

ON THE ORIGIN OF SPECIES
BY MEANS OF
NATURAL SELECTION

Charles Darwin

edited by Joseph Carroll



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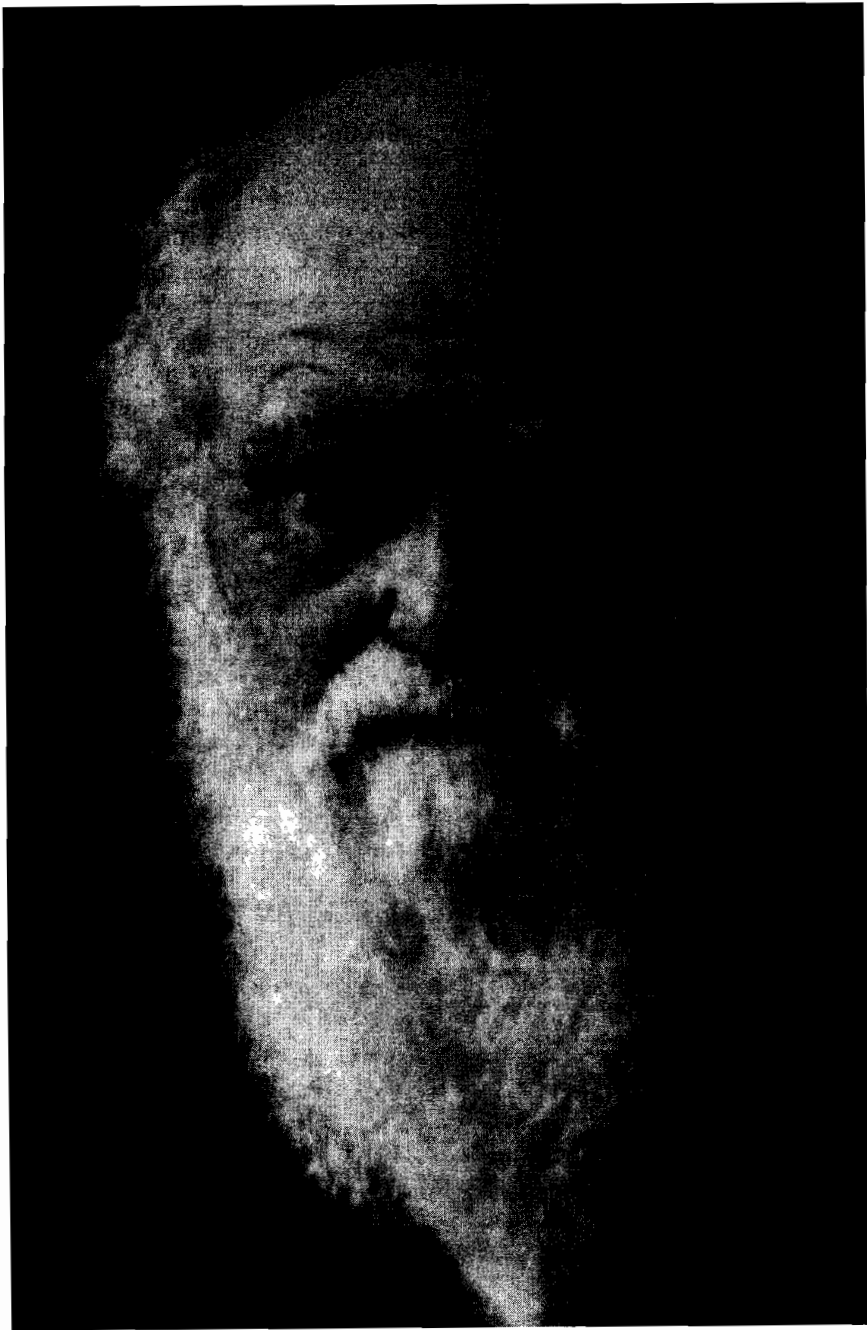
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Through its research leaves, the University of Missouri has provided valuable time in which to work on this edition.



Portrait of Charles Darwin by John Collier (1881)
Reproduced by permission of the Linnean Society of London.

Introduction

I. The Classic Status of *The Origin of Species*

The Origin of Species has special claims on our attention. It is one of the two or three most significant scientific works of all time—one of those works that fundamentally and permanently alter our vision of the world. At the same time, it is one of the few great scientific works that is also a great literary classic. It is written for the educated general reader and requires no specialized scientific training. It is argued with a singularly rigorous consistency, but it is also eloquent, imaginatively evocative, and rhetorically compelling. Although it is now nearly a century and a half old, it remains the single most comprehensive and commanding exposition of its subject, and its subject—the development of life throughout all of time—has a sublime scope and a unique significance.

Many fine scientists, scholars, and writers have now dedicated their lives to the subject of evolutionary biology, but none of this work has rendered Darwin's own contribution obsolete. Ernst Mayr, both a biologist and a historical scholar of the first rank, maintains that modern evolutionists differ from Darwin "almost entirely on matters of emphasis" (*One Long Argument*, 164). Mayr himself is one of the main contributors to the "Modern Synthesis," that is, the integration of Darwin's theory of natural selection with Mendelian genetics. Despite the advances in modern technical understanding, he notes that "a modern evolutionist turns to Darwin's work again and again," and he observes, rightly, that "Darwin frequently understood things far more clearly than both his supporters and his opponents, including those of the present day" (vii). His summary judgment of Darwin's lasting historical significance is that "no one has influenced our modern worldview—both within and beyond science—to a greater extent than has this extraordinary Victorian" (ix). In confirmation of these claims, we may look to a recent, comprehensive textbook of evolutionary biology, Mark Ridley's *Evolution* (1993). Ridley informs his audience that "the classic case for evolution was made in Darwin's *On the Origin of Species*" and that Darwin's "general arguments still apply" (3). Further, on the specific and central topic of the evidence for evolution, Darwin gives "the classic account" (59). Michael Ghiselin, another distinguished biological theorist and Darwin scholar, also affirms the enduring value of Darwin's commanding perspective. "To learn of the facts, one reads the latest journals. To understand biology, one reads Darwin" (232). Given such testimony as this, it would not be too much to say that if a student were to read only one book on evolution, the best book to read would still be *The Origin of Species*.

2. Plan of the Introduction

The extraordinary canonical position occupied by the *Origin* depends on three elements: the subject, the time, and the man. Darwin had a subject full of mystery and power, the one subject of the deepest possible significance for all living things; the time was right for the comprehension of that subject; and Darwin was the right man to achieve that comprehension. In this section of the introduction, I shall explain the sequence of topics for the introduction as a whole, and then in the next three sections I shall take up each of these three elements in turn. After commenting on Darwin's subject, the historical background to his work, and the character of mind that made it possible for him to discover and develop the theory of natural selection, I shall describe the one main evolutionary theory that stood as an alternative to Darwin's—the theory of Lamarck and Spencer. Turning then to the development of Darwin's own theory, I shall discuss the inception and gestation of the *Origin*, and I shall also discuss Darwin's effort, in *The Descent of Man*, to incorporate human beings within the phylogenetic order—that is, within the classificatory system that derives from the common descent of all living things. ("Phylogeny" is the evolution of a genetically related group of organisms and is distinguished from "ontogeny," the development of an individual organism.) In locating Darwin in relation to both his sources and his successors, I shall use the idea of scientific revolutions as a leading theme. I shall compare Charles Lyell's revolution in geology with Darwin's revolution in evolutionary biology, and I shall examine the complex way in which Darwin assimilates his sources, incorporating some elements and using others as foils. Taking issue with Thomas Kuhn's notion of a simple paradigm shift or gestalt switch, I shall also examine the long delay before Darwin's own revolution was completed in the Modern Synthesis, a process that lasted from about 1920 through about 1950. In the final segment of the introduction, I shall offer a brief guide to further reading.

The Works Cited section at the end of the introduction will contain references to the source texts for the selections in the appendices, to the works cited in the introduction as a whole, and to the works cited in the guide to further reading.

3. Darwin's Subject

Before commenting on the nature, sources, and development of Darwin's theory, it will be helpful to present a brief outline of the theory itself. Darwin's own summary of his theory, in the introduction to the *Origin*, is admirably succinct:

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. (In this volume, p. 97)

The logic of reasonable presuppositions and conditional inferences in this formulation is luminously clear and simple—so clear and simple that Darwin's young colleague, T. H. Huxley, first responded to the theory by exclaiming to himself, "How extremely stupid not to have thought of that!" (in this volume p. 627). The apparent simplicity of the theory is deceptive and is in fact a measure of its extraordinary depth and power. Huxley was a man of exceptionally quick and sharp intellect, but he lacked Darwin's deep consistency and his power of formulating and sustaining a wholly original vision of the world. (When we speak of "genius," it is to such power that we refer.) Huxley saw instantly into the logic of the case, but he did not see instantly, and perhaps never fully and consistently grasped, the all-encompassing character of the theory, the way it implied and was implicated in every conceivable aspect of the structure and function of all living things—both of their internal organization and of their external relations to the physical world and to other living things. The significance of a scientific theory can be measured in good part by the ratio between simplicity of causal explanation on the one side and the extent of explanatory scope on the other. The most significant theories bring the largest range of phenomena within the smallest compass of causal explanation. Judged by this criterion of significance, the theory that Darwin squeezes succinctly but adequately into the few lines quoted above ranks with the theories of Copernicus, Newton, Einstein, and Crick and Watson. That is, it is one of the few most successful efforts at scientific explanation in the history of science.

The succinct summary quoted above has a dry, logical, almost arithmetical character. Such is the nature of simplicity in causal explanation. But the full scope of the world of phenomena encompassed by the theory has a magnitude that staggers the imagination, and this magnitude has a specific aesthetic character. Since the time of Longinus, the definition of the sublime has been that of a grandeur that expands the imagination to its limits and then escapes those limits. Darwin himself understood this effect and had the imaginative capacity simultaneously to explain and to wonder. In his autobiography, he complains that in his later life he had lost all capacity

for aesthetic pleasure, for poetry and art, though he still much enjoyed novels. For this apparent atrophy of the aesthetic faculties, he blames his exclusive concentration on scientific work (in this volume p. 443). A perhaps more just apprehension of the case is to say that Darwin's aesthetic and imaginative energy had gradually become wholly absorbed into the creative vision that became his life's work. In the final sentence of the *Origin*, after once again summarizing succinctly the presuppositions and logical linkages of his theory, he gives full rhetorical and emotional expression to his imaginative apprehension of his subject:

There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

Darwin's imagination poises over two kinds of tension. One is the tension between the simplicity of life's origin and the multifarious complexity into which natural forms have evolved and continue to evolve. The other kind of tension is that between the invariable, unitary law of gravity, producing only an endless, cyclical repetition of planetary motion, on the one side, and on the other the perpetual change of living forms through time. Darwin envisions the whole progression of life on earth within the cosmic scope of Newton's celestial mechanics, and in his imaginative response to this progression he integrates the austere intellectual satisfaction of causal explanation with a luxuriant delight in the complexity of life.

In his chapter on geological succession, Darwin observes that through his theory "we can understand how it is that all the forms of life, ancient and recent, make together one grand system; for all are connected by generation" (in this volume p. 309). The *Origin* is full of impressive rhetorical passages, but its larger imaginative effect derives from the quietly meditative and methodical exposition of this whole "grand system" in its diverse aspects. The first and most apparent aspect is that of systematics, the classification of all living things within a hierarchical order. In the century before Darwin, the great Swedish systematist Linnaeus (Carl von Linné, 1708-78) had created a workable system of classification. He had thus provided an indispensable platform for Darwin's own work, but Linnaeus' system had no causal mechanism and no temporal dimension. As Ghiselin observes, in Darwin's theory, "classification ceased to be merely descriptive and became explanatory" (83). The hierarchical order of systematic classification exists *because* all living beings are connected in a phylogenetic line. They are connected, as Darwin says, by "generation."

Darwin's insight into the phylogenetic basis of systematic order is a true insight—an insight that peers into the reality of things. Consequently, once he has in possession this one central clue to the organization of life, he can use it as a guide to every other aspect of natural history. It becomes his golden thread through the mazes of anatomy, development (ontogeny), reproductive interactions, ecology, paleontology, and the geographical distribution of living things. Darwin gives extended expositions to his findings in all these fields of inquiry. These expositions serve as evidence for his core theory, and his core theory serves as an explanatory hypothesis for the organization of the evidence.

In the generation before Darwin, in rough parallel to Linnaeus, the distinguished French anatomist and paleontologist Georges Cuvier had established two grand principles of anatomy: (1) that all animals can be arranged into a few basic body plans (in Cuvier's system, vertebrates, molluscs, articulates [for ex., insects], and radiata [for ex., jellyfish]; and (2) that the internal organization of all animals displays an integrated functional order; one part or organ requires and implies another part of a particular kind. For instance, an animal with the teeth and claws of a predator will also predictably have a digestive tract designed for the digestion of meat. An animal with wings designed for flight will also have a heart that beats fast enough and a skeletal structure light enough for sustained flight. The same logic of phylogenetic connection that explains the classificatory order described by Linnaeus explains also the organization of life under a few distinct body plans. And the idea of adaptation by means of natural selection explains the integrated functional order in the internal organization of organisms. Animals make sense as integrated functional wholes not because they have been created in that way, once and for all, but because they have evolved in adaptive relation to the conditions of their existence.

The theory of special creation and the theory of natural selection are both compatible with the integrated functional organization of animals—and indeed integrated functional organization is the primary evidence put forth in the argument of natural theology: the argument that "design" implies a designer (see the selections from Paley in this volume). But the theory of special creation, in contrast to the theory of natural selection, is not a causal explanation so much as a simple appeal to divine intervention—the *deus ex machina* of biology. More importantly, from the standpoint of causal logic, while special creation can account for integrated functional organization simply by claiming that such organization displays the wisdom and beneficence of the Creator, it cannot account for *imperfections* in functional organization. If God created animals to be perfectly adapted to their environments, why did he provide them with rudimentary organs such as the human appendix? Why did he provide upland geese with

webbed feet that they never use for swimming? Moreover, why did he manage things in such a way that the same sequence of bones appears in the forelimbs both of reptiles and of mammals, and in the wings both of birds and of bats? Was this sequence of bones optimally efficient for the diverse activities of all these animals? To questions such as these, special creation can provide no answer. In contrast, Darwin's theory of descent with modification—the theory that all organisms have descended from previous organisms, and that in the course of descent the form of organisms has gradually become modified through a process of adaptation by means of natural selection—provides an answer. By invoking this theory, we can understand that all adaptive structures derive from previous structures; adaptation never begins from nothing, and inherited structure places necessary constraints on all functional organization.

