to the same hostile reception. He decided to amass much more evidence to support his theory before going public with it.

As it turned out, it would be another fifteen years before Darwin would be ready to present his theory to the world, during which time he continued to work on various biological problems.[2] The crucial event that forced his hand was the arrival in the post in June 1858 of a paper by another English naturalist, Alfred Russel Wallace (1823–1913), which sketched out a theory so similar to Darwin's own that Darwin wrote to his friend and confidant the geologist Charles Lyell, "If Wallace had my MS [manuscript] sketch written out in 1842, he could not have made a better short abstract!" (F. Darwin 1887, vol. 1, p. 473). Darwin immediately set to work on composing an "abstract" of his theory. The result was *On the Origin of Species*, published in November 1859.

The *Origin* was an instant bestseller, quickly selling out its entire first printing of fifteen hundred copies on the day it was published (24 November 1859). In Darwin's lifetime it sold over twenty-seven thousand copies in Britain alone. Much of its success can be attributed to the fact that Darwin wrote it as a summary of his theory rather than as the more extensively documented tome he had originally intended, thus making it accessible to a much wider audience. Others had proposed evolutionary views before. What was novel in Darwin's theory was the central role given to what he called "natural selection," a seemingly simple idea with profound implications. In the "Introduction" Darwin provides the best concise statement of evolution by natural selection anyone has ever given:

> As many more individuals of each species are born than can possibly survive; and as, consequently, there is a frequently recurring struggle for existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be *naturally selected.* From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form. (Darwin 1859, p. 5; emphasis in original)

Later we will examine various aspects of Darwin's theory in detail, but at the outset it is important to understand what was different – and to many of his contemporaries, objectionable – about this theory. As a number of writers have pointed out, it wasn't so much Darwin's advocacy of evolution that was novel or disturbing. By 1859 evolutionary ideas had become almost commonplace. Rather, what was disconcerting was the idea that natural selection operating on chance variations produced the diversity and apparent design in nature. Darwin's theory seemed to make evolution more blind and haphazard than anyone had imagined. One way to appreciate the novelty of these aspects of Darwin's theory is to contrast it with an account of evolution in which chance variation and natural selection are *not* key explanatory elements. We can then return to examine specific aspects of Darwin's theory more closely.

"Nature's Plan of Campaign"

Jean Baptiste Pierre Antoine de Monet, Chevalier de Lamarck (1744–1829) stands out as the most important evolutionary theorist before Darwin. Some previous thinkers, for example, George Louis Leclerc, Comte de Buffon (1707–88), had toyed with the idea of limited species change based on different environments, but no fully developed evolutionary theory appeared before Lamarck's at the beginning of the nineteenth century. His evolutionary speculations appear in three works: In the introduction to his *System of Invertebrate Animals* (1801); more fully in his most famous work, *Zoological Philosophy* (1809); and finally, in the introduction to his *Natural History of Invertebrates* (1815).[3]

In keeping with the natural history tradition since Aristotle, Lamarck accepted the idea that the major classes of organisms can be arranged in a linear series of increasing complexity. But, whereas Aristotle was content simply to describe this series, Lamarck wanted to explain it as a true historical sequence produced by a gradual evolutionary process taking place over an immense period of time. According to Lamarck, “Nature, in successively producing all species of animals, beginning with the most imperfect or the simplest, and ending her work with the most perfect, has caused their organization gradually to become more complex” (Lamarck 1809, p. 60). The various classes of organisms we observe today (e.g., insects, fishes, amphibians, reptiles, birds, mammals) were explained as the result of this primary complexifying process.

To explain this process Lamarck postulated an “endowment” (or “law”), according to which animal life has the inherent power of acquiring progressively more complicated organization. As organisms move up this ladder of organization, vacant morphological space at the bottom is continually being replenished with lower forms (e.g., worms) arising from spontaneous generation from inanimate matter. In Lamarck’s view, biogenesis (the origination of life from nonlife) was not a singular unique event in the history of the earth, but rather a continuous and ongoing process. It follows that different lineages begin their ascent up the ladder of complexity at different times. Thus part of the diversity we observe is simply the result of different lineages having begun at different times, with the secondary result that each has so far progressed to a different stage in its upward ascent. The lineage that includes *Homo sapiens* is the oldest, because it alone has reached the highest stage of development. Given the movement involved in this picture, an escalator rather than a ladder is perhaps a better representation.

This complexifying process is the primary cause of organic diversity. As Lamarck realized, however, another force must also be at work: “If the cause which is always tending to make organization more complex were the only one affecting the form and the organs of animals, the increasing complexity of organization would everywhere follow an extremely regular progression. But this is not the case” (Lamarck 1809, p. 130). That is, were the intrinsic tendency toward increasing complexity the *only* cause of evolutionary change, then one might expect to observe a single linear sequence of forms, grading smoothly from the simplest to the most complex. In fact, however, the living world is characterized by tremendous diversity in which it is difficult to locate every species on a simple scale of increasing complexity. A second biological datum requiring explanation is the diversity of forms *within* each major class of organism. “Mammals” comprise many different kinds of animals, for example, rodents, canines, felines, etc. Likewise, “felines” are represented by leopards, lions, jaguars, tigers, ocelots, and so on. As Lamarck noted, "The organization of animals, in its growing complexity, from the least to the most perfect, presents only an *irregular gradation* of which the whole extent displays a large number of anomalies or deviations which have no apparent order in their diversity" (Lamarck 1809, p. 221). In order to account for this diversity of forms, Lamarck realized, there must be other forces at work besides the intrinsic drive toward perfection.

To explain this level of diversity Lamarck posited a secondary process of adaptation to environmental conditions. To survive, organisms must be able to interact successfully with their environments which are always changing. As environments change, new needs (*besoin*) are induced within organisms. These needs result in changes in the animal's "efforts" or "habits," with a corresponding increased use of relevant parts of the body. Lamarck postulated "vital fluids" that are forced into specific parts of the body, causing these body parts to hypertrophy, thus helping the organism to meet its needs more effectively. Likewise, if an organ or part is no longer needed, it falls into disuse and gradually atrophies, eventually disappearing altogether. Structural changes thus induced are then passed on to offspring. The cumulative effect of this process is the appearance of different kinds of organisms, and eventually entirely different species. This is the infamous "inheritance of acquired characteristics" doctrine usually associated with Lamarck, but that he neither originated nor was specifically criticized by his contemporaries for holding, since it was widely accepted in his day. The controversial part of Lamarck's theory for his contemporaries was the way he incorporated the idea of "vital fluids" as responsible for naturally-occurring structural changes. Lamarck's view was radical because, rather than being fitted by God or nature with a constant structure for specific environments, he saw organisms as undergoing changes simply as a result of natural processes operating within and upon organisms in the particular environments in which they found themselves. It was the speculative *naturalism* of Lamarck's account, rather than its evolutionary character *per se*, that so many of his contemporaries found objectionable.

In summary, Lamarck viewed the production of living things as the result of two different kinds of forces. On the one hand, there are forces that underlie the natural tendency of living things to complexify according to a preordained scale of perfection, an inherent power of acquiring progressively more complicated organization that tends toward the production of a *regular gradation* of living things from simple to complex. On the other hand, interfering forces orthogonal to these prevent living things from arriving at their idealized natural state. Adaptation to different environmental conditions disrupts the smooth progression in complexity, resulting in diversity. As Lamarck described this twofold process: "The progression in the complexity of organization suffers, here and there, in the general series of animals, from anomalies produced by the influence of the circumstances of the environment, and by those of the habits contracted" (Lamarck 1809, p. 133). Consequently, only the main types of organization (families or classes) could be arranged in a single series of increasing complexity. Because of adaptation to changing environments, species cannot be arranged in a simple series of higher or lower. Thus the central upward tendency of nature "only appears in a general way, and not in the details" (Lamarck 1815, p. 52). The following quote nicely captures Lamarck's overall view:

> Nature's plan of campaign in the production of animals is clearly marked out by [a] primal and predominant cause, which endows animal life with the ability to complicate organization progressively, and to complicate and perfect gradually, not only the total organization, but also each system of organs in particular. . . . But a quite separate cause, an accidental and consequently variable one, has here and there cut across the execution of this plan, without however destroying it. . . . This cause . . . has given rise to whatever real discontinuities there may be in the series, and to the terminated branches which depart from it, at various points, and diminish its simplicity, and finally to the anomalies to be seen in the various organ-systems of the different organizations. (Lamarck 1815, p. 133)

Despite the fact that Lamarck is now considered to have gotten it almost completely wrong, his theory was nonetheless a serious effort to explain certain accepted but problematic facts about nature. First, many forms uncovered in the fossil record are no longer extant. Likewise, there is no evidence in the fossil record of many of the forms we see today. Clearly there has been a tremendous replacement of organic forms over time. Second, an inspection of extant animals shows that they form a graded series of increasing complexity. Organisms can be more or less arranged along a *scala naturae* ranging from bacteria to *Homo sapiens,* with each step along the ladder exhibiting greater complexity. Third, organisms display amazing diversity, which must be explained in some way. Finally, organisms seem exquisitely well-suited for their particular environments. Organic replacement, increasing complexity, diversity, and fitness are four primary biological phenomena Lamarck correctly recognized as in special need of explanation. Providing correct explanations of each is, of course, important, but the importance of correctly identifying and taking seriously the problems to be solved should not be underestimated. Lamarck's contributions in this regard were seminal.

Ideals of Natural Order

Clearly there are fundamental differences between Lamarck's and Darwin's theories, differences that are critical for understanding both the nature of Darwinian evolution and the nature of Darwinian explanations. Stephen Toulmin (1961) suggests that every scientific explanation presupposes an "ideal of natural order" that permits the inquirer to distinguish between what is the "natural," normal state of a thing, to be taken for granted and used in framing explanations, and which phenomena depart from this natural state and therefore require explanation. A short digression into the history of physics will help to bring Toulmin's central idea into focus.

Consider the very different starting points for Aristotelian and Galilean dynamics. Aristotle formulated his physics of motion by generalizing from a commonsense explanation of a moving object: A cart being pulled by a horse. The cart continues to move just insofar as the horse continues to pull it along. Two factors are at work: The external agency (the horse) keeping the body in motion, and resistance (the weight of the cart) tending to bring the motion to a stop. Aristotle realized that this explanation could be generalized for any moving body. Explaining the motion of any body means recognizing that a body moves at the rate appropriate to an object of its weight, when subjected to just that particular balance of force and resistance. In order for an object to remain in motion, a force must be continually exerted. Relax the force being exerted, and the object in motion will eventually come to rest. Being "at rest" is the natural state of any natural substance, and requires no special explanation. Being "in motion" requires special explanation. Complete rest, or steady motion under a balance of actions and resistances, is the natural motion of an object. Anything that can be shown to exemplify this balance will thereby be explained.

As is well known, the science of motion underwent a dramatic revolution in the seventeenth century in which the ideal of natural order at the heart of Aristotelian physics was abandoned and replaced by another, quite different conception. The most radical single step was taken by Galileo, who argued that rest and uniform motion are equally "natural" for bodies, with neither in need of explanation. Only *changes* in motion, for example, acceleration, require special explanation. This looks, at first glance, very like our modern "law of inertia." Yet Galileo's conception of motion is no more identical with our own than is Aristotle's. In some important respects it is closer to Aristotle's conception than it is to ours. Whereas Aristotle's model of motion was a cart being pulled by a horse, Galileo's model was that of a ship moving steadily across the ocean and disappearing over the horizon, its motion describing a curve. Only some active force could deflect the ship from its circular path. He thus took *circular* motion to be entirely natural and therefore not in need of explanation. Such a conception proved extremely useful for "explaining" the motions of the heavenly bodies. Because they move with uniform speed in perfect circles (Galileo believed), their motion is entirely natural and therefore in need of no special explanation.