By explaining both the internal organization of organisms and their classificatory order, Darwin enabled himself to give an intelligible account of life in three of its main dynamic aspects: (1) the internal development of individual organisms (ontogeny); (2) the distribution of species over space in time; and (3) the interactions of organisms within ecological systems.

By positing the selection of adaptive characteristics at differing points in the life history of an organism, Darwin was able to explain, correctly, the partial parallelism between embryonic development (ontogeny) and the place a species occupies within the generational sequence (phylogeny). The human embryo, for instance, at one stage contains gills, and at another a rudimentary tail. (Darwin comments on this topic in the *Descent of Man*; see this volume pp. 500–502.) Darwin's disciple Ernst Haeckel later exaggerated this insight into embryonic development into the misleadingly overgeneralized claim that *ontogeny recapitulates phylogeny*, but Darwin's own observations (in this volume pp. 373–74) display the judicious precision and circumspection that usually characterize his work, and these observations form an integral part of the network of logic and evidence in his exposition. In his history of embryology, John Moore makes a point about Darwin's historical significance very similar to the point that Ghiselin makes about Darwin's place in the history of systematics. "The Darwinian paradigm shift of 1859 changed not only what biologists did but also provided an explanation for what they observed. The new paradigm was able to offer a satisfying explanation for much that had already been learned. In fact, the data themselves seemed to be awaiting some organizing theory, and Darwin's basic idea provided it" (407). The theory of natural selection "did far more than make some otherwise confusing embryological phenomena understandable. It accounted for the grand phenomenon of organisms belonging to sets or taxonomic groups," and as a result it "gave embry-

ologists a mission of first-rate theoretical importance—the search for lineages in the minutiae of development" (409–10).

By identifying phylogenetic organization, Darwin was able to situate plants and animals in distinct lineages and to observe the way these family groups have distributed themselves geographically through migration and the dispersal of seeds. In the later chapters of the *Origin*, Darwin reconstructs the changes over geological time in the ecosystems that have occupied specific portions of the earth. It is worth emphasizing that the "one long argument" of the *Origin* is not just the exposition of a *theory*. It is also a geographical and ecological *history*. The theory provides the crucial clues for the history, and the history in turn supports and illustrates the theory. The historical portions of the *Origin* constitute a dramatic narrative that is immense in its scope and detail. In the first of his two chapters on "Geographical Distribution," for instance, Darwin gives a masterful and compelling account of the flow of life forms over vast continental land masses, driven by the advance and retreat of ice sheets and the oscillations of the earth's crust, over millions of years.

Darwin's understanding of adaptive form links the internal organization of animals with their environmental conditions—conditions consisting both of the physical environment and also (a point to which Darwin gives special emphasis) of the other organisms with which they interact. This interdependency of organisms is the subject of ecology, and the *Origin* offers both a classic exposition of the principles at work in ecological analysis and also a series of narrative and rhetorical evocations that are among the most striking and memorable passages in the book. In these passages, logical argument interlinks symbiotically with naturally poetic imagery, each expanding and supporting the other. Here is an instance:

A corollary of the highest importance may be deduced from the foregoing remarks, namely, that the structure of every organic being is related, in the most essential yet often hidden manner, to that of all other organic beings, with which it comes into competition for food or residence, or from which it has to escape, or on which it preys. This is obvious in the structure of the teeth and talons of the tiger; and in that of the legs and claws of the parasite which clings to the hair on the tiger's body. But in the beautifully plumed seed of the dandelion, and in the flattened and fringed legs of the water-beetle, the relation seems at first confined to the elements of air and water. Yet the advantage of plumed seeds no doubt stands in the closest relation to the land being already thickly clothed by other plants; so that the seeds may be widely distributed and fall on unoccupied ground.

In the water-beetle, the structure of its legs, so well adapted for diving, allows it to compete with other aquatic insects, to hunt for its own prey, and to escape serving as prey to other animals. (in this volume pp. 142)

Darwin envisions the world as a ceaseless process of biotic interactions leading to transformations of organic form. The driving force behind these interactions is the drive toward survival and reproduction.

Natural theologians such as William Paley had examined ecological interactions from within the constraining need to affirm a beneficent order aimed at the production of the highest happiness for the highest number. Darwin's ecological vision, in contrast, takes a radically naturalistic turn. In one celebrated passage, contemplating "the plants and bushes enclosing an entangled bank," Darwin insists that the appearance of randomness or "chance" in their distribution is delusory and that in reality all happens according to "definite laws." These laws are those of a struggle and conflict that in terms of human moral order are mere anarchy and chaos:

What war between insect and insect—between insects, snails, and other animals with birds and beasts of prey—all striving to increase, and all feeding on each other or on the trees or their seeds and seedlings, or on the other plants which first clothed the ground and thus checked the growth of the trees! (in this volume p. 141)

Darwin takes full account of symbiotic relationships, and also of cooperation among social animals such as bees, ants, and wolves (and, in *The Descent of Man*, human beings), but his vision is fundamentally one of competitive struggle. He repeatedly uses phrases such as "the great battle of life," and the "war of nature." As one of the several possible empirical findings that could falsify his theory, the most striking and decisive that Darwin cites is his contention that if even one instance could be found of a species having developed an adaptation solely for the benefit of some other species, "it would annihilate my theory" (in this volume p. 220). The vision of nature Darwin offers is not that of some broad, abstract, intellectual pattern, but that of living impulse, eager, frantic, animating every single organism, vast and minute, in inconceivable numbers, everywhere on earth, persisting throughout all the time of organic life. In his own generation, this vision was startling in its novelty and strangeness, but it was also massively convincing. It was as if the fog had been dispersed, and for the first time people saw the living world as it really is and said, "Of course, yes, that's it."

Darwin's vision of nature can be disturbing in its recognition of ferocity and ruthlessness, but it can also be ennobling in its response to beauty and

power. Darwin's own response to his subject has a quality of adult realism that, in retrospect, makes the fantasies of anthropomorphic providentialism seem puerile and sentimental. In the concluding sentence to the central chapter "Natural Selection," Darwin finds a poetic image that recapitulates his phylogenetic diagram of branching lineages and that also captures the tonal extremes in the subjective qualities of his vision:

As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feeble branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications. (in this volume p. 177)

Death and destruction are inseparable parts of the organic process. No small part of Darwin's achievement is to have had the strength of mind necessary to rise above our partial human identifications and to stand, clear of eye and unabashed, before the total order of nature.

4. The Historical Moment of *The Origin of Species*

In the latter half of the eighteenth and the first half of the nineteenth century, natural history had made huge strides in a wide array of specialized disciplines. The tradition of "natural theology," or the study of adaptive structure and ecological relations—interpreted as indications of providential order or "design"—had already extended from the time of John Ray (1627-1705) to that of William Paley (1743-1805). In the course of the eighteenth century, Linnaeus had for the first time set taxonomy—the classification of living things in coherently related groups—on a sound footing. The Comte de Buffon (1707-88), the greatest of the naturalists among the French encyclopedists, had pioneered the study of geographical distribution—the designation of distinct groups of plants and animals in different parts of the world. Explorer naturalists, typified for Darwin by Alexander von Humboldt (1769-1859), had transformed the genre of travel writing into a medium of research into biogeography and ecology. (Darwin's own research as a naturalist during the voyage of the *Beagle* made important contributions to this tradition.) The deliberate breeding of animals and plants had of course gone on since before the beginning of recorded history, but the methodical study of breeding—of hybridism and of variation and the inheritance of variations—had emerged only within the previous century. The development of modern scientific embryology can be dated from Karl Ernst von Baer's discovery of the mammalian egg in

1827. The embryological researches of Darwin and his contemporaries provided important new insights into the structure and development of organisms and opened the way for Darwin's speculation into the relations between the individual development of a single organism (ontogeny) and the development over generations of species and higher taxa (phylogeny). ("Taxa" is the plural of "taxon." Taxa are distinct groups of organisms of any rank. The taxonomic system locates all organisms within a classificatory hierarchy, thus: kingdom, phylum, class, order, family, genus, species, individual organism.) In the decades immediately preceding Darwin's maturity, Cuvier had established a strong scientific foundation both for comparative anatomy and for paleontology and had thus provided an indispensable basis for using anatomical structure to analyze the phylogenetic relations among organisms. In the work of Thomas Malthus (1766-1834), economics had turned its attention to the elemental biological interaction between population pressure and the supply of food. Most importantly of all, in a period from about 1750 to 1830, geology had emerged from the realm of fantastic speculation, established itself as a progressive empirical science, extended the scale of geological time from thousands of years to thousands of millions of years, and provided a model for the idea of massive alterations in structure resulting from the accumulation of changes so minute as almost to escape notice within the scale of a human lifetime.

Darwin's academic career at Cambridge was undistinguished, but while in university he had pursued natural history as a hobby and had made scientific friends. One of these friends, the botanist John Henslow, recommended Darwin for a post as unofficial naturalist on board *H.M.S. Beagle*, assigned to take soundings along the coast of South America and circumnavigate the globe for the purpose of making chronometric calculations. The *Beagle* set sail late in 1831 and returned to England nearly five years later. Much of that time, while his shipmates went about their different duties, Darwin was ashore, exploring, geologizing, and collecting specimens in natural history. Just before Darwin set out on the voyage of the *Beagle*, Robert Fitzroy, the captain of the ship, gave him what was probably the single most important intellectual gift of his life, the newly published first volume of Charles Lyell's *Principles of Geology*. (Volumes two and three reached Darwin in the course of the voyage.) Darwin assimilated Lyell's geological vision and used it as the main guide to his own geological observations on the voyage, and indeed for the rest of his life.

From Lyell Darwin inherited both substantial intellectual property and a burden of intellectual debts—unsolved scientific problems—that helped give direction to his own work. Lyell was both a geologist and a species theorist. In the former field, he achieved lasting distinction and provided an indispensable basis for the development of Darwin's own theories. As a

species theorist, Lyell's creative work merely registered the stresses and perplexities of the species problem as it had developed up to his own time.

As a geologist, Lyell adopted the uniformitarian views of James Hutton. In *Theory of the Earth* (1795), Hutton had described the earth as a homeostatic system in which the slow and perpetual building up and wearing away of land over billions of years maintains a large-scale equilibrium. In the four decades between Hutton's work and Lyell's publication of the *Principles of Geology*, empirical geologists had made major advances in reliable knowledge about volcanic activity, erosion, stratigraphy, fossils, and other aspects of practical geology. Lyell assimilated this information, supplemented it with his own original and highly perceptive observations about crustal movements, and organized it within the basic framework of Hutton's theory of a homeostatic equilibrium between erosion and the formation of new land masses.

The principles of geology propounded by Lyell were fundamentally sound and relatively comprehensive. Since the time of his initial synthesis, there have been only two really fundamental additions to geological theory. The first was the theory of glaciers that was developed by Louis Agassiz during Lyell's own lifetime and that Lyell assimilated into later editions of the *Principles of Geology*. The second was the theory of continental drift, eventually expanding into the theory of plate tectonics, that was first sketched out by Alfred Wegener in the first and second decades of the twentieth century. The theory of plate tectonics has solved many interesting puzzles in geology, paleontology, and the geographical distribution of animals and plants, but this theory has only extended and expanded Lyell's synthesis, not replaced it. Darwin's theory of evolution by means of natural selection, in contrast, decisively demonstrated that Lyell's hypotheses as a species theorist were fundamentally wrong. Darwin could incorporate certain aspects of Lyell's thinking about species, and especially the idea that species become extinct through failure to adapt to environmental change—but the larger structure of Lyell's theory was erroneous, and what Darwin did was not to assimilate it but rather to reject it and to replace it with an alternative, better theory.

At the time that Lyell took up the species problem, the main alternatives for explaining the distribution of species over time were those of Jean-Baptiste de Lamarck and Georges Cuvier. In his *Philosophie Zoologique* (in this volume, pp. 573-80) and other works, Lamarck had formulated a radical alternative to the idea that species had been created in their fixed and final form. He had proposed that species evolve over time, driven forward by some mysterious internal impetus toward ever-increasing complexity of structure and directed ultimately toward transformation into the supposedly highest of all anatomical forms—the human. Along the way, Lamarck

speculated, the pure impulse of complexification leading to anthropomorphic perfection is deflected and distorted by the need of organisms to adapt to the various stresses of local environmental conditions. Cuvier had flatly rejected Lamarck's evolutionary theses and had affirmed that all species are specially created in a single, primary act of creation, that of Genesis. Since he also recognized the reality of extinction, he necessarily supposed that the actual number of species is declining over time.

Cuvier did important work in assessing fossils and strata in the Paris basin, but he drew erroneous conclusions from the discontinuities in both the sedimentary sequences and the fossil record. He did not recognize the basic stratigraphic principle with which William Smith (1769-1839) can be credited. (Stratigraphy is the branch of geology that concerns itself with analyzing the sequence of sedimentary strata.) Smith was the founder of English stratigraphy, and through his stratigraphical map of England, he established the principle that strata are complete in no one area; sediments have been both laid down and eroded over widely dispersed areas, with the result that a complete stratigraphical column—a complete sequence of all actual strata in their chronological order—can be obtained only by collating strata from different regions. This act of comparison and collation was the main business of practical geology from the time of Hutton and of the stratigraphical pioneer Abraham Werner (1750-1815) through the time of Adam Sedgwick (1785-1873), the Cambridge stratigrapher who gave Darwin his first lessons in practical geology (and who later, incidentally, violently opposed his theory of evolution on religious grounds). Since Cuvier's formative period came a little too early for him to assimilate Smith's principle, he was both a geological and a biological catastrophist. He accounted for discontinuities in the fossil record by supposing that a series of catastrophic floods or sudden ice invasions had eliminated the biota in any given area multiple times. He accounted for the different fossils in more recent strata by supposing that after each catastrophe somewhat different (but already existing) plants and animals had migrated in from neighboring regions. (In the most extravagant of all theories of special creation, Cuvier's catastrophist disciple Louis Agassiz, among others, supposed that whole new biotas—new assemblies of plants and animals—had been specially created after each successive catastrophe.)

Both Lamarck and Cuvier perceived certain aspects of the species problem correctly, but neither formulated a plausible total theory. Cuvier believed that some species represented in fossils had become extinct, and Lamarck believed they had evolved into currently living forms. Thus far each was at least partly correct (not all extinct species have evolved into living species), and their views were complementary, but other aspects of their views prevented the complementarity from being perceived as part of the

whole, larger picture. Lamarck denied the possibility of extinction (except in rare cases of human depradation), did not adequately recognize basic differences of body plan among distinct groups of animals, and provided no plausible mechanism for evolutionary development. Through his paleontological researches into the extinct fauna of the Paris basin, and especially the large extinct mammals such as mammoths, Cuvier decisively established the reality of extinction, but he rejected Lamarck's correct contention that species could change over time.