When we turn to Newton we find that the ideal of natural motion has changed once again. The paradigm example of motion is now a body moving at uniform speed in a Euclidean straight line, completely unaffected by any external forces. A body's motion is treated as natural and not in need of explanation only when it is unaffected by all forces, including its own weight – a situation that is never observed in the real world. But the ideal example doesn't need to be observed because it provides a standard against which a body's actual motion requires explanation. Newton's first law of motion, the principle of inertia, represents an ideal of natural order supplying a standard of rationality and intelligibility for understanding and explaining natural phenomena. Once this new theoretical ideal was accepted, and with a little help from the hypothesis of universal gravitation, dozens of previously puzzling phenomena fell into an intelligible pattern. Newton's ideal of natural order structured physical explanations right up to the twentieth century, when Einstein's development of relativity theory fundamentally altered our conceptions of the physical world once again.

Stepping back now from the details of the different models just described, it becomes clear that what counts as a successful explanation in physics, and indeed even of what natural phenomena require explanation, is intimately related to ideas about the fundamental order of nature. Any dynamical theory involves some explicit or implicit reference to a paradigm example which specifies the manner in which, in the natural (or ideal) course of events, bodies may be expected to move. By comparing the motion of any actual body with this paradigm example, that which requires explanation can be determined. Every step of the explanatory project is governed and directed by the fundamental conceptions of the theory.

What is true in physics is equally true in biology. As Ernst Mayr (1988) notes, others before Darwin had attempted to explain the diversity of living things, but Darwin provided a new *kind* of theory by reversing what could be taken for granted, and what required special explanation. Once again, Aristotle made the significant original contribution to explaining biological phenomena. As in his physics, so, too, in his biology, Aristotle employed a natural state model according to which the forces acting on an entity or set of entities can be partitioned into two kinds: Forces that ground the natural tendency of the kind of entity being considered, and interfering forces which may prevent the entities in question from arriving at their natural state. A familiar nonbiological example is water, which has a natural tendency to flow from higher to lower elevation, but whose actual movement in that direction can be obstructed by interfering forces such as a dam, becoming frozen, and so on. Aristotle's favored biological example was an acorn whose natural tendency to develop into an oak tree can be thwarted by any of a number of interfering forces, such as drought, consumption by a squirrel, and so on. In Aristotle's model, individual organisms (oak trees, squirrels, etc.) are specimens of types each of whose essence is fixed and immutable. Individual variability is real but represents departure from the ideal type defining each species. Departure from this ideal type therefore requires explanation. Aristotle devotes considerable attention in the *Generation of Animals* to accounting for "monsters" and other less dramatic deviations from the ideal species type. As in his physics, so, too, in his biology, a natural-state model determines which natural phenomena are and are not in need of explanation.

From our current perspective, Lamarck's theory can be seen as transitional between Aristotle's and Darwin's. Like Aristotle, Lamarck held that species themselves are fixed and immutable. Species themselves do not change.[4] Unlike Aristotle, Lamarck believed that the living world is characterized by significant change and replacement over time. Organisms come to occupy different rungs (i.e., instantiate different species) as they progress up the ladder of phylogenetic development. On this scheme, individual organisms evolve; species do not. The apparent replacement of some species by others is to be explained by individuals of the former being gradually transformed, that is, evolving, into individuals of the latter – something that is unintelligible in Aristotle's biological theory.

Darwin's approach differs fundamentally from that of both Aristotle and Lamarck. According to Aristotle's essentialist, "typological" approach to variability, the type (species) is fixed and primary, and individual variability is derived and in need of explanation in terms of interfering forces. Likewise, for Lamarck, "All of the races of living bodies continue to exist *in spite of* their variations" (Lamarck 1809, p. 55). Individual variations are viewed as a kind of "noise"' disrupting the directional process from the simple to the complex. They are evolutionary dead-ends, not leading to new lines of development. Darwin's "populational" theory entails a complete reversal of these approaches (Mayr 1963, 1976; Sober 1980, 1985). According to this view, individual variability is fundamental (and largely unexplained), and the existence of types (e.g., species) requires special explanation. Species exist precisely *because* of naturally occurring variations. Organic variation is the natural result of the absence of interfering forces. Uniformity (species) results from interfering forces (e.g., geographical isolation, which prevents individuals from interbreeding). For example, whereas Aristotle and Lamarck would explain variations in the height of oak trees as due to interfering forces affecting the oak's natural tendency, Darwin would treat the variation as natural (as reflecting a "norm of reaction" in contemporary parlance), with the fact that the trees instantiate the restricted height distribution they do as in need of explanation (e.g., in terms of selection against individuals that depart significantly from the mean). In Darwin's hands the explanandum (that which requires explanation) and the explanans (that which does the explaining) are reversed. Aristotle and Lamarck each treat variations as somewhat unfortunate consequences of imperfections in the process; Darwin treats variations as the indispensable precondition of continuing evolutionary development.

The contrast between Lamarck's and Darwin's theories of organic change can be understood in another way as well (Sober 1984, 1994). Lamarck's theory is premised on a "developmental stage" (or ontogenetic) conception in which phylogeny (the series of changes characterizing a lineage through time) is modeled upon ontogeny (the series of developmental changes undergone by an individual), in two distinct ways. First, the overall process of evolution is modeled on the development of individual organisms. Just as individual organisms develop according to a preset plan (laid down in their hereditary material), so, too, evolution as a whole is viewed as a directional unfolding from lesser to greater complexity according to "nature's plan of campaign," as Lamarck called it. Second, in Lamarck's scheme evolution is driven by changes in individuals, not in species. The explanation for why giraffes have long necks is that in the past individual giraffes stretched their necks to reach the higher foliage, this altered feature was passed on to offspring, and the process was repeated until the long-necked creatures of today appeared. Changes among individual organisms drive the process.