Lyell rejected Cuvier's view of geological history as a series of catastrophic floods and sudden massive invasions of ice, but he also reacted with alarm to Lamarck's evolutionary speculations. These speculations seemed to conflict with his uniformitarian convictions that the current state of the earth has been the result of past actions very similar to the actions we see occurring around us at the present time. An even more important objection was that the speculations implied continuity between human beings and the primates (specifically, "orang-outangs"). In reaction to Lamarck, Lyell sought to modify the idea of special creation in such a way that he could acknowledge the reality of extinction and still integrate special creation with his own uniformitarian geology. Lyell hypothesized that only a small proportion of the biota existing at any given geological period becomes extinct and that the extinct species are replaced with species that have been newly created. Replacements of the biota would thus be slow, gradual, and continuous. Lyell suggested that species went extinct because of a failure to adapt to changing environmental conditions, but he offered no causal mechanism for the introduction of new species. Like Cuvier, and in stark conflict with the paleontological evidence, he denied any "progressive" character—any increase in morphological complexity—in the stratigraphic column. He suggested instead that newly introduced species always replaced, with some slight differences, other species within the same general class (in this volume p. 610). Certain species of birds or fish, say, would become extinct, and new but not too dissimilar species of birds and fish would be created to replace them. As a species theorist, then, what Lyell mainly offered Darwin, apart from his exposition and critique of Lamarck (in this volume pp. 608-609), was a set of puzzles and perplexities that it became the chief occupation of Darwin's life to solve.

Darwin himself was always generous in his appreciation of Lyell's achievements and open in his avowals of how much his own work had benefitted from Lyell's influence. In the *Origin*, Darwin speaks of the *Principles of Geology* as a work that "the future historian will recognise as having produced a revolution in natural science" (in this volume, p. 271). For the purpose of understanding the nature of the Darwinian revolution, and of scientific revolutions generally, it is instructive to compare the relation of

two great revolutionaries to their chief predecessors: Lyell's relation to Hutton, and Darwin's relation to Lyell himself. At the time Lyell produced the first edition of *Principles of Geology*, Hutton was largely in eclipse. His views on the importance of volcanic activity in creating land masses had received less credence than the Neptunist theory of Abraham Werner, who had hypothesized that all the sediments had been precipitated from a universal ocean. At the time of Lyell's work, the dominant, received view in geology was the somewhat different version of catastrophism—the theory of successive, relatively local floods and ice invasions—propounded by Cuvier. In this climate, given Cuvier's daunting prestige, to advocate a Huttonian view—the idea of continuous, relatively slight changes in the earth's surface over incalculable immensities of geological time—required considerable boldness and originality. Nonetheless, within just a few years, Lyell had established his new, Huttonian synthesis as the dominant, mainstream view. Toulmin and Goodfield lucidly characterize Lyell's historical position in relation to his predecessor.

Lyell's position differed from Hutton's in only two serious respects. Firstly, he sets less store on the providential character of geological change.... Secondly, where Hutton's account of geological development had inevitably been only schematic, his own could be elaborate and detailed. The intervening forty years had left their mark.... [Lyell] had at his disposal a much larger and more varied range of examples, and the range of mechanisms he could illustrate and establish was correspondingly larger and more varied. Instead of the earlier crude opposition between fire and water, he could demonstrate the geological effects of a dozen different agencies, acting either in combination or against one another; and it was the marginal balance between all these agencies, at any one place and time, which determined whether the Earth's crust was being built up or worn down at that point. (169)

Lyell established uniformitarianism as a historical phenomenon and as a methodology. The method is that of reasoning from present causes to past events, and the factual presupposition that justifies the method is the idea that geological change results from small natural changes working over vast periods of time. (Historians of biology designate the factual presupposition as "actualism.") Both the fact and the method presupposed a time scale greater by orders of magnitude than that of any previous human imagining. Hutton must be accorded credit for the original conception of deep geological time, but Lyell gave it definitive confirmation and made it fully available to the empirical imagination.

By integrating empirical information within a Huttonian theoretical framework, Lyell established geology firmly as a science. He thus brought to a close the long phase of fanciful speculation in geology, a phase that included all ancient myths—pre-literate, classical, and Biblical—and also the quasi-mythic cosmogonic speculations of theorists such as Burnet, Buffon, and Werner. (Thomas Burnet [1635-1750] was a clergyman and author of *Sacred Theory of the Earth*, an extravagant exercise in geological fantasy.) Cuvier had made major advances in paleontology, and Lyell assimilated those to his system, thus correcting Hutton's failure to take adequate account of the fossil record, but Cuvier's catastrophism also constituted the last major flutter of the old speculative fancy in the construction of stories about the earth. Lyell himself acutely diagnoses this fancy as an inevitable imaginative consequence of a radically foreshortened time scale in which to compress the titanic transformations in the earth's crust. (See this volume pp. 606-607.)

Lyell was overwhelmingly the most important single influence on Darwin's work. Through his uniformitarianism—his vision of change as the consequence of small natural changes working over vast periods of time—Lyell provided the basis for Darwin's formulation of a scientifically correct theory of the development of life on earth. Darwin began his career on the *Beagle* voyage at least as much a geologist as a biologist. His first mature work of scientific discovery—what Ghiselin rightly calls his first great synthesis—was his theory of coral reefs (see pp. 461-62 in this volume). This theory deploys a chief principle of Lyell's geology—the perpetual rising and falling, the slow undulation, of the earth's crust. On the basis of this theory, Darwin corrected Lyell's own erroneous theory about the formation of coral reefs. (Lyell hypothesized that they grew upward from stable undersea mountains; Darwin correctly surmised that most of them grew at the edge of mountains that were gradually sinking beneath the surface of the ocean, and that others grew at the fringes of land masses undergoing elevation.) By revising Lyell's specific theory about coral reefs, Darwin solved a geological puzzle, and he thus also brilliantly confirmed Lyell's larger principle.

Lyell and Darwin may be envisioned as a triumphal scientific succession—one great monarch succeeding another. Lyell definitively shifted geology from the realm of fanciful speculation to that of science, and Darwin did the same for biology. Among the fanciful speculations that Darwin replaced, we may count Lyell's own theory about the extinction and succession of species. In one respect, Darwin's achievement looms larger than that of Lyell. Though a geologist of genius, Lyell was not a theoretical discoverer of the first magnitude. His work was that of synthesis and integration. He adopted Hutton's basic scheme and used it to assimilate the more recent work in vulcanism, paleontology, and stratigraphy. Darwin both discovered

the basic theory of descent with modification by means of natural selection and also produced the synthesis of empirical disciplines that confirmed it. If we compare *The Origin of Species* with the *Principles of Geology*, we can still greatly admire Lyell's achievement, and we can perceive its vital importance to Darwin, but in comparison we can also appreciate all the more fully the singular, world-historical character of Darwin's book—the magnitude of its scope and the depth of its significance, its originality, the grandeur of its design, the intricate unity of its argument, and the sustained, symphonic power of its exposition.

5. Darwin's Intellectual Character

The middle of the nineteenth century was the right time for the formulation of the theory of natural selection because this whole network of naturalistic research had finally produced all the elements that were necessary to it. Darwin was the right man to undertake the formulation for several reasons. He had the rare capacity for original, creative thinking about elemental realities. He had both the training and the depth of mind that were necessary to recognize the significance of his subject, and he had the ambition that drove him to seize the unique opportunity history had given him. He had the social and material conditions that made it possible for him to dedicate himself to his project. He had an extraordinary capacity for sustained, detailed, multifarious inquiry oriented to one large, synthetic aim. He had an exceptional gift for insight into the mechanisms of living things, and an equally exceptional gift for integrating all his observations and inquiries into a unified theoretical vision. As Matthew Arnold said of the Greek dramatist Sophocles, Darwin saw life steadily, and he saw it whole.

In one important respect, Darwin's virtue was negative: he was not able *not* to conceive his subject in a profoundly coherent way. He had no capacity for evasion or equivocation. His mind did not admit of getting lost in details or of becoming stymied in inconsequential implications. He did not respond to the allurements of specious inferences. Partisan bias and special pleading were wholly alien to him. He weighed counterevidence or arguments that told against his views not simply as a matter of obligation, grudgingly, or as a strategy of argument. He cared for the full weight of an argument. As Henry James might put it, he wanted its full value, and he understood instinctively, as a part of his intellectual personality, that the weight of an argument consists of the conclusions that emerge from the combined force of all the evidence and all the reasons that can be brought to bear on a subject.

Darwin's integrity enters crucially into the standing of the *Origin* as both a scientific and a literary classic. Michael Ghiselin has registered the impor-

tance of intellectual integrity as a source of strength in the construction of Darwin's theories. "Darwin's success may readily be explained by a very simple hypothesis which seems not to have occurred to his critics: he thought. He reasoned systematically, imaginatively, and rigorously, and he criticized his own ideas" (232). Such qualities were apparent also to the most astute among Darwin's contemporaries. Speaking on the occasion of Darwin's death, T.H. Huxley, one of the most effective public proponents of Darwin's views, described "a certain intense and almost passionate honesty by which all his thoughts and actions were irradiated, as by a central fire" (in this volume p. 623). Huxley explains how this "rarest and greatest of endowments" worked in Darwin both as a productive force and as a disciplinary constraint. As a productive force, it led him to undertake "prodigious labours of original investigation and of reading," and it drove him "to obtain clear and distinct ideas upon every topic with which he occupied himself." As a disciplinary constraint, it "kept his vivid imagination and great speculative powers within due bounds" and "made him accept criticisms and suggestions from anybody and everybody." One of the people from whom Darwin most eagerly sought criticism was his closest personal friend, the eminent botanist Joseph Hooker. In his review of the *Origin*, Hooker describes Darwin's integrity not merely as a feature of intellect but also as a social quality. It is an index of civilization that reveals itself in the tone and manner of Darwin's writing. "Whatever may be thought of Mr. Darwin's ultimate conclusions, it cannot be denied that it would be difficult in the whole range of the literature of science to find a book so exclusively devoted to the development of theoretical inquiries, which at the same time is throughout so full of conscientious care, so fair in argument, and so considerate in tone" (in Hull, *Darwin and His Critics*, 83).

Much has been made of Darwin's supposed dullness, exemplified, it is thought, by his respectable but undistinguished performance as a student. In his *Autobiography*, Darwin himself contributed to this tradition. He assessed his own abilities with unfeigned modesty and with the dispassionate weighing of pros and cons that had long since become the governing habit of his mind. He concluded, "With such moderate abilities as I possess, it is truly surprising that thus I should have influenced to a considerable extent the beliefs of scientific men on some important points" (in this volume, p. 444). The surprise is perhaps justifiable on the grounds, as he himself explained, that he had not the "quickness of apprehension or wit" of a sort that distinguished Huxley. He acknowledged further that his memory was "extensive, yet hazy" (in this volume, p. 443), but since his scholarly methods were highly organized, memory was not a significant handicap. When he needed information, he could "generally recollect where to search." In counterweight to his deficiencies or limitations, Darwin credited

himself with methodical habits of observation and with an instinct of reasoning. "From my early youth I have had the strongest desire to understand or explain what I observed,—that is, to group all facts under some general laws" (in this volume, p. 444). Darwin's mind readily generated hypotheses—this is what we mean by creativity in science—but Darwin made a conscientious and effective effort to submit all hypotheses to dispassionate scrutiny. "I have steadily endeavoured to keep my mind free, so as to give up any hypothesis, however much beloved (and I cannot resist forming one on every subject), as soon as facts are shown to be opposed to it."

Darwin's combination of inventive fertility and self-critical rigor is singular, and singularly efficacious, particularly when it is combined with the power of sustained inquiry—"the patience to reflect or ponder for any number of years over any unexplained problem" (in this volume, p. 444). Although he puts the case modestly and fairly, such qualities as Darwin ascribes to himself actually contain the whole organon of the scientific ethos. Darwin could succeed as an independent and original thinker of the first magnitude because he encompassed within his own method and character all the necessary phases or aspects of generating and testing hypotheses that are normally distributed throughout the scientific community and that constitute a long-range institutional process.

Biographers not infrequently speak of Darwin's easy circumstances with a measure of resentment or disdain, as if he was somehow cheating or taking undue advantage of an unearned and illegitimate privilege deriving from an unjust distribution of wealth. In *The Descent of Man*, Darwin himself observes that the existence of a leisure class is an absolute prerequisite to the achievements of high civilization. "The presence of a body of well-instructed men, who have not to labour for their daily bread, is important to a degree that cannot be over-estimated; as all high intellectual work is carried on by them, and on such work material progress of all kinds mainly depends" (in this volume, p. 539). In our own time, such work is done by a professional class trained and commissioned for it. Darwin himself notes that in his own class many people no doubt made no very good use of their privileged circumstances. But resentment is an appropriate response to privilege only if the opportunities are wasted. Darwin did not waste them.

Darwin's supposed dullness as a student needs to be assessed with some care. His dispositions were not toward classical scholarship and language study but toward natural science. He was thus never a prize student, but whole generations of prize students can now be recollected only by digging deep into the decaying documents that register forgotten names. A few prize students have presumably been genuinely animated by the conventional curriculum of the Greek and Roman classics; they were fortunate in that this field just happened to answer to their real talents and interests.

Probably most prize students, though, in achieving prizes, have given evidence less of inherent interest in philology than of social ambition and a willingness to accept conventional guidelines of activity. As a boy, Darwin pursued natural science purely as a hobby, and because it was a hobby he and others could not help but regard it, with some mild disapproval, as a form of dissipation, as a leisure pursuit to be indulged a little guiltily as a distraction from the serious work of deciphering the same standard texts in classical languages that many generations of students had already deciphered. In some biographical accounts, too little is made of the fact that to pursue natural science at all, with delighted if guilty eagerness, gave important evidence of spontaneous curiosity and intellectual animation.

As a boy and a young man, Darwin read widely in the course of liberal studies that was common for educated gentlemen of his age. And again, too little is often made of this phase of Darwin's education. Independently and for purely personal pleasure, he read the major English poets. As a boy, he read Shakespeare with rapt and absorbed attention (*Autobiography* 43, and see this volume, p. 442). On the *Beagle*, when he went ashore, the one book he took for pleasure, when he could take only one book, was *Paradise Lost* (in this volume, p. 430). Though he was not keen on the minutiae of language study, and though his own genius was oriented mainly to science and not to literature, Darwin had a large general intelligence that responded with spontaneous delight to the finest artistic language the English literary tradition could supply. Such responsive aptitudes are not so common as we might suppose, particularly if our sense of the norm for literary intelligence is derived almost exclusively from reading biographies of novelists and poets.

In assessing Darwin's academic career, it would be well to recall other men who were regarded, in their student days, as rather dull dogs, but who consoled themselves for their mediocrity in conventional academic performance by reading widely and with absorbed delight in the liberal arts and by pursuing artistic or intellectual activities of their own devising. By answering to this description, Darwin joins a company that includes, among others, the Duke of Wellington and Winston Churchill. It would perhaps be too much to say that success in conventional academic pursuits in one's youth is a certain sign of ultimate mediocrity, but such success is by no means incompatible with mediocrity, and the reverse proposition—that mediocrity in school work is an unpassable barrier to originality and to greatness of achievement—is quite certainly false.

The one scholar who has most fully and adequately grasped the nature of Darwin's intellectual character is Michael Ghiselin. Carefully weighing the evidence of Darwin's aptitudes in various areas, he concludes, "By the conventional indices, his intelligence quotient would probably indicate

intellectual superiority, but not genius. Yet such standards can have little meaning in judging a unique individual with such unusual talents. Whatever may have been Darwin's intellectual resources, he used them with almost superhuman effectiveness" (237). Balancing off raw IQ against intellectual character, Ghiselin suggests that "perhaps we should attribute his accomplishment less to intelligence than to wisdom" (237). By the word "wisdom," Ghiselin means something more than and rather different from moral and emotional judiciousness, though Darwin also possessed these qualities in abundance. He means the whole array of characteristics that enable a scientist to get at the truth of a subject. Darwin's curiosity and inventiveness, his caution and circumspection, his ambition, objectivity, and patient determination all play a part in his success, and as Ghiselin rightly observes, "in the final analysis, the real criterion of greatness in such matters is success" (238). Had he not possessed a mind of a truly extraordinary quality, he could not have succeeded as he did.

The nature of Darwin's success has puzzled some scholars in part because each of his mental characteristics, though admirable, is not in itself unique or even extraordinary. Insofar as Darwin's achievement depends on the quality of his own mind, what accounts for his greatness is the way all of his mental characteristics enter into combination. The combination of Darwin's characteristics was truly exceptional, and the evidence for the exceptional nature of this combination is that it enabled him to grapple effectively with the problem with which history presented him. Ghiselin concisely summarizes Darwin's career as a theoretical biologist. "On seeing that there was evidence for evolution, in spite of what others had concluded, he had the courage and ability to seek out and to discover its mechanism. Grasping the potentialities of his discovery, he had the audacity to develop a comprehensive system of biological ideas on a scale which has scarcely been appreciated" (243). Courage, audacity, and sustained constructive energy are all virtues on a heroic scale, but in Darwin's case they were made effective by being placed under the command of a characteristic that seems rather quiet, mild, and modest. Of all the characteristics that contribute to Darwin's achievement, Ghiselin and Darwin concur in believing that the one most important characteristic was a simple matter of disposition or preference—the disposition "to prefer having an opinion which is true" (243). As simple and even modest as such a disposition might seem, Huxley is right in designating it as the "rarest and greatest of endowments."

6. The Lamarckian and Spencerian Alternative to Darwinism

The Chevalier de Lamarck (1744-1829) has received more respectful attention from his modern commentators than he received from most of his

contemporaries. Mayr notes that Lamarck was the first scientist to propose a consistent theory of gradual evolution (*One Long Argument*, 43), and Simpson argues that Lamarck is historically important because he explicitly described evolution as "a general fact embracing every form of life in a single historical process" (*The Meaning of Evolution*, 266). In his own day, as an evolutionary theorist, Lamarck had little standing among reputable biologists. He was overshadowed and overborne by the great Cuvier, who proved, contrary to Lamarck's own views, that extinction was a reality of the paleontological record. Lamarck envisioned a progressive transformation of species that began with the spontaneous generation of simple microorganisms. Over evolutionary time, driven by an internal need for a complexification of structure leading ultimately to the perfected human form, these microorganisms gradually moved up the scale of nature. Along the way in this progression, species were deflected and a little distorted by being compelled to adapt to specific environmental conditions, but their finely graded variations of structure nonetheless ultimately constituted the unbroken links in a temporalized Great Chain of Being.

The quasi-Lamarckian intimations of evolutionary development in the work of Darwin's grandfather, Erasmus Darwin (particularly in *Zoonomia*), were only slight and undeveloped poetic fancies and had little or no impact on subsequent biological theory. In contrast, Darwin's near contemporary Robert Chambers made a great popular sensation with the publication of his quasi-Lamarckian theory of evolution in *Vestiges of Creation* (1844), but Chambers was a journalist, not a serious scientist, and his fanciful speculations drew little sympathetic scientific attention. Darwin and other commentators have sometimes suggested that Chambers prepared the public mind to be more favorably receptive to Darwin's evolutionary theory, but as Huxley's violently hostile reaction to Chambers suggests, Chambers might have done the cause of evolutionary theory more harm than good by casting it into the range of fantastic pseudo-science. Lamarck had been little known in England until Lyell gave an exposition of his views in the second volume of *Principles of Geology* (1832), and Lyell had expounded these views only for the purpose of repudiating them. When Darwin himself took up the cause of evolution, he was consistently eager to distance himself from Lamarck and emphatic in his expressions of disdain (see the comments in his letters, this volume pp. 475, 477-78, 493). In the *Origin*, Darwin seldom cites Lamarck as a source of valid observation, and he does not even take him as a primary foil or alternative. The main polemical foil against which Darwin constructs his own positive arguments is that of special creation.

Lamarck's theory of evolution is progressive and teleological. That is, like almost all theorists of historical development in the nineteenth century, Lamarck believed that historical change was a form of improvement and

that these improvements were directed toward some ultimate goal. In Lamarck's theory, as in most such theories, the movement is animated by some internal dynamic, but this internal dynamic is simply the mechanism for the realization of an essentially providential design instituted by a beneficent deity. Familiar versions of teleological progressivism include widely divergent ideological constructions: Hegel's absolute idealism—the idea of a World Spirit manifesting itself in the dialectical progression of culture and particularly well-disposed to the Prussian State; Marx's dialectical materialism, a theory of class-based social interactions leading inevitably to the egalitarian utopia of communism; the utilitarian utopianism of Comte and St. Simon, in which all culture progresses reliably through the stages of supernatural and metaphysical development finally to come to poise in the “scientific” humanitarianism of positivism; and the schemes of various British Victorian constructors of cultural theories, including Carlyle, Mill, and Arnold (see Carroll, *Evolution and Literary Theory*, 21–24, 184–91, 200–01).

Darwin's theory of natural selection has so successfully eliminated teleology from the pool of common metaphysical ideas that many casual modern commentators forget that the most fundamental element of Lamarck's evolutionism was orthogenic progressivism—that is, an innate tendency to development along some “straight line” directed toward a determinate end. The inheritance of acquired characteristics was for Lamarck a secondary or subsidiary mechanism. Darwin himself conceded some limited scope to this latter principle, and progressively more in later editions of the *Origin* as he sought to hedge his bets against criticisms based on problems in the theory of inheritance and the extent of geological time. (See the section entitled “The Nature of the Darwinian Revolution” for comments on Jenkin's critique of blending inheritance and on Kelvin's arguments about the age of the earth.) The idea of the inheritance of acquired characteristics was largely disconfirmed by the proto-geneticist August Weismann in the late nineteenth century and was dealt decisive blows by the consolidation of the Modern Synthesis and by the discovery of DNA, but it appears as at least a minor issue as late as 1982 (see Maynard Smith, *Evolution Now*, 91–92).

When Darwin scoffs contemptuously at Lamarck, he is not attacking the one idea with which Lamarck is now most familiarly associated—the inheritance of acquired characteristics. He is attacking two things. One is a subsidiary mechanism for the inheritance of acquired characteristics, the mechanism of “willing” (Darwin notes this could hardly apply to plants); he replaces this with simple “use and disuse,” as in the loss of sight by moles or cave-dwelling animals. The other and more important object of Darwin's scorn is the idea of an inherent tendency to progress. Lamarck's theory is heavily inflected by the spirit of theodicy—that is, the effort to explain away or rationalize the existence of evil and thus to reconcile it with the

existence of an omnipotent and benign deity. It is a biologized version of the Leibnizian idea that our world is the best of all possible worlds. (Gottfried Wilhelm Leibnitz [1646–1716] was a German polymath and optimist philosopher.) As in the case of Paley's natural theology, the need to affirm the benevolence of Providence is a central underlying motive and a primary regulative principle for the formulation of the theory. In that respect, it is not a scientific theory but a theological theory. In fundamental and decisive contrast, Darwin's theory is scientific both in motive and in character. Its motive is to provide a causal explanation that makes the best sense of the total body of available evidence, and its character is mechanistic. Darwin recognizes various metaphysical implications of his theory, with their attendant emotional sensations, but in seeking confirmation of the theory, he appeals not to the consonance of the theory with a preconceived metaphysical order but rather to the explanatory adequacy of the causal mechanism he has identified. These differences of orientation have a correlative in method and manner. Darwin was given over heart and soul to the scientific method, and he responded with almost instinctive disgust to the general slackness of argument in Lamarck and to the license he gave to his unconstrained speculative fancy.

Lyell gives a vivid and compelling summary of Lamarck's thesis, and on the descriptive level this thesis has a lot to say for itself—it takes in the progressive development of species and the lability of the species form. In contrast, Lyell's own views on this issue are relatively weak; they look like desperate counter-measures, and they were never widely accepted. In expounding Lamarck's theory, rather than approaching the problem, as Lamarck does, as a set of theological propositions, Lyell concentrates on the biological problem of the instability of species. As a result, Lyell makes Lamarck's theory seem more attractive and plausible than Lamarck himself makes it seem. He does not make it plausible to Darwin, but he does provide a point of entry into Lamarck's general vision for the second most prominent English evolutionist of the nineteenth century—Herbert Spencer (1820–1903). As Spencer notes in his *Autobiography* (see this volume pp. 592–93), he first became acquainted with Lamarck, when he was only about twenty years old, through Lyell's exposition. Despite Lyell's rejection of Lamarck, Spencer himself found the ideas immediately attractive. He absorbed them into the innermost fiber of his intellectual life, and from that time forward he never deviated in his devotion to them.

Spencer was primarily a social philosopher, and his first book, the *Social Statics* (1851), is an exercise in integrating Lamarckian teleological progressivism, utilitarian ethical theory, and an extreme form of libertarian individualism associated with laissez-faire economics. Substantial passages from this work have been included in this present volume because they provide par-

ticularly vivid and virulent instances of the social ideology that is commonly mislabeled "social Darwinism." As the date of publication for *Social Statics* makes clear, this ideology was formulated before the publication of the *Origin of Species* in 1859; the ideology was in no way influenced by Darwin's own work. Spencer envisions an ultimate utopian social order that will be achieved by gradually eliminating social undesirables and perfectly synchronizing the symbiotic interactions in a population of maximally efficient egoists. In rough parallel to the idea of natural selection, he envisions the gradual perfecting of the human type through the elimination of relatively unsuccessful human organisms and the transmission of acquired improvements, by Lamarckian inheritance, in the offspring of the strong and successful members of the population. That is, in contrast to Darwin's view, Spencer's view is that the members of a species adjust to their circumstances with varying degrees of success. These adjustments bring about structural modifications in their constitution, and the more successfully "adapted" pass on their improved constitutions to their offspring. Darwin allows for Lamarckian adaptation only as a minor, subsidiary process. For him, adaptation occurs not through behavioral changes within a single life cycle but rather through random variation and the differential survival of offspring over many generations.

The evolutionary theory propounded in *Social Statics* does not present the evolutionary process as a mechanism for the transmutation of species but rather as a means for the perfecting of the latent ideal form within a species, particularly the human species. In this important respect, Spencer is still presupposing the Aristotelian concept of species as an "archetype," that is, an ideal form with an unchanging essence. Spencer has used Lamarck as a means of modifying this Aristotelian concept, but only in such a way as to extend the concept over evolutionary time. That is, the ideal form of the species gradually fulfills or realizes itself not in a single generation but in the course of many generations.

The moral and social theories propounded in Darwin's *Descent of Man*—his one substantial essay in the field of evolutionary psychology and social ideology—are very different from the "social Spencerism" of *Social Statics*. Darwin's moral psychology is founded on the principle not of egoistic competition among isolable units in a social group, but on the principle of evolved social sympathy. Spencer has almost unconsciously incorporated into his social psychology an idea derived from utilitarian economics and utilitarian ethics: that humans are in origin and essence non-social, that they are self-contained units designed to maximize individual pleasure, and that they incorporate into social groups only as a matter of convenience or necessity. Darwin, in contrast, with his far greater intuitive penetration into human nature, perceives that human beings are social animals and that their

whole motivational and emotional organization is geared toward interdependent interaction with other humans. The evolved basis for that interdependence is social sympathy. Accordingly, Darwin's own vision of a utopian perfecting of the human social order consists not in maximizing the egoistic efficiency of individuals but in a gradual expansion of social sympathy so that it includes first all other human beings, of all nations and races, and then finally all living things (in this volume pp. 532–33). It is still a utopia—Darwin was to that extent bound within the ideological constraints of his age—but it is a utopia of enlightened humanitarian ecologists, not of finely honed utilitarian egoists.

Darwin and Spencer run parallel courses, with neither having any substantial influence on the other. Spencer formulated his main ideas and wrote some of his foundational works while Darwin was still a relatively obscure naturalist working in specialized areas such as the geology of coral reefs and the classification of barnacles. Darwin formulated his own core theory in 1838, when Spencer was only eighteen and Darwin had never heard of him. After his first foray into social ideology, Spencer developed a much larger, more grandiose theory of evolution on a cosmic scale. This general theory of cosmic evolution first appeared, in nucleus, in an essay of 1852 entitled "The Development Hypothesis" and was then given an elaborate, full-dress formulation in his definitive philosophical work, the *First Principles* (1862). The cosmic theory depends on intrinsic formal processes abstracted from any specific field of action; it is basically a theory that uses abstract terms to describe a process of increasing organizational complexity—the simultaneous proliferation of smaller units of organization and their incorporation into ever larger systemic units. This is a descriptive pattern that Spencer mistakenly regarded as a causal mechanism and hence as a form of explanation. He could make this mistake because he presupposed an intrinsic principle of progress as a first principle and needed only to deduce, as he believed, the logical order through which that principle would necessarily articulate itself. It is to this order of problem that Darwin refers when he complains that what Spencer trades in are not explanations but only "definitions" (see this volume p. 436).