The contrasts with Darwin's theory are striking. Whereas Lamarck's theory treats evolution as preprogrammed, in Darwin's theory whatever direction there is in the process is dictated by changing environments and the ability of populations to respond, both of which are highly contingent. Darwin also separates ontogenetic and phylogenetic explanations, restricting each to just one stage in the overall evolutionary process. Developmental ontogeny explains individual characteristics, while selection explains populational characteristics, and hence phylogeny. Why does *this* giraffe have a long neck? Because it inherited long-neck genes whose instructions were expressed in an appropriate environment. Why do giraffes (as a species) have long necks? Because in the past individuals with long necks enjoyed greater survival and reproductive success than those with shorter necks, and these more successful individuals differentially passed on their characteristics to offspring. So far as evolution is concerned, organisms are essentially fixed in their attributes, while species evolve.

Natural Selection

In its essentialism regarding species, Lamarck's theory harkens back to Aristotle; in its transformism concerning life as a whole, it anticipates Darwin. As a conceptual bridge between pre-evolutionary biology and contemporary evolutionary biology it thus occupies a historically crucial position. Yet as daring and novel as it was, Lamarck's theory was a dead-end in the history of evolutionary theorizing, whereas Darwin's theory has given rise to a vigorous research program extending far beyond anything that even Darwin could have imagined. But it has also given rise to numerous controversies, many of which center on the operation of natural selection. Given the centrality of natural selection in Darwin's theory, it is of fundamental importance to understand how selection operates. This turns out to be considerably more difficult than it first seems. In a seminal article, Richard Lewontin noted that "The generality of the principles of natural selection means that any entities in nature that have variation, reproduction, and heritability may evolve" (Lewontin 1970, p. 1). That seems clear enough. However, this seemingly straightforward observation, as Lewontin was well aware, harbors difficult problems. Selection is often thought of as operating on individual organisms. In principle, at least, it could operate on other sorts of biological entities as well. But which ones? What kinds of characteristics must a biological entity have in order for it to be subject to selection? How would selection of these other entities relate to selection of individual organisms? Even if selection could operate on these other biological entities, which ones does it in fact operate on, and what are the consequences for understanding the evolution of life on Earth?

Consideration of these problems has led to one of the most vigorous controversies in contemporary evolutionary biology: the "units of selection" debate (Brandon and Burian 1984; Sober and Wilson 1994). Whereas some biologists have asserted that selection operates exclusively on individual organisms, others have advocated models according to which selection operates on other biological entities as well. The issues dividing these biologists are complex and multifaceted, and will be the subject of later chapters, but they were prefigured in Darwin's writings. Understanding his view on this issue is thus essential to making sense out of subsequent debates. Consequently, it is worthwhile to examine Darwin's views on such issues in some detail, with the aim of finding out precisely how he conceived of the operation of natural selection in the evolutionary process. Did he have a settled view about the entities upon which selection can or does operate? If so, what was it?

Darwin and Organism Selection

According to a contemporary slogan intended to unambiguously identify biological entities with their respective evolutionary roles, "genes mutate, organisms are selected, and species evolve" (Hull 1988). Darwin knew nothing about genes, of course, but it seems obvious that he would have accepted the claim that organisms are selected, and that species evolve. After all, those are two of the key ideas constituting his theory. It is also easy to show that Darwin *generally* viewed selection as operating amongst individual organisms rather than on biological entities at some higher (or lower) level of organization. Despite the subtitle of the *Origin of Species*, the "preservation of favoured races" is construed as an *effect* of the struggle for survival at the level of individual organisms. It seems quite clear that when Darwin writes "Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life" (Darwin 1859, p. 63), the struggle being described is between individual organisms. He was even willing to be more precise. Most often, Darwin thought, the struggle will be intraspecific: "[T]he struggle almost invariably will be most severe between individuals of the same species" (Darwin 1859, p. 75).

Just as the struggle for existence is primarily between individual organisms, so, too, is selection primarily for or against the individual. In a pack of wolves, the swiftest and slimmest will be more effective predators, and hence there will be selection for wolves possessing such characteristics (Darwin 1859, p. 90). Sexual selection, too, in which possessing some feature attractive to the opposite sex gives one an edge in the competition for mates, is presented in such a way that individuals are selected because they have some advantage over other individuals within their immediate group. By definition, sexual selection takes place within a species, pitting conspecific against conspecific, and thus represents individual selection in the clearest sense (Darwin 1859, pp. 87–90). Similar examples of Darwin's preference for explanations in terms of individual selection are easy to produce. Clearly, whenever a biological phenomenon required a selectionist explanation, Darwin preferred to construe selection as operating amongst individual organisms. This point is simply not controversial.

"One Special Difficulty"

This tidy picture is complicated when one considers Darwin's treatment of certain "special difficulties." Special difficulties require special explanations including, in this case, consideration of selection operating on biological entities other than (or in addition to) individual organisms. For example, in Chapter VII of the *Origin,* Darwin considers "one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters or sterile females in insect-communities" (Darwin 1859, p. 236). Later in the same chapter he declared that castes of sterile workers in the social insects pose "by far the most serious special difficulty, which my theory has encountered" (Darwin 1859, p. 242). The "special difficulty" for Darwin was not (as it became for later Darwinians) to explain sterility and extreme altruistic behavior (although, as we shall see, Darwin did offer an explanation for these puzzles) but, rather, to explain how natural selection could produce a neuter caste whose members were so structurally different from their parents and from one another: "[F]or these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, being sterile, they cannot propagate their kind" (Darwin 1859, p. 236). "[T]he difficulty," Darwin wrote, "lies in understanding how such correlated modifications of structure could have been slowly accumulated by natural selection" (Darwin 1859, p. 237).