After formulating his grand scheme of cosmic evolution, Spencer dedicated the rest of his life to using it as a pattern within which to organize every field of knowledge. He wrote books giving what he and many of his admirers took to be definitive formulations of all the knowledge that could possibly be contained within the fields of astronomy, geology, biology, sociology, psychology, and ethics. Each field was passed through the abstract formula of complexification—of "an advance from a diffused, indeterminate, and uniform distribution of Matter, to a concentrated, determinate, and multiform distribution of it," that is, "from a confused simplicity to an

orderly complexity" (this volume p. 591). In passing through biology, or passing biology through this filter of preconceived ideas, Spencer pauses long enough to incorporate, as he believes, Darwin's theory of natural selection, but he never so much as glimpses the way in which Darwin's theory actually supplants and cancels his own merely formal exposition (see this volume pp. 591-92, 593, 594).

In his *Autobiography*, Darwin declares, rightly, that while he was sometimes impressed with Spencer's apparent brilliance, he never derived much of value from him in the way of scientific propositions (in this volume p. 436). It nonetheless remains the case that Spencer is responsible for coining the one phrase, "the survival of the fittest," which is most often used as a kind of short-hand code phrase for the theory of natural selection. This phrase was first used by Spencer in the *Principles of Biology* in 1864. On Wallace's advice, Darwin adopted it in the fifth edition of the *Origin* in 1869. The advice was ill-considered, both in the giving and the receiving of it. From that one phrase has emerged a persistent pseudo-issue in the philosophical critique of Darwinism. It has been a source of unnecessary, purely semantic confusion. The argument runs thus: if fitness is defined by survival, "the survival of the fittest" means only that survivors survive. The phrase offers a good instance of the way in which the "definitions" that were Spencer's stock-in-trade incline toward "tautologies." But the putative problem is not in the concept the phrase is meant to encapsulate but in the phrase itself. Darwin's own formulations of the idea of natural selection have nothing tautological about them. Organisms vary in the characteristics that enable them to survive and reproduce; such variations are heritable; and the differential transmission of heritable variations leads over many generations to fundamental changes in adaptive structures, and hence, eventually, to speciation. Darwin adopted Spencer's phrase only on the tacit understanding that it would serve as a shorthand term implying all the content in his own concept of natural selection, but if one takes Spencer's phrase at face value, it strips out the elements of heritable variations and differential reproductive success. In order to avoid giving occasion for confusion, it is probably a good idea simply to avoid using the phrase.

Spencer was the most promising of Lamarck's offspring, but however splendidly he flourished in his own generation, Spencer's lineage long since faded into obscurity and has now sunk into extinction. In this respect, Spencer and Lamarck are to modern Darwinism what Neanderthals were to Cro-Magnons, not ancestors in a direct line of descent, but separate species running parallel to one another and (in all likelihood) interbreeding little or not at all. The Neanderthals survived for hundreds of thousands of years in Ice-Age Europe and the Levant, but they co-existed with Cro-Magnons for only a few thousand years. Between forty and twenty-seven

thousand years ago, as the ice retreated and the Cro-Magnons migrated in from the South, the Neanderthals disappeared from the earth, either directly exterminated or simply pushed out of viable habitats by the better equipped and more highly organized invaders who replaced them. The many volumes of Spencer's encyclopedia of universal knowledge are like the skeletal remnants of an extinct people, kept in cabinets as objects of antiquarian curiosity, a little dusty and strange, icons of an evolutionary dead end, and thus melancholy mementos of an ultimate failure and futility.

7. The Inception and Gestation of Darwin's Theory

i. The Place of *The Origin* in Darwin's Career

Before looking more closely into the development of Darwin's theory, I shall sketch out the familiar story of Darwin's career. Darwin was the son of a wealthy country doctor and the grandson of an Enlightenment scientist and poet—Erasmus Darwin. After an abortive effort at attending medical school in Edinburgh, he studied at Cambridge with the intention of taking orders and entering the church. His appointment as unofficial naturalist aboard the *Beagle* rescued him from his clerical destiny and enabled him to find his vocation as a serious student of geology and natural history. He sent home large and valuable collections of flora, fauna, and fossils, along with letters containing scientific observations, and when he returned to England, he was met with scientific acclaim and welcomed warmly into the community of practicing geologists and naturalists.

Darwin did not discover natural selection or evolution while on his voyage, but as he himself observes in the first paragraph of the *Origin*, the biogeographical and paleontological observations he made on the voyage were the primary stimulus for the development of his theory. Shortly after returning to England, he began reading and meditating on the species question and jotting down his reflections in a series of Notebooks. As he explains in his autobiography, the catalytic event in the formulation of his theory was his reading of Thomas Malthus' *Essay on Population* (in this volume, p. 438). Malthus' mathematical conception of the way birth rates inevitably exceed the food supply—what we might call the carrying capacity of the environment—formed the final, essential link in the chain of reasoning that constituted Darwin's theory. Darwin "discovered" or formulated the theory of descent with modification by means of natural selection in 1838. In 1842, he wrote a sketch of the theory at about the length of a standard scholarly article. The sequence of topics in this sketch was essentially the same as that which he used for the sequence of chapters in the *Origin*. In 1844, he expanded this sketch into a book-length manuscript,

which he set aside with instructions that in case of his death his wife should find someone to edit and publish it.

From 1844 until 1858, Darwin worked on a variety of projects. For the first few years after his return, he was occupied mainly with the materials from the voyage. In addition to the travel narrative itself, he published commentaries on the collections from his voyage and important works of geological inquiry that had resulted from his observations on the voyage. From 1846 to 1854, Darwin devoted himself to mastering the classification and anatomical structure of both the living and extinct species of a single class of animals, that of the cirripedes or barnacles. The eight years Darwin spent on the study of barnacles made important contributions to several developing fields of inquiry—to systematics, paleontology, embryology, and comparative anatomy—and it gave Darwin himself a firm professional grounding in all these areas. Moreover, by exploring the intricate variations on hermaphroditism and sexual polarity among related species of barnacles, Darwin opened an entirely new field of inquiry into the evolution of sex. During all this time, he never ceased collecting information, conducting experiments, and reflecting on the origin of species. At various points along the way, he confided his ideas to a few close associates—to his friend and botanical colleague Hooker, to his geological mentor Lyell, to his young admirer and anatomical colleague Huxley, and to his main American correspondent, the botanist Asa Gray.

Having finally completed his exhaustive study of cirripedes, in 1856, at Lyell's urging Darwin finally began writing his big book on species. He planned the work on such a massive scale, so enormous in its detail and so circumspect in its consideration of sources and facts, that it seems to have been intended to forestall and overwhelm all conceivable objection. In the *Origin* itself, Darwin often speaks with regret of having to pass over the extensive catalogues of facts that he promises to make available at some future time. However dense and concise the *Origin* itself might be, it is still quite a long and hefty book, and I think it safe to assume that most readers do not share Darwin's regret at not being able to linger over the massive documentation he has had to pass by.

Darwin had completed several hundred pages of his "big species book" when, in June of 1858, he was suddenly given a rude shock. Alfred Russel Wallace (1823-1913), fourteen years Darwin's junior, was one of Darwin's many scientific correspondents. Wallace was in the Malay Archipelago studying natural history much as Darwin had done in South America. While recovering from an attack of malaria, he recalled his reading of Malthus from years before, and this recollection precipitated in his mind the theory of descent with modification by means of natural selection—just as reading Malthus had precipitated the theory in Darwin's mind. (Wallace

was not one of the people to whom Darwin confided his own ideas on evolution.) Wallace sent a short paper to Darwin sketching out his ideas on the subject (in this edition, pp. 610-18). In the accompanying letter, with some diffidence, he asked Darwin to assess the paper, and if he saw any merit in it, to publish it.

Darwin's consternation was extreme. He had been working on the theory of natural selection for nigh on twenty years. He had already elaborated his theory at book length, had amassed huge quantities of evidence, and was in the process of producing a tome that was to have been simultaneously original and definitive. And now he was being scooped by a young colleague who had, during a fit of malaria, had a sudden insight into the same logic that had animated all of Darwin's efforts. Darwin was determined to do nothing mean or dishonorable, but he was understandably anxious not altogether to lose the credit for priority in the discovery of his theory. He turned for advice to the two men he trusted most, Lyell and Hooker. They proposed simultaneous publication and suggested that Wallace's paper be presented, side by side with a paper by Darwin, at a meeting of the Linnean society. This solution was acceptable to everyone concerned. Darwin's paper consisted of two separate pieces stitched together for the occasion: one a chapter on natural selection from the manuscript of 1844, and the other an excerpt from a letter of 1857 to Asa Gray in which Darwin had given a complete outline of his theory (in this volume, pp. 471-74 and 482-84).

After the shock of receiving Wallace's paper, Darwin decided to postpone completion of his "big species book" and instead to produce a shorter, denser work, devoid of footnotes, an "abstract" of the larger project. (Darwin initially proposed to the publisher that the book be entitled "*An Abstract of an Essay on the Origin of Species and Varieties through Natural Selection*," but the editor sagely dissuaded him from so tentative and cumbersome a title.) The big species book was never taken up again, but the "abstract," ultimately titled *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, became the definitive and original work Darwin had wished to produce. As he himself says in his *Autobiography*, "It is no doubt the chief work of my life" (in this volume p. 440). It was published on November 24, 1859. It was an immediate success, rapidly sold out, and a second edition, with a few revisions mainly of a copyediting character, was published six weeks later, on January 7, 1860. Four other editions followed, the last in 1872, and the book gradually expanded in size, as Darwin incorporated new information and included responses to some of the criticism that had been published. The sixth edition is nearly a third again as long as the first edition.

In the remaining two decades of his life, in addition to these revised edi-

tions of the *Origin*, Darwin published a long sequence of monographs and papers on specialized topics in the field of evolutionary biology that he had himself invented—notably on variation and inheritance, botanical adaptations of many kinds, sexual dimorphism and sexual selection, human moral psychology, the anatomy of emotional expression, and the ecology of earthworms. These more particular studies partly fulfilled the promises, made repeatedly in the *Origin*, that Darwin would provide more supporting evidence on particular points in some later work. Darwin continued doing original research until the end of his life, and his later works incorporated the results both from his studies and from his own experiments in botany and ecology.

The Notebooks reveal that Darwin had gained the essential insights of his work two decades before it was published, and the essays of 1842 and 1844 demonstrate that he was already at that time able to give a coherent exposition of the basic theory of descent with modification by means of natural selection. What then, if anything, did Darwin gain through waiting for fourteen years before writing the final version of his work? There were three main forms of gain: (1) vastly more detail both in apt illustration and in considered inference, (2) an extended compositional process that resulted in an extraordinary density, coherence, and clarity in the exposition; and (3) one new idea, or at least a latent idea rendered explicit and available for development. The process of composition consisted of alternating phases of expansion and condensation, of filling in details and then of abstracting and summarizing. The one new idea is described in Darwin's *Autobiography*. He explains that there was one basic problem he had not adequately formulated in 1844—the problem of “divergence” or branching speciation, as opposed to linear descent (in this volume, pp. 438–39).

ii. Darwin's Discovery of Divergence

There is some uncertainty about what Darwin's discovery of divergence means and what it amounts to. As Darwin's son and editor Francis Darwin observes in an introduction and a note for the 1844 manuscript, the idea of divergence—the gradual diversification of species from a parent stock—is strongly implied in the 1844 manuscript (Darwin and Wallace, *Evolution by Natural Selection*, 33–34, 215n), and indeed, Darwin's Notebooks contain diagrammatic sketches of branching evolution similar to that which he presents formally in the *Origin* (in this volume, pp. 168–69). What Darwin seems to mean by his discovery of divergence is the idea of ecological niches as a source of diversification. This meaning is obliquely apparent in the passage from the *Autobiography* in which Darwin describes his moment of insight about divergence, and it is much more clearly apparent in the chap-

ter on divergence (chapter seven) in the unfinished big species book and in the letter of 1857 to Asa Gray (part VI) that became part of Darwin's Linnean Society paper of 1858 (in this volume, p. 484; for other references that support this supposition, see chapter seven of Ospovat's *The Development of Darwin's Theory*, and see the commentary by Glick and Kohn in *Charles Darwin on Evolution*, 127–30).

In Darwin's own account of the development of his theory, the idea of ecological niches hit him with the force of sudden revelation, as if it were the last of that whole series of brilliant flashes of insight that fill the Notebooks. The problem with Darwin's account is that the idea of ecological niches as a means of speciation is already clearly present both in the 1844 manuscript and in the second, revised edition of the *Voyage of the Beagle*, published in 1845. In the *Beagle* passage, commenting on the variation of finches in the Galapagos, Darwin makes a statement that, in retrospect, seems to contain in nucleus the whole of the theory of the *Origin*. “Seeing this gradation and diversity of structure in one small, intimately-related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends” (in this volume, p. 457). In the 1844 manuscript, in a passage on the “Variation of Organic Beings in a Wild State”—immediately preceding the passage that was included in the Linnean Society paper of 1858—Darwin asks the reader to envision natural selection as a sort of magnified human breeder seeking to form a new species on a volcanic island. The ecological conditions of the island would be somewhat different from those in the original home of the species, and the species would thus need to be “adapted to new ends” (*Evolution by Natural Selection*, 114). Starting from this example, obviously inspired by his own Galapagos findings, Darwin proposes that we take an expansive view of the principle involved. “With time enough, such a Being [that is, the Magnified Breeder] might rationally ... aim at almost any result” (115). Darwin takes mistletoe as an example. “Let this imaginary Being wish, from seeing a plant growing on the decaying matter in a forest and choked by other plants, to give it power of growing on the rotten stems of trees” (115), and from there the plant may be supposed to develop the capacity for growing on “sound wood.” With naturalistic verve, Darwin describes the way in which, throughout its adaptive transformations, mistletoe would have evolved in co-adaptive relation with the birds and insects that help it to propagate. It was a felicitous example, and in the *Origin* Darwin continued to use mistletoe to illustrate the co-adaptation of species in an ecosystem (in this volume p. 96). (Glick and Kohn suggest that it was only after 1844 that Darwin came to believe that “new species could be formed without geographic isolation” [130], but as the mistletoe example indicates, Darwin had already recognized ecological

speciation in 1844, and indeed the same example appears in the sketch of 1842; see *Evolution by Natural Selection*, 45.)