More precisely, Darwin recognized and attempted to resolve two distinct problems concerning sterile castes of workers in social insects. The first problem concerned the origin and maintenance of sterile castes. Why this should be a problem for Darwin's theory is clear. Sterile individuals, by definition, do not reproduce. Instead, they appear to sacrifice their reproductive interests for the benefit of the rest of the hive or colony. If natural selection favors those individuals more proficient at reproducing themselves, then sterile individuals are obviously at a distinct disadvantage relative to their more prolific conspecifics, and should be eliminated from the struggle for existence in short order. Yet social insects, with their sterile castes, are among the most widespread and successful living systems on earth. The existence of sterile castes among social insects seems inexplicable on the assumption that all selection is for individually advantageous characteristics. What possible individual advantage can accrue to being sterile? There appears to be none. How, then, is the presence of sterile castes to be explained?

Despite the serious threat it posed to his theory, Darwin apparently thought that this problem could be handled rather easily, and so his discussion of it is surprisingly brief:

> How the workers have been rendered sterile is a difficulty; but not much greater than that of any other striking modification of structure; for it can be shown that some insects and other articulate animals in a state of nature occasionally become sterile; and if such insects had been social, and it had been *profitable to the community* that a number should have been annually born capable of work, but incapable of procreation, I can see no very great difficulty in this being effected by natural selection. (Darwin 1859, p. 236; emphasis added)

The key idea in this passage is that in addition to operating on individually advantageous characteristics, selection can also operate on characteristics "profitable to the community." Apparently, Darwin was willing to entertain the idea that there could be selection for characteristics beneficial to the community, even though they were of no use (and actually detrimental) to the individuals possessing those characteristics.[5]

But did Darwin really entertain the idea of selection operating on more inclusive entities than individual organisms? Michael Ruse (1980) offers a spirited defense of the claim that, contrary to appearances, Darwin never departed from a strict individual selectionist perspective. According to Ruse, by the end of the 1860s "there was nothing implicit about Darwin's commitment to individual selection. He had looked long and hard at group selection and rejected it" (Ruse 1980, p. 620).[6] Again: "In the nonhuman world Darwin was a firm, even aggressive, individual selectionist . . . [who], for organisms other than man . . . unequivocally invoked individual selection" (Ruse 1980, p. 629). On this view, when Darwin does seem clearly to come out in support of some sort of higher-level selection process, such lapses constitute a "quaver in his commitment to individual selection" when he "for once did lose sight of the individual and allow that possibly the unit of selection may have been the group" (Ruse 1980, pp. 626–7).

How, then, should Darwin's apparent group selectionist explanation of sterile neuters be understood? According to Ruse, there is no appeal to higher-level selection here. Rather, the key to understanding Darwin's argument is to note that the sterile altruists are genetically related to the fertile members of the colony. Although they are themselves reproductively disadvantaged by being sterile, nonetheless by helping their relatives to survive and reproduce they are assisting in the propagation of copies of their genes, many of which are shared with close relatives. Instead of passing on their genes directly through producing offspring, sterile individuals do so indirectly through the offspring of their fertile relatives. Such a process (later named "kin selection") cannot be considered higher-level (i.e., community-level) selection, Ruse argues, because selection is not preserving characteristics exclusively of value to nonrelatives. Consequently, "Darwin was certainly an individual selectionist at this point" (Ruse 1980, p. 619).

Despite the attractions of this interpretation in simplifying our image of Darwin considerably and even allowing him to anticipate important developments in twentieth-century evolutionary biology, it suffers from two serious difficulties. First, it depends on the assumption that Darwin could not have been proposing a higher-level selection process if the individuals in question are genetically related. In other words, it assumes that higher-level selection requires that individuals sacrifice themselves for nonrelatives. The rationale for this assumption is far from clear. Second, and more directly relevant in the present context, it is unclear that *Darwin* made any such assumption. Ruse's interpretation depends on familiarity with a solution to the problem that was not clearly understood until well over a century after the publication of the *Origin.* It is true that recent explanations (from the mid-1960s on) of sterile castes among social insects have focused on explanations in terms of benefits conferred on genetic relatives by sterile individuals (e.g., Hamilton 1963, 1964). But clearly such explanations cannot be simply read back into Darwin's account if we wish to understand how *he* approached the problem.[7] Our best guide to what Darwin thought is what he actually said, interpreted in the context of his other remarks on similar issues. Interpreting Darwin as offering a "kin selection" solution to the problem of sterile castes runs the risk of reading back into Darwin's writings what we, now, believe to be the correct explanation of the problem at hand, rather than considering Darwin's solution on its own terms.

Fortunately, there is plenty of material to help us bring Darwin's views about the operation of selection into sharper focus. His answer to the second problem concerning sterile neuters, in particular, provides important further clues to his thinking. Recall the essential difficulty: "[W]ith the working ant we have an insect differing greatly from its parents, yet absolutely sterile; so that it could never have been transmitted successively acquired modifications of structure or instinct to its progeny. It may well be asked how is it possible to reconcile this case with the theory of natural selection?" (Darwin 1859, p. 237). Darwin thought that the problem of explaining how natural selection could produce a neuter caste differing widely in instinct and in structure from both the males and fertile females was much greater than the problem of explaining how natural selection could have rendered the workers sterile in the first place. But he thought that the problem was solvable:

> I can see no real difficulty in any character having become correlated with the sterile condition of certain members of insect-communities . . . when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end. . . . Thus I believe it has been with social insects: a slight modification of structure, or instinct, correlated with the sterile condition of certain members of the community, has been advantageous to the community: consequently the fertile males and females of the same community flourished, and transmitted to their fertile offspring a tendency to produce sterile members having the same modification. (Darwin 1859, pp. 237–8)

Here Darwin seems to draw an explicit contrast between "selection applied to the family" and selection applied "to the individual," suggesting that he was well aware of the distinction between the two processes. The explanation offered for the existence of sterile castes is the fact that such a condition "has been advantageous to the community" in relation to *other communities* lacking this feature. This suggests that he was thinking of a selective advantage accruing to the community that is distinct from, and in this case contrary to, benefits for at least some of the individual members of that community. In this way, individually deleterious traits might nonetheless be selected for if such traits are linked to some advantage for the community as a whole.

This interpretation has the virtue of taking Darwin's own statement of his view seriously. Unfortunately, this straightforward interpretation is complicated by the fact that Darwin's remarks still contain some ambiguities. When he cautions that we should not forget that "selection may be applied to the family, as well as to the individual," does he intend to remind his readers that there is another kind of selection *in addition to* individual selection? Or does the "as well as" clause in his remark indicate that he thinks that selection at the level of the family acts *in concert with* selection at the level of individuals, with both processes conjointly producing the phenomenon to be explained? His remark later in this passage that some "slight modification of structure, or instinct, correlated with the sterile condition of certain members of the community, has been advantageous to the community" implies that he is thinking of selection at the level of the family or community *rather than* selection at the level of individuals as the preferred explanation of sterility. Yet elsewhere he writes: "In social animals [natural selection] will adapt the structure of each individual for the benefit of the community; if each in consequence profits by the selected change" (Darwin 1859, p. 87). This supposes that selection will adapt the structure of each individual to the benefit of the community *only if* such adaptation *also* benefits the individual. So in this case benefit to the individual is primary. However, in the sixth edition of the *Origin* (1872) the passage is changed to read as follows: "In social animals [natural selection] will adapt the structure of each individual for the benefit of the whole community; if the community profits by the selected change" (Darwin 1959, p. 172). The change of emphasis has now been reversed! Darwin's view is not altogether as clear as we might like, so we are left with some uncertainty in representing his thought.

To make matters worse, another interpretive problem arises when we consider the remarks elided from the long quote above. There Darwin uses the following comparisons with sterile insect castes to make his point: "Thus, a well-flavoured vegetable is cooked, and the individual is destroyed; but the horticulturist sows seeds of the same stock, and confidently expects to get nearly the same variety . . ." (Darwin 1859, pp. 237–8). In this example, it is not the family as a discrete unit that is the object of selection but, rather, the *characteristics* of the family that are carried in the seeds. Neuter insects are presumably meant to be analogous to the "well-flavoured vegetable" that is cooked, in that neither is individually reproductively successful, yet the characteristics of each are preserved in other members of their family. There are, of course, disanalogies as well. In the case of the vegetables, "tastiness" is a characteristic of both parents and offspring, whereas sterility is a characteristic of certain individuals only (i.e., a certain subset of the offspring of fertile parents). Whereas the characteristics correlated with the sterility of neuter insects are supposed to be of benefit to their community, the tastiness of certain individual vegetables is not obviously of benefit to the "community" of which they are a part. Finally, what is missing from this example is some characteristic correlated with tastiness whose existence is to be explained in terms of selection for being "well-flavoured" in the way in which sterility is supposed to be explained by being correlated with (for example) large mandibles in the soldier caste of some ant species.

Darwin's second example is somewhat more helpful, inasmuch as it introduces the issue of sterile offspring: "I have such faith in the powers of selection, that I do not doubt that a breed of cattle, always yielding oxen with extraordinarily long horns, could be slowly formed by carefully watching which individual bulls and cows, when matched, produced oxen with the longest horns; and yet no one ox could ever have propagated its kind" (Darwin 1859, p. 238). Here the analogy with neuter insects is closer. A particular characteristic had by sterile offspring but not by their parents (e.g., long horns in oxen, large mandibles in soldier ants) can become correlated with the sterile offspring, even though (by definition) such individuals cannot pass on this characteristic to their offspring. Where the analogy breaks down, however, is in the causes responsible for the correlations in question. In the case of the long-horned oxen, the cause is artificial selection operating on their parents. Having extraordinarily long horns is presumably of no benefit to the parents nor to the herd, although it may be valued by the breeder. In the case of the neuter insects some structure correlated with sterility proved to be advantageous to the community, including their parents. As a result, the fertile individuals who produced such useful offspring flourished and continued to produce sterile offspring having the same modification.

As Darwin concludes a bit later, "With these facts before me, I believe that natural selection, by acting on the fertile parents, could form a species which should regularly produce neuters..." (Darwin 1859, p. 241). Darwin's talk of selection acting on the fertile parents might lead one to conclude that they, rather than the community, are the beneficiaries of the presence of neuters. As he proceeds to note, however, he conceives of neuter castes as benefiting the entire community of which they are a part: "We can see how useful their production may have been to a social community of insects, on the same principle that the division of labour is useful to civilized man" (Darwin 1859, pp. 241–2). Who, then, is the primary beneficiary of the division of labor – the community or individual men? Darwin doesn't say. If we want further clarity, we'll have to look elsewhere to see whether he ever resolves these ambiguities.