Darwin himself clearly believed that at some point after 1844 he had suddenly received a new and important inspiration about ecological diversification. In order to reconcile this belief in the novelty of his insight with the evidence of what he had already written in 1844, we shall perhaps be compelled to make a distinction between having an idea available in latent form, on the one side, and making it present as an active and conscious source for further reflection, on the other. Making it explicit gave Darwin the impetus for some actual observations and experiments. For instance, it presented to him the idea that a single bit of ground could provide a large arena for adaptation and selection (see this volume, pp. 164-65). More importantly, Darwin seems to have had a sudden, far-reaching insight into the scope and significance of ecological diversification as a central organizing principle within the whole economy of nature.

In 1844, Darwin had been thinking of ecological diversification mainly as a means of speciation, that is, as a causal mechanism that explains the morphological transformations and diversification of a species over time. His new inspiration might well have been the realization that this temporal dimension does not exhaust the explanatory significance of the mechanism. The idea of ecological diversification associates itself in Darwin's mind with the co-adaptation of species, and it thus provides a point of entry into the intricate and dynamic interactions that take place *at any given moment in time* within a total network of biotic interdependencies. These interdependencies are in turn an integral part of the total environmental situation that conditions and constrains evolutionary change. Hence Darwin's strong and repeated emphasis, in the *Origin* itself, that, among the factors regulating adaptive change, interaction with other species is even more important than the physical environment. By articulating the idea of ecological diversification, Darwin extended the explanatory reach and the range of supporting evidence for his theory—and not just for the theory of descent with modification but specifically for the theory of natural selection. This idea was also the source and subject for some of the greatest rhetorical moments in the *Origin*. In passages like that of the “entangled bank,” the rhetoric rises as a stylistic register for the scope and depth of Darwin's imaginative vision.

iii. A Tale of Two Manuscripts: 1844 and 1859

Apart from the one problematic conceptual development involving divergence, the chief difference produced by the long gestation of Darwin's work lies in the composition. How much of a difference is that? If Darwin had died and his widow had fulfilled his wishes, getting Hooker, say, to edit

and publish the 1844 manuscript, what effect would this book have had, compared to that of the *Origin*? The basic components of the core argument are all there, as indeed they are in Wallace's short and sketchy paper, but the *Origin* works out that argument in rigorous detail, with an accumulated wealth of information that places it at the apex of biological knowledge available in Darwin's own time. The *Origin* makes vividly clear the rigorous coherence of the argument as it is carried out through the essayistic or discursive equivalent of experimentation. Darwin's implied position with respect to the reader is something like this: “Here is my idea; let us see how it stands up against all the information now available in all the relevant fields of inquiry—classification, paleontology, geographical distribution, geology, comparative anatomy, embryology, the breeding experiments of hybridizers and domestic breeders, and the study of instinct in social insects. Let us pose all the most difficult questions we can, as if we were the devil's advocate—our own most serious and probing critics—and impartially weigh the evidence. Let us see whether the theory I have advanced can provide a coherent and reasonable explanation for all this information. And particularly, let us perpetually test my hypotheses by posing them as alternatives to the theory of special creation.” The result of this experiment is of course that special creation breaks down repeatedly. It is unable to account for the information Darwin presents. His own theory not only accounts for that information piecemeal, in individual cases and in each field; it demonstrates that the information in each field forms a seamless web of interlocking explanation for the information in all the other fields.

In 1838 and 1839, Darwin had sudden brilliant bursts of insight into the essential mechanism and into its “metaphysical” or psychological implications. In 1842 and 1844, he formulated the theory in a discursively coherent form. But it was not until 1857 through 1859 that he was able to marshal his theories and his facts into a vision both massive and minute, saturated at every point with concrete evidence and matured reflective analysis. Probably, if only the 1844 manuscript had been published, other scientists would have taken up the project and in fragmentary, collective efforts have pieced together the whole puzzle. The logic and reality of the case would have led inexorably, though perhaps slowly, to that result. The final outcome for science might possibly have been little different from what it has been. The outcome for literature would have been utterly different, because the world would have been deprived of one of its great masterpieces—arguably the only work of this scientific magnitude that is also fully accessible as a work of literary imagination.

Both the 1844 manuscript and the *Origin* begin with a chapter on variation under domestication. This is an analogical argument based on homely and familiar associations, especially on the popular hobby of pigeon breed-

ing, and it is designed not as a proof but rather as an illustrative parallel for Darwin's theory of natural selection. It is designed to open the reader's imagination to the general process of variation, selection, and divergence in organic form. The core theoretical argument of the *Origin*, the argument about actual causal processes in nature, occupies three central chapters (chapters two, three, and four): "Variation under Nature," "Struggle for Existence," and "Natural Selection." In the 1844 manuscript, this core argument is outlined in just a few pages in part of chapter two (see this volume, pp. 471-74), and the other topics in that chapter are not very coherently related either to the core argument or to one another. More than half of chapter two is devoted to the topic of hybridism, to which Darwin devotes a whole chapter (chapter eight) in the *Origin*. In the 1844 manuscript, the discussion of variation in nature forms a small part of chapter two. In the *Origin*, this topic occupies all of the second chapter ("Variation under Nature") and all of chapter five, "Laws of Variation." The other chapter topics in the 1844 ms. have counterparts in the *Origin* ("Instinct," "Geographical Distribution," and the rest), but the earlier versions are far less detailed and lack the tight consecutivity of argument—the dense interweaving of observation and inferential reasoning—that distinguish the concordant discussions in the *Origin*. The topic of "Difficulties on Theory," a whole chapter in the *Origin*, appears in the 1844 ms. as a patchy set of comments parceled out into sections of chapters three and six.

iv. The Style of Argument in the *Origin*: An Instance

It might be well to compare two passages in order to provide at least one detailed example of the kind of difference that fifteen years made in the work we read today. In chapter two of the 1844 ms., Darwin discusses the distinction between varieties and species. At the end of the chapter, under the heading "Limits of Variation," he makes a speculative inference on the stabilization of species in nature:

I repeat that we know nothing of any limit to the possible amount of variation, and therefore to the number and differences of the races, which might be produced by the natural means of selection, so infinitely more efficient than the agency of man. Races thus produced would probably be very "true"; and if from having been adapted to different conditions of existence, they possessed different constitutions, if suddenly removed to some new station, they would perhaps be sterile and their offspring would perhaps be infertile. Such races would be indistinguishable from species. But is there any evidence that the species, which surround us on all sides, have been thus

produced? This is a question which an examination of the economy of nature we might expect would answer either in the affirmative or negative. (*Evolution by Natural Selection*, 135)

This is the very end of the central theoretical chapter, but the conclusions are conjectural and tentative. The style is abrupt and choppy. The appeal to "the economy of nature" is vague and inconclusive. The succeeding chapter, "On the Variation of Instincts and other Mental Attributes under Domestication and in a State of Nature, [etc.]" does not take up the question left hanging at the end of chapter two.

One could contrast the fade out at the end of this chapter to the rhetorical climax of the magnificent "Tree of Life" image with which Darwin concludes the chapter "Natural Selection" in the *Origin*. Here I wish to make a somewhat different comparison, a comparison not only of rhetorical effect but of argumentative style. I shall quote one long passage from chapter five of the *Origin*, "Laws of Variation." This passage is the conclusion not to a core theoretical sequence nor even to a whole chapter. It is the conclusion to a sub-section of a labeled section of a chapter. The section is labeled by being introduced with an italicized proposition that itself constitutes a positive, unqualified affirmation. "*A part developed in any species in an extraordinary degree or manner, in comparison with the same part in allied species, tends to be highly variable*" (in this volume, p. 189). The sub-section of this labeled section is introduced by a firm development of this proposition, and the development is supported by a confident appeal to a bit of established common knowledge in natural history. "The principle included in these remarks may be extended. It is notorious that specific characters are more variable than generic" [that is, that characteristics distinguishing species vary more than characteristics distinguishing whole genera] (in this volume, p. 192). This particular observation does not appear in the 1844 ms. In the *Origin*, it helps confirm and clarify the larger, sustained vision of morphological features emerging out of the flux of minute individual differences and assuming, over almost unimaginable expanses of geological time, ever higher rank in the classificatory hierarchy. Such features first stabilize as characteristics of species and then as characteristics of genera, and on up the hierarchy through families, orders, classes, phyla, and kingdoms. As each feature assumes higher classificatory rank, it becomes the shared property of a branching, diversified array of lower-ranked forms. In the passage I am about to quote, the particular point Darwin makes concerns only the relative variability of species and genera, but the tight logic of evidence and reasoning through which he makes this point invokes the core logic of natural selection, and this one point thus becomes yet another microcosmic confirmation of the total theory:

Finally, then, I conclude that the greater variability of specific characters, or those which distinguish species from species, than of generic characters, or those which the species possess in common;—that the frequent extreme variability of any part which is developed in a species in an extraordinary manner in comparison with the same part in its congeners; and the slight degree of variability in a part, however extraordinarily it may be developed, if it be common to a whole group of species;—that the great variability of secondary sexual characters, and the great amount of difference in these same characters between closely allied species;—that secondary sexual and ordinary specific differences are generally displayed in the same parts of the organisation,—are all principles closely connected together. All being mainly due to the species of the same group having descended from a common progenitor, from whom they have inherited much in common,—to parts which have recently and largely varied being more likely still to go on varying than parts which have long been inherited and have not varied,—to natural selection having more or less completely, according to the lapse of time, overmastered the tendency to reversion and to further variability,—to sexual selection being less rigid than ordinary selection,—and to variations in the same parts having been accumulated by natural and sexual selection, and having been thus adapted for secondary sexual, and for ordinary specific purposes. (in this volume, pp. 194-95)

This whole long passage consists of only two sentences, but Darwin has learned all the most important lessons about syntactic parallelism and subordination that more than a century of classic English prose had sought to teach. The first half of the passage consists of a sequence of precise factual observations tied together in parallel substantive phrases by the word “that.” The pivot or hinge of the passage is the main clause of the sentence: “are all principles closely connected together.” The main clause of the second sentence follows immediately and answers with almost colloquial ease to the main clause of the first sentence: “All being mainly due to . . .” And then follows a second sequence of parallel subordinate phrases, introduced by the word “to” [= due to], providing a causal explanation for the facts adduced in the first sentence. The causal explanation is presented not as a random list of causes but rather as a tightly linked causal sequence that outlines the actual historical sequence and that also incorporates, as fine and relevant embellishment, a reflection on the subordinate and ancillary character of sexual selection—that is, the selection of characteristics adapted for the purpose not of survival but of advantage in propagation.

The sustained symphonic power of Darwin’s composition in the *Origin*

depends on the mastery of many such local units of argument and exposition. As it happens, few historians of science are also trained analysts of rhetoric and composition, and few literary scholars have been sufficiently receptive to Darwin’s subject matter to give adequate attention to the rhetorical and literary characteristics of the *Origin*. One consequence of this gap between what C.P. Snow called “the two cultures” is that the splendid literary quality of the *Origin* has never received its due meed of praise. A more serious consequence is that many otherwise competent readers have failed to grasp the sheer density and coherence of logical argument that is the foundation for that literary quality.

v. “Why the Delay?”

This one example could be replicated by many others, and it should make clear that the *Origin* represents an immense advance over the 1844 ms. in the quality of composition, and it should be clear further that the word “composition” involves more than cosmetic or aesthetic qualities. It involves articulated argument interwoven with matured observation. Virtually every commentator on Darwin’s career broaches the question, “Why the delay?” If Darwin had a book-length ms. prepared in 1844, why did he wait another fifteen years before publishing his book? One common answer to that question is that he delayed because he was *afraid* to publish—afraid to offend the public, afraid to endanger his social and professional position, afraid even to upset his wife. In its most extreme form—as it appears for instance in the biography of Darwin by Desmond and Moore—proponents of this view attribute Darwin’s severe, chronic gastrointestinal disorder to hysterical anxiety about the potential public reception of his work. This view of the case has a certain *National Inquirer* flavor of lurid headline sensationalism. *Radical Scientist Crippled by Terror of his Own Theory!* But even in its milder forms—as it appears for instance in Ruse’s *The Darwinian Revolution*—this line of interpretation evinces a certain cynicism and betrays a basic deficiency in interpretive judgment. It fails to register the difference in the quality of argument between a lightly and not very coherently sketched outline, on the one side, and a dense, comprehensive, tightly woven fabric of argument on the other.

The *Origin* manifests on virtually every page the results of intense study and absorbed reflection sustained over a period of nearly two decades by a scientific genius in the most robust phase of his development. Darwin could no doubt have spent two or three years polishing and refining the composition of the 1844 ms., and the published result would presumably have been a respectable contribution to scientific speculation. But no amount of attention devoted merely to polishing the 1844 ms. could have

produced a work even remotely so dense and thorough as the *Origin*. Darwin did not yet know enough, and had not thought enough, to produce the definitive work his theory had the potential to produce. From 1844 to 1859, the efforts that went into Darwin's studies in geology and natural history, and particularly his work on barnacles, enabled him to master entire fields of information in respect to which, in 1844, he was but a novice. In addition to his published work, over those years he collected an immense quantity of information—of facts accompanied by analytic reflection—that were slated for publication in the big species book. Though not directly cited, this information was an active force behind the momentum of argument that goes into passages like that which I have quoted above. Some people write many books very quickly, but the speed and frequency usually result in thinness and repetition. Books like the *Origin* take time—just exactly as much time as Darwin did in fact take. There was no “delay,” only a protracted preparation. Did the result justify all the time and effort that went into it? Most emphatically, it did.

vi. Impact and Aftermath

In order to assess the value of Darwin's two decades of preparation for the public impact of his work, we can compare it with the impact made by the Linnean Society papers and the *Origin*. The papers had almost no impact; they went virtually unnoticed. In his summary of the Society's activities for that year, the Society's president, Thomas Bell, expressed regret that the year had not been “marked by any of those striking discoveries which at once revolutionise, so to speak, the department of science on which they bear” (cited in Oldroyd, *Darwinian Impacts*, 84). In a letter to Darwin in 1864, Wallace himself draws the appropriate inference. “As to the theory of Natural Selection itself, I shall always maintain it to be actually yours and yours only. You had worked it out in details I had never thought of, years before I had a ray of light on the subject, and my paper would never have convinced anybody or been noticed as more than an ingenious speculation, whereas your book has revolutionised the study of Natural History, and carried away captive the best men of the present age. All the merit I claim is the having been the means of inducing you to write and publish at once” (*More Letters of Charles Darwin*, 2:36). The modern historian of biology David Hull seconds Wallace's opinion. “If all Darwin and Wallace had done was to publish their Linnean papers, it is very unlikely that biology would have been revolutionized. These papers were mere sketches” (*Science as a Process*, 279). In the *Origin* itself, in contrast, Darwin “scanned the wide range of phenomena that his theory had to explain and showed which cases it could handle without any difficulty, which were doubtful cases, and which anomalies.”

The result was that he “converted a promising sketch into a scientific theory.”

The rhythm of composition for the *Origin* peaked in the first edition. After his two decades of preparation, there was one last phase of intensive editing. Darwin heavily rewrote the whole manuscript once it was in proofs. (Lyell's wife had read the penultimate version and complained of obscurities of expression.) The second edition, which appeared about six weeks after the first, offered only some minor editorial polishing and can reasonably be considered part of the compositional apex. After the second edition, the apex was clearly past, and in subsequent editions Darwin's further work on his manuscript became counterproductive. He became entangled with contemporary criticisms, and he undertook retrenchments and elaborated qualifications in response to scientific criticism based on inferences—about the mechanism of inheritance and geological time—now known to be erroneous. The result is a diffuse expansiveness and a slight blurring of the clear outlines of the argument. Accordingly, for this present edition, I have chosen to use the first edition as a primary text, correcting it against only minor copyediting revisions in the second edition.

vii. Darwin's Use of Malthus

Since Darwin's discovery predated that of Wallace by nearly two decades, one cannot precisely characterize the case as one of “simultaneous” discovery, but the timing is close enough, on a historical scale, to support the contention that time was ripe for the discovery, that all the essential elements were in place. One of those elements, the first-hand experience of a practicing naturalist in the wild, would have been available to relatively few people at the time. The other elements were all publicly accessible and in wide possession among an educated lay public for whom natural history was a much more common and absorbing preoccupation than it is at the present time. (Many a country parson, like Mr. Farebrother in George Eliot's *Middlemarch*, had his private cabinet of prize specimens.) And yet, only Darwin and Wallace came across the idea, and they had an almost identical experience of revelation. In both cases, the crucial, crystallizing experience was that of reading Malthus' *Essay on Population*.

Why was Malthus so important? In a word: food. In our own day, in the affluent West, our main problem concerning food is that we have too much of it and thus have to make strenuous efforts of restraint and disciplined physical activity to avoid obesity. If we examine some of the contextual material assembled in this volume, we shall realize how anomalous this present situation is. In the passages from the Bible, Paley, Lamarck, Spencer, Malthus, Lyell, and Wallace, one is forcibly struck by the preoccupation

with hunger and death converging on the question of population. Even God, at the end of the first chapter of Genesis, is concerned about food, and everyone else is preoccupied with the question of burgeoning and unfeedable masses of reproducing organisms. This preoccupation will be the more intelligible if we consider the conditions of life at the time. Famine was a regular feature of life in England itself up until the beginning of the nineteenth century. Famines recurred often on the continent into the 1830s, and in Ireland through the middle of the century. The 1840s in England are commonly referred to as "the hungry forties," and in Ireland, in the potato famines of the late 1840s, hundreds of thousands of people starved to death. In the early-middle decades of the nineteenth century, Dickens' novels register the prevalence of chronic hunger and malnutrition as a pervasive feature of life among large masses of the common people. Even well-fed people like Darwin and Wallace could not help but perceive the pressure of hunger in the population as a whole. Nonetheless, by presenting this phenomenon as an arithmetical calculation, Malthus made it vividly and dramatically apparent to them in a way simple observation had failed to do.

Darwin and Wallace both were fine and experienced observers of nature, but neither of them had actually, directly, observed the mass death that accompanies each generation. For each of them, this was an inference derived from the Malthusian calculation and transferred readily to animal populations. Darwin and Wallace both instantaneously saw how it applied across the whole animal kingdom. They simply had not registered it before: if animal populations remain stable, and the numbers born to sets of parents exceed two, the excess must be presumed to have died. Since the numbers born do in fact regularly exceed the number of parents, the annual cycle necessarily involves a holocaust, a vast dying, as regular as the clockwork that serves Paley as a metaphor of benevolent providential design. If one factors in heritable variation and takes account of the way these variations affect survival and reproduction, the conclusion has a stunning simplicity: natural selection.

Darwin's use of Malthus presents us with an exemplary instance in the history of scientific discovery. Darwin adopted Malthus' specific arithmetical insight and incorporated it as a component of a much more complex theory. This is a classic instance in the growth of scientific ideas, and it provides us with an occasion to compare two fundamentally different views of science: (1) the social constructionist or Marxist view that any given scientific theory merely reflects the larger set of social, economic, and ideological forces at work in the scientists' world, and (2) the realist and objectivist view that science constitutes a developing knowledge of the actual world.

Malthus saw human population as a homeostatic system, that is, a system that sustained an equilibrium in numbers through an internal, self-regulat-

ing mechanism. If people become better off, they produce more offspring. If they produce more offspring, they starve, and the population remains stable. Darwin did not see evolution itself as a homeostatic system, but he affirmed Malthus' observation about the relative stability of population sizes, and he extended that observation from humans to all populations. The reproductive behavior of individual organisms has a predictable systemic effect on the population. If, as Malthus maintains, the population of a given species remains relatively stable in numbers over time, and if individual members vary in their ability to survive and propagate, and if those variations are heritable, then over time the population as a whole will change in adaptive structure. *Stability in the numbers of a population* thus becomes an integral logical component of an explanation for *change in adaptive structure in a population*. Both the stability of population numbers and the idea of a population as a self-regulating system are essential components of the whole argument. As Ghiselin observes, "Seeing in Malthus how the interaction of individuals in the same species may be affected by the intrinsic properties of each organism, and how there could be cumulative effects, Darwin and Wallace were able to conjoin all the disparate elements into a unitary system which constituted the theory of natural selection" (77). In Darwin's much larger formulation, that system includes both the element of stability in numbers, taken directly from Malthus, and also the element of adaptive change that results from the interaction of variation and differential reproductive success.

viii. Context of Discovery and Context of Verification

In terms of the philosophy of science, this account of the relation between Darwin and Malthus is realist and objectivist in orientation. (In the modern philosophy of science, the most prominent proponent of this orientation has been Karl Popper.) In contrast, the social constructionist or Marxist conception of Darwin's theory presents that theory as an analogue to economic competition and takes Malthus as a primary inspiration for the formulation. Social constructionists treat Malthus as a source for an analogy rather than a component of a logical and empirical structure, and they typically do not directly assess the empirical validity of Darwin's theory. Instead, they cast doubt on Darwin's theory through a form of argument that we can describe as guilt by association. Social constructionists reject Malthus and capitalism on both moral and economic grounds; and they present Darwin's theory as itself a mere reflex of capitalist ideology. In this way, Darwin's theory can be presented as both scientifically arbitrary and morally retrograde. (For a prominent example of this approach, again see the biography of Darwin by Desmond and Moore.)

John Maynard Smith is both a confirmed Marxist in his political orientation and also a convinced Darwinian. Indeed, he is one of the two or three most creative and influential evolutionary theorists in the latter half of the twentieth century. His account of Darwin's relation to Malthus can serve to illustrate how a commentator can have an intelligent respect for the objective validity of science but still also reasonably and plausibly assess the way social context enters into the formation of scientific theories. He comments on the "subtle processes whereby ideas derived from a study of social relationships influence the theories of natural scientists," and he notes that "Darwin was consciously influenced by the ideas expressed by Malthus in his *Essay on Population*" (*Theory of Evolution*, 43). Maynard Smith is by no means sympathetic to what he takes to be Malthus' own motive in writing his book—"to justify the existence of poverty among a considerable section of the population"—but he nonetheless acknowledges that Malthus' main thesis is correct: "that animal and plant species, including the human species, are capable of indefinite increase in numbers in optimal conditions." Maynard Smith has thus tacitly invoked the distinction between "context of discovery" and "context of verification." Whatever Malthus' motives might have been, the only real question, from a scientific point of view, is whether his observation is sound.

The distinction between context of discovery and of verification shapes Maynard Smith's assessment of Darwin's relation to the larger social and economic context in which he worked. Maynard Smith observes that "Darwin must also have been influenced by the fact that he lived in the era of competitive capitalism, when some firms were improving their techniques, and increasing in size and affluence, while others were going bankrupt, and old crafts were dying out. It is unlikely that the concepts of competition and the struggle for existence in nature would have occurred to him so readily had he lived in a more static feudal society." The condition of society makes Darwin more receptive to certain observations than he otherwise might have been, but to say this much is not to say either that social conditions wholly cause or control the formulation of Darwin's theories, nor that those theories are incorrect. Maynard Smith invokes certain social conditions to explain, in part, how Darwin's imagination might have been primed or made ready for the observation of certain facts and the formulation of certain ideas. To determine whether those observations and ideas are in fact true, one must invoke specifically scientific criteria of judgment.

A serious effort to bring criticism to bear on the scientific validity of Darwin's theory must look either to the factual basis of his propositions, their logical connection, or their implications for a variety of empirical areas: genetics, biogeography, paleontology, comparative anatomy, and embryology. If it turned out, for instance, that Malthus, Darwin, and Wal-

lace were wrong in assuming that population numbers tend to remain relatively stable over time, and if they were wrong in the inference that many more members of a given population are born than survive to reproduce—if a population could expand indefinitely, without limitation through the availability of resources—then one main element of Darwin's theory would collapse, and the whole complex of ideas would be invalid. Or, if modern genetics had proven that heritable variations could not be sustained beyond a few generations, again, the system would collapse. This was an implication of the faulty inheritance theory of Darwin's own time—the idea of "blending inheritance"—and it presented one of the most serious challenges to his system. And again, if Lord Kelvin had been right, and the earth were only somewhere between twenty million and forty million years old, the scale of geological time required by Darwin's system would have failed. If the catastrophist view of the fossil record had been vindicated because paleontologists had turned up cases in which one whole animal group was succeeded by a different group, suddenly and contiguously, without any intervening forms, and with no possibility of migration, the idea of "special creation" would have received strong vindication, and Darwin's system would have been seriously challenged. One can imagine, for instance, an Australian discovery in which marsupials were suddenly supplanted, in the fossil record, for a period of a few thousand or million years, then just as suddenly replaced by mammals of the more modern type, only to be succeeded once again by Marsupials. This is not empirically impossible; it is consistent with the hypothesis of special creation; but it is altogether inconsistent with the theory of descent with modification by means of natural selection. And of course, it never happened.

8. Darwin's Evolutionary Psychology

The Descent of Man was published in 1871, twelve years after the publication of the *Origin*, but the implications for man are a distinct and powerful part of the initial inspirations that Darwin scribbled into his Notebooks in the late 1830s (see this volume, pp. 465–68). In the introduction to the *Descent*, Darwin explains that for diplomatic reasons he chose to avoid any extensive consideration of human beings in the *Origin*, but that for the sake of his integrity he had felt obliged to observe, toward the very end of the book, that his theory had human implications. "In the distant future, I see open fields for far more important researches. Psychology will be based on a new foundation, that of the necessary acquirement of each mental power and capacity by gradation. Light will be thrown on the origin of man and his history" (in this volume p. 397). Following Darwin's lead, most commentators cite this one passage as the only reference to man in the *Origin*, but they

thus overlook, as did Darwin himself, two references that are, in their own quiet way, even more effective. In the chapter "Struggle for Existence," Darwin cites "slow-breeding man" as an instance of potentially geometric reproductive rates, and in "Difficulties on Theory," Darwin casually takes human racial differences as yet another example of our ignorance concerning "slight and unimportant variations" such as skin color or hair (in this volume pp. 134, 218-19). Human beings are included in these passages along with examples drawn from wild species and from domesticated animals. The implication is that human beings are simply one more animal species and that their characteristics have the same causes and provide evidence for the same principles that enter into the discussion of plants, elephants, turkeys, vultures, and cattle (the other examples that are used in the passages).

In the *Descent*, Darwin carries the implications of these passages to their logical conclusion. He locates human beings in their phylogenetic heritage, as primates, and in support of his phylogenetic analysis, he brings forward arresting evidence from comparative anatomy and embryology. Regarding humans as social animals, he examines their forms of behavior and social organization as natural manifestations of their elementary biological dispositions for survival and reproduction, and he locates them within an ecological context that restricts all conditioning influences to those that also affect other animals.

The *Origin* succeeded in effecting a sudden and massive transformation in the educated public's view of descent with modification. Emboldened by this success, Darwin set out in the *Descent* to complete his survey of "the higher animals" (in this volume p. 398). In some respects, this earliest of all essays in evolutionary psychology is still one of the best and most profound. It points the way toward a mature social science methodology that incorporates information from studies in anatomy, embryology, psychology, and anthropology. In company with his excellent methodology, Darwin brought to his subject a fine moral consciousness that helped direct his insights into the evolved social psychology of human beings. He gave a classic analysis of the two basic components of human moral psychology: (1) an evolved social sympathy, and (2) a capacity for reflective judgment that situates all present action in relation to longer temporal sequences and thus makes "conscience" possible. The incisiveness of this analysis has yet to be surpassed in even the most recent and sophisticated works of evolutionary psychology and evolutionary ethics. It nonetheless remains the case that it is the *Origin*, and not the *Descent*, that is "the chief work" of Darwin's life. Darwin brought to the study of man the same naturalistic intuition that he brought to the question of species, but the time was less ripe, and by the time he wrote his book, he was himself past the peak of his productive power.

Lyell effected a revolution in geology, and Darwin in biology. We are still waiting for a similar revolution in psychology and the other social sciences. After the first decade of the twentieth century, the leading figures in the social sciences instituted a long phase of ideological suppression in the service of an ideology of cultural autonomy, and we are only just now, in the past few decades, finally taking up again the naturalistic methodology that Darwin pioneered. Prediction involving timing in such a matter is of course risky, but I shall take the risk and affirm that we are just now on the verge of completing the Darwinian revolution in the social sciences.

In order to understand what that revolution would entail, we can compare the *Descent* with the *Origin*. The *Descent* is full of fascinating observations and penetrating insights, but it lacks the deep systematic order that distinguishes the *Origin*. In the *Origin*, every fact and observation has a clear place within the tight logical structure outlined in the introduction and in the last paragraph of the book. The *Descent* is more casually organized, looser, more impressionistic. As is commonly observed, it is actually two separate books, awkwardly joined. One book is an anthropological essay on human nature, with some specific reference to evolved sex differences. The other book is a lengthy and highly detailed technical treatise on sexual dimorphism in the animal kingdom. In the selections for this volume, I have deleted the technical treatise and somewhat abridged the anthropological essay. Even apart from the question of awkwardly combining two distinct books, the anthropological essay in the *Descent* lacks the extraordinary logical rigor that distinguishes the *Origin*. The array of motives, emotions, and cognitive dispositions analyzed in the book have no tight, necessary relation to one another within a total system of motivational structures that are rooted in the elementary principles of natural selection. The level of conceptual organization in *Descent* is less like that of the *Origin* than, say, that of John Locke's seminal but big and baggy *Essay Concerning Human Understanding*. It is a classic work, but not the kind of authoritative and definitive work Darwin achieved in biology proper.