Of "Well-Endowed Men"

Talk of a "division of labour" within an insect community naturally invites further comparison between human and nonhuman societies. If appeal to selection at the level of communities might help to explain some otherwise puzzling features of insect societies, might not the same be true for understanding how human communities come to have the characteristics they do? Darwin took up this challenge in his major work on human evolution, *The Descent of Man* (1871), where he again invoked selection at the level of communities or groups in response to the problem of explaining how a characteristic apparently detrimental at the individual level could nonetheless evolve. The particular problem in question was "how within the limits of the same tribe did a large number of members first become endowed with [their] social and moral qualities, and how was the standard of excellence raised?" (Darwin 1871, vol. 1, p. 163). The problem is that this seems difficult to explain in terms of selective benefits for those individuals displaying exceptional levels of sociability and morality, as Darwin goes on to explain:

> It is extremely doubtful whether the offspring of the more sympathetic and benevolent parents, or of those which were the most faithful to their comrades, would be reared in greater numbers than the children of selfish and treacherous parents of the same tribe. He who was ready to sacrifice his life, as many a savage has been, rather than betray his comrades, would often leave no offspring to inherit his noble nature. The bravest men, who were always willing to come to the front in war, and who freely risked their lives for others, would on an average perish in larger numbers than other men. Therefore it seems scarcely possible . . . that the number of men gifted with such virtues, or that the standard of their excellence, could be increased through natural selection. (Darwin 1871, vol. 1, p. 163)

Just because we are all acquainted with acts of self-sacrifice, of parents for children, of comrades for their friends, and so on, the seriousness of the problem should not be underestimated. If natural selection favors characteristics exclusively of benefit to the individuals possessing them, then acts of self-sacrifice (i.e., of "altruism"), in which an individual's reproductive fitness is lowered, become genuinely puzzling from an evolutionary perspective.

As we might expect by this point, Darwin's solution to this problem lay in considering benefits accruing to *tribes* constituted by such virtuous men:

> It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe, yet . . . an advancement in the standard of morality and an increase in the number of well-endowed men will certainly give an immense advantage to one tribe over another. There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection. (Darwin 1871, vol. 1, p. 166)

Because the variation is between tribes, rather than between individuals within tribes, selection at the level of *groups* of individuals is apparently being proposed. This interpretation is strengthened by the recognition that the characteristic benefiting the group often involves the sacrifice of the individual – either literally, in cases in which an individual dies for the benefit of the group, or in the sense that individuals take greater risks and thus reduce their reproductive potential. It is this disadvantage for the individual that seemed to Darwin to require an explanation in terms of selection at the level of a more inclusive entity.

Some interpreters have flatly denied that Darwin entertained supra-individual selection to explain human morality. According to Ruse, for example, Darwin "saw the individual man or woman as being the crucial unit in the selective process. There was no question that, when faced with his own species, he was going to swing around suddenly and start to argue as a general policy that for *Homo sapiens* alone the group . . . is the key element in the evolutionary mechanism" (Ruse 1980, p. 626). Ruse insists that "apart from some slight equivocation over man, Darwin opted firmly for hypotheses supposing selection always to work at the level of the individual rather than the group" (Ruse 1980, p. 615). Yet as we have seen, there is nothing equivocal about Darwin's position. He was willing to entertain a group selectionist explanation, not only for the evolution of human morality, but for other puzzling biological phenomena as well. Indeed, Darwin was perfectly willing to generalize and extend this sort of explanation to account for other similarly puzzling social phenomena in a way that leaves little doubt that he believed that selection can and does operate at the level of communities:

> With strictly social animals, natural selection sometimes acts indirectly on the individual, through the preservation of variations which are beneficial only to the community. A community including a large number of well-endowed individuals increases in number and is victorious over other and less well-endowed communities; although each separate member may gain no advantage over the other members of the same community. (Darwin 1871, vol. 1, p. 155)

In this view, selection at the level of groups might still positively affect the individuals within the groups, because the individuals in one group may, on average, be more reproductively successful, precisely by being members of that group, than are the individuals belonging to other groups. But in such cases selection does not operate directly on the individuals *within* a given group, because the properties that selection operates upon are properties of the entire group, not of its individual members. Such a selection process is thus clearly distinct from the sort of selection that Darwin believed explains the properties of individual organisms. Consequently, in addition to selection operating on differences among individual organisms ("organism selection"), Darwin also recognized selection operating on differences among groups of organisms ("group selection").

The best guide to understanding what Darwin actually thought are his actual words, taken at face value if possible, and only reinterpreted if absolutely necessary. When Darwin writes that "certain mental faculties . . . have been chiefly, or even exclusively, gained for the benefit of the community" (Darwin 1871, vol. 1, p. 155), we should take this as a genuine expression of his thoughts on the matter. When we do this, it becomes evident that although Darwin preferred explanations in terms of selection operating on individual organisms, he was perfectly willing to entertain explanations in terms of selection at the level of groups when the situation warranted it.

Possibilities and Boundaries

As we have seen, an alternative to thinking of selection as operating exclusively among individual organisms is to think of it as operating as well on *groups* of organisms ("group selection"). I have been suggesting that there are good reasons to conclude that Darwin seriously entertained this idea, and attempted to apply it to solve several otherwise puzzling biological phenomena. It is noteworthy that the two instances in which Darwin most clearly appears to offer group selectionist explanations – for sterile castes among social insects and for the evolution of the human moral sense – both involve *social* phenomena. A brief consideration of the *development* of Darwin's thinking on such phenomena provides important clues to understanding why he believed that social phenomena merit a different sort of evolutionary explanation.

Social Evolution

One such clue appears for the first time in the fourth edition of the *Origin* (1866), as well as in a later work, *The Variation of Animals and Plants under Domestication* (1868). Once again, Darwin is considering the peculiar case of sterile neuters:

> With sterile neuter insects we have reason to believe that modifications in their structure have been slowly accumulated by natural selection, from an advantage having been thus indirectly given to the community to which they belonged over other communities of the same species; but an individual animal, if rendered slightly sterile when crossed with some other variety, would not thus indirectly give any advantage to its nearest relatives or to any other individuals of the same variety, thus leading to their preservation. (Darwin 1959, pp. 444–5; 1868, vol. ii, pp. 186–7)

The sixth and final edition of the *Origin* (1872) includes "fertility" along with "structure" and adds that the communities being discussed are *social* communities (Darwin 1959, p. 445). It is significant that in these additions Darwin explicitly contrasts the relevant explanations of sterile castes among social insects with that of interspecific and hybrid sterility. Whereas in the former case sterility can be explained by natural selection operating through advantages accruing to social communities, in the latter case no such socially mediated community-level advantage can be invoked. The addition of this passage, with its striking emphasis on an animal's membership in a "social community," suggests that Darwin considered sociality to be a distinct factor in evolution, one that in some cases perhaps licenses (or requires) the postulation of selection operating at a level more inclusive than that of the individual organism.

Selection and Individuality

This also suggests that in reading Darwin's frequent remarks to the effect that a given biological phenomenon "could not have been effected through natural selection [because] it could not have been of any direct advantage to an individual animal . . ." (Darwin 1959, p. 444) one has to take into account whether he is referring to a feature bearing only on the well-being of an individual organism or whether the feature in question is a structural property of a more inclusive social organization having a biological significance of its own. Darwin may well have been committed to explanations of the former solely in terms of selective advantages for individual organisms, while allowing for explanations of the latter in terms of selection operating on entities above the level of individual organisms, *precisely because he viewed these higher-level entities as "individuals" in their own right.* Significantly, in a letter to Wallace discussing his proposed explanation of hybrid sterility, Darwin wrote: "I believe, that Natural Selection cannot effect what is not good for the *individual, including in this term a social community*" (Darwin to Wallace, April 6, 1868; in F. Darwin and Seward 1903, vol. 1, p. 294; emphasis added; also in Wallace 1916, p. 170). What is especially striking about this remark is that Darwin explicitly includes in the denotation of the term "individual" a "social community." This means that it would be correct to attribute to Darwin the view that selection can only act upon "individuals," but a mistake to ascribe to him the view that only organisms can be individuals in the relevant sense. Social communities, too, can be individuals, and hence can be directly available for selection to act upon. In this interpretation, Darwin was indeed a strict "individual selectionist," but one whose conception of an "individual" included not just individual organisms but extended as well to certain other sorts of biological entities.[8]

What Natural Selection Cannot Do

Before leaving this topic it is important to note that, despite the ambiguity of some aspects of Darwin's treatment of natural selection, there is one related issue about which he could not have been clearer. Although he was at times willing to entertain the idea that selection might act upon and benefit some more inclusive entity than the individual organism, for example, the community, the variety, or even the species,[9] there is one issue concerning selection that was *never* an issue for Darwin, namely, whether selection might operate on one species for the good of another. He was absolutely clear that natural selection could never be understood to act in this way:

> Natural selection will modify the structure of the young in relation to the parent, and of the parent in relation to the young. In social animals it will adapt the structure of each individual for the benefit of the community; if each in consequence

profits by the selected change. What natural selection cannot do, is to modify the structure of one species, without giving it any advantage, for the good of another species; and though statements to this effect may be found in the works of natural history, I cannot find one case which will bear investigation. (Darwin 1859, pp. 86–87; Darwin 1959, p. 172)

Later in the same work Darwin put the point in the strongest possible terms:

Natural selection cannot possibly produce any modification in any one species exclusively for the good of another species; though throughout nature one species incessantly takes advantage of, and profits by, the structure of another. . . . If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced by natural selection. (Darwin 1859, pp. 200–1)

For example, some authors had asserted that the rattlesnake's rattle is a mechanism for warning potential victims of danger, and thus of giving them a fair chance of escape. Darwin heaps scorn on this claim: "I would almost as soon believe that the cat curls the end of its tail when preparing to spring, in order to warn the doomed mouse" (Darwin 1859, p. 201). It is true that organisms of different species sometimes behave in ways that are mutually beneficial (e.g., symbiotic relationships between ants and acacia trees, termites and the cellulose-digesting bacteria that inhabit their guts, etc.), but all such cases can be explained as organisms acting for their own, rather than for their associate's, benefit. Darwin made his own view of the matter crystal clear: "Natural selection will never produce in a being anything injurious to itself, for natural selection acts solely by and for the good of each" (Darwin 1859, p. 201).

Summary: Darwin and Natural Selection

Natural selection is the central theoretical principle that distinguished Darwin's explanation of living things from all those that preceded him. In addition to offering a new explanation for the origin and nature of living things, Darwin proposed a new *kind* of explanation, based on a novel ideal of natural order according to which variation (rather than uniformity) is fundamental. Stated abstractly, how natural selection operates seems entirely unproblematic. Yet the very generality that gives the principle its broad explanatory power also raises difficult questions about its actual operation. On what sorts of "biological entities" can and does natural selection operate? How did Darwin approach this issue? As we have seen, for the vast majority of problems requiring a selectionist explanation, Darwin was content to appeal to selection at the level of individual organisms. He was, however, willing to countenance selection operating at some higher level of organization when the biological phenomenon under consideration did not lend itself to an analysis in terms of selection for individual benefit. So, for example, in the *Origin,* Darwin explained the otherwise puzzling case of sterility among certain members of insect communities by noting that "selection may be applied to the family, as well as to the individual, and may thus gain the desired end." In *The Descent of Man* (1871) he offered a similar explanation of the evolution of the human moral sense. Explaining the evolution of social behaviors, in particular, seemed to him to require extending the range of natural selection beyond the narrow compass of the individual organism but not necessarily beyond the scope of the individual understood as a biological entity having some significant degree of functional integration. In this way selection could, in principle, operate among communities as functionally integrated individuals. Interpretations of Darwin's thought that present him as strictly adhering to the view that selection only operates on individual organisms gain in simplicity but sacrifice appreciation of the subtlety of Darwin's attempts to solve some of the most difficult problems facing the theory of natural selection. His was an individualistic perspective at heart, but he refused to straightjacket himself into offering just one kind of evolutionary explanation. Darwin was too much of a pluralist for that.