In order to complete the Darwinian revolution in the social sciences, we shall have to integrate at least two schools of modern Darwinian psychology. One school is that of "sociobiology," which concentrates on the ultimate regulative principles of inclusive fitness and that can be criticized for too crudely or simply reducing human motives to the drive toward reproductive success. The second school is that of "evolutionary psychology," which aims at identifying a disparate array of "cognitive modules" or genetically derived and physiologically based behavioral mechanisms targeted to the solution of specific adaptive problems. In order to extend this synthesis from the social sciences to the humanities, we shall also have to be able to take account of the adaptive functions of the arts and to understand the for-

mal organization of the arts as prosthetic extensions of evolved cognitive aptitudes. What is missing, up to this point, is the complete causal integration of elementary biological principles with complex psychological structures, complex forms of social organization, and complex forms of cognitive activity. Many talented researchers are now working in these fields, and there is a vast amount of information to be assimilated. We are waiting only for the touch of genius to bring all this information into the kind of order that Lyell achieved in the *Principles of Geology* and that Darwin achieved in *The Origin of Species*.

9. The Nature of the Darwinian Revolution

The history of evolutionary theory after 1859 can be divided into a few distinct phases. In the period from 1859 to that of Darwin's death in 1882—a period strikingly described by T.H. Huxley (in this volume, pp. 619-29)—Darwin radically transformed the received view of evolution. Within just a few years, most reputable scientists came to accept that evolution, the transformation of species over time, had in fact occurred. But most scientists did not confidently accept natural selection as the primary mechanism through which those transformations took place. There was a long interregnum, lasting from about 1859 to about 1920, in which uncertainty over the mechanism of heredity and the extent of geological time placed the theory of natural selection in doubt. Fleeming Jenkin (1833-85) pointed out that if inherited variations were “blended” in each successive generation, any variation would inevitably be swamped by the common characteristics of the species, and the physicist William Thomson (later Lord Kelvin, 1824-1907), on the basis of ingenious calculations about the dissipation of heat from the earth, argued that the earth was much younger than Lyell and Darwin had supposed, so that far too little time had passed for evolutionary change on Darwin's model. Around the turn of the century, Kelvin's theory of heat loss was corrected by the discovery of continuous, heat-producing radioactive decay from within the earth. Gregor Mendel (1822-84) had discovered particulate inheritance in 1856—providing the solution for the problem of blending inheritance—but his theories were not recognized and assimilated until the turn of the century, and even then geneticists mistakenly believed that evolutionary change would require macromutational leaps, not the gradual accumulation of adaptive changes required by the theory of natural selection. Around 1920, three distinguished geneticists, Ronald Fisher (1890-1962), John Haldane (1892-1964), and Sewall Wright (1889-1988), began publishing the papers that reconciled Mendelian genetics with natural selection. In the period from about 1920 to about 1950, biological theorists from a wide array of specialized disciplines—natural history, sys-

tematics, paleontology, ecology, and other areas—integrated their work with that of the geneticists and thus produced the “Modern Synthesis.” The Modern Synthesis is the culmination of the Darwinian revolution and forms the basis for the authoritative current framework of scientific evolutionary theory. The discovery of the structure of DNA in 1953 has only confirmed and strengthened the basic theoretical structure of the Modern Synthesis. By identifying the specific molecular mechanisms that regulate variation, sexual recombination, mutation, and inheritance, the discovery of DNA has empirically validated key components of Darwin's theory, and has given decisive proof for his hypothesis that all of life on earth, through all its multifarious transformations in structure, forms a single, unbroken chain of hereditary transmission.

Mayr sets the Darwinian revolution in opposition to two distinct models. One is the idea that advance in science is “steady and regular” (*One Long Argument*, 132). He attributes this view to no specific authority, and it is not clear that any serious theorist actually holds by it, though it might roughly describe some level of vague popular belief. The other model is that of Thomas Kuhn, which Mayr characterizes, fairly enough, as “a series of revolutions separated by long periods of steadily progressing normal science.” Mayr describes a range of possible developments considerably wider than that envisioned within Kuhn's model:

When we study particular scientific disciplines we observe great irregularities: theories become fashionable, others fall into eclipse; some fields enjoy considerable consensus among their active workers, other fields are split into several camps of specialists furiously feuding with one another. This latter description applies well to evolutionary biology between 1859 and about 1940.

As Huxley explains (in this volume, pp. 624-29), within ten years of publishing the *Origin*, Darwin had effected an almost complete transformation in the received view about one chief component of his theory—the contention that species had not been separately created and are not fixed and stable; that all species derive from descent with modification. Huxley suggests also something of the uncertainty that still hovered over the other main component of Darwin's theory: natural selection as the central mechanism of change. Mayr is more emphatic than Huxley about the opposition to natural selection, and in this respect he reflects the now authoritative consensus. He maintains that “the opposition to natural selection continued unabated for some eighty years after the publication of the *Origin*. Except for a few naturalists, there was hardly a single biologist, and certainly not a single experimental biologist, who adopted natural selection as the exclu-

sive cause of adaptation" (*One Long Argument*, 132).

In the concluding paragraph to the introduction of the *Origin*, Darwin himself tacitly anticipated a development not unlike that which Kuhn describes for scientific revolutions. Assuming provisionally that his main arguments would prove persuasive, he cautioned, "No one ought to feel surprise at much remaining as yet unexplained in regard to the origin of species and varieties, if he makes due allowance for our profound ignorance in regard to the mutual relations of all the beings which live around us" (in this volume p. 98). The ignorance Darwin has in mind evidently concerns the detailed ecological knowledge about the relations of species to their habitats and the co-evolutionary, interdependent adaptations of species connected to one another within an ecological web. Such problems, however important, would constitute, on the level of theory, details. That is, they would correspond to what Kuhn identifies as "puzzles" or matters of detailed inquiry wholly within the framework of an established theory. And puzzles of that sort there certainly have been. Darwinism has constituted an immense research program for naturalists—pointing the way toward their detailed inquiries into adaptive structure, embryology, geographical distribution, systematics, and ecological organization. But Darwin's own hopes for the completeness of his theoretical revolution were, as it turned out, too sanguine. One of the problems of detail within his theory, the nature of inheritance, proved so large a puzzle, with so many false leads and incomplete solutions, that one major element of his total theory—natural selection—remained in doubt for at least sixty years, until Fisher, Haldane, and Wright began to publish the papers on Mendelian genetics and natural selection that laid the foundations for the Modern Synthesis.

Mayr is correct in affirming that the Darwinian "paradigm shift" took several decades to complete. For the theory of natural selection, there was never any sudden "gestalt" switch. As Mayr describes it, giving the inside view of a major contributor to the process, there was instead a gradually accumulating body of theoretical genetic work that slowly converged with the work of "naturalists" (ecologists and systematists) and paleontologists. The combined weight of these different fields eventually convinced the majority of scientists qualified to judge in the case. Ridley confirms Mayr's account, and he concurs with Mayr in locating the consolidation of the Modern Synthesis in the late forties. He observes that by the mid-forties "the modern synthesis had penetrated all areas of biology. The 30 members of a 'committee on common problems of genetics, systematics, and paleontology' who met (with some other experts) at Princeton in 1947 represented all areas of biology. But they shared a common viewpoint, the viewpoint of Mendelism and neo-Darwinism. A similar unanimity of 30 leading figures in genetics, morphology, systematics, and paleontology would have

been difficult to achieve before that date" (*Evolution*, 18).

The history of Darwinism offers an opportunity for assessing the most important epistemological issue raised by Kuhn's model: the question as to whether scientists are capable of reflecting critically on their own ideas and, on the basis of these critical reflections, modifying their views. Kuhn describes paradigms as a total structure of ideas that regulates what scientists can think and even what they can actually see. In Kuhn's presentation, if certain phenomena do not fit within a paradigm, scientists are unable to perceive those phenomena. Mayr's description of the slow and messy progress of the Darwinian revolution subverts Kuhn's notion of a simple, total framework, a "paradigm" that scientists either accept, blindly, or reject and replace with another paradigm that they then also accept in an equally uncritical fashion. On this issue, Kuhn's most effective theoretical opponent has been Karl Popper, who identifies Kuhn's "Myth of the Framework" as "in our time, the central bulwark of irrationalism" ("Normal Science and Its Dangers," 56).

Kuhn's model has an at best imperfect fit to the process of scientific theory formation in the period after Darwin presented his theory. How does it fit in the other direction? That is, how well does Darwin's own transformation accord with the notion of a sudden and radical gestalt switch? Darwin radically altered the prevailing view about the origin of species, and he proposed a mechanism that had never been considered as the central mechanism that regulated all of phylogenetic history. But the "switch" that occurred in his own thinking was no complete and total replacement of all previous ideas and information about species. As we have seen in considering the background to Darwin's work, he absorbed information and ideas from a very wide range of sources. His relations to both Malthus and Lyell are particularly instructive in this respect. Darwin assimilated Malthus' insight into population pressure and food supply as one central component of his own theory, but he also incorporated it into a much larger theory that involved adaptive structural changes of which Malthus had no inkling. Darwin assimilated major elements of Lyell's geology, developed them further (as in the theory of coral reefs), and used them to help explain essential points about geographical distribution and the fossil record. He rejected Lyell's general theory, if an idea so tentative and sketchy can be called a theory, about the origin of species, but he also incorporated Lyell's argument that a chief engine of extinction is the failure of a species to adapt to change of climate. In none of this do we see anything remotely like the sudden and total replacement of one structure of ideas by another. What we see instead is a steadily accumulating body of ideas and information that many individual scientists piece together into local groups—as if they were working out segments of a picture puzzle in which the segments remained,

for the time being, disconnected from one another—until one scientist (or in this case two, if one also counts Wallace), sees the way in which all the partial segments fit into one total larger pattern.

To conceive of Darwin's achievement in this way need not diminish our sense of the importance of the creative, innovative power of the individual scientist. Ghiselin cites Kuhn's idea that "scientific revolution results from the failures and contradictions of the prevailing system," and while he grants that "such may well be the case for conventional scientists," he insists that "Darwin was an exception. He restructured traditional fields and erected new paradigms when the positive development of his ideas suggested something new" (45). Darwin's case thus confirms, he argues, that "the success of at least some revolutionary thinkers" may be attributed "not to sociological forces, but to an innovative mentality." This is a false antithesis. One can see the way it presents itself in Ghiselin's thinking, and indeed the Kuhnian model has often been taken, by its proponents, in the light in which Ghiselin sees it. The antithesis depends on an overly simple opposition between two kinds of productive force. In this overly simple formulation, either the whole social context produces a theory, or the individual genius of the scientist produces the theory. In reality, both elements are necessary parts of scientific discovery. Science is a collective, social enterprise. Darwin depended on the findings of an extended network of researchers—his scientific correspondents number in the hundreds—and a long tradition of geological and biological investigation. He did indeed observe the failures and contradictions of the prevailing system, and through the positive development of his ideas he provided solutions for them. If there had been no unsolved problems within the prevailing system, there would have been no need to formulate new explanations. To acknowledge that the existence of problems is a prerequisite for the formulation of solutions need not derogate from the "innovative mentality" of creative scientific genius. Maynard Smith gets this issue into proper focus. After listing the various kinds of information and inspiration that fed into the formulation of Darwin's theory, he observes that all these elements "provided Darwin with the necessary methods of attack and materials for study; it required his individual genius to weld them into a comprehensive theory of organic evolution" (*Theory of Evolution*, 43).

The fortunes of Darwin's theory in the period that lay between the publication of the *Origin* and the consolidation of the Modern Synthesis offer us one signal measure of the quality and magnitude of Darwin's genius. In his *Autobiography*, Darwin notes that "some of my critics have said, 'Oh, he is a good observer, but has no power of reasoning'" (in this volume, p. 443). Mildly but astutely, Darwin comments, "I do not think that this can be true, for the *Origin of Species* is one long argument from the beginning to the

end." What Darwin saw, and what almost everyone else (including Huxley) failed to see, for nearly a century, was that his theory consisted of interconnected and interdependent bodies of evidence and reasoning. The theory has a total logical structure, and that structure has a kind of tough validity that should have rendered it presumptively correct from the beginning.

Even Mayr, distinguished biologist and historian though he undoubtedly is, wrongly believes that the different elements of Darwin's theory are isolable. The evidence he brings forward to confirm that view is that in the minds of most of Darwin's contemporaries the idea of descent with modification was in fact isolated from the idea of natural selection (*One Long Argument*, 37). Mayr acknowledges that Darwin himself regarded the elements of his theory as "a unity," so that in disputing this claim he is placing the combined weight of Darwin's contemporaries and successors against the weight of Darwin's own judgment. In order to support the judgment thus rendered, Mayr asserts that "natural selection is dealt with in the first four chapters" but that "in the remaining ten chapters natural selection is not featured" (*One Long Argument*, 95). These latter chapters, Mayr maintains, deal only with descent, not with the mechanism of natural selection. In both this specific affirmation and the larger claim it is intended to support, Mayr is demonstrably mistaken.

Darwin saw clearly the logical necessity of all the parts of the theory fitting together. He understood that natural selection "almost inevitably induces extinction and divergence of character in the many descendants from one dominant parent-species" (in this volume, p. 363). Divergence itself "explains that great and universal feature in the affinities of all organic beings, namely, their subordination in group under group," and in this strict logical sense natural selection is an integral causal component of systematics or classification. The systematic classification of all living things involves both linkages and gaps; the gaps reflect extinction, and extinction is an effect of selection. As with classification, so also with geographical distribution. The radiation of dominant groups of flora and fauna within distinct geographical regions is a result not merely of descent but of the dominance of certain groups over other groups, and this dominance is the result of selection (in this volume, pp. 131, 323-24, 330, 346). Even more apparently, ecology is a matter not of descent over time but of current interactions regulated by the adaptation of organisms to their environments—environments in which other organisms are at least as important as the physical features of the land, water, or air. Ecosystems are "systems" precisely because they involve elaborate interactions among organisms that have co-evolved in adaptive relation to one another, as predator, prey, parasite, and symbiont.

If we shift our focus from large-scale populational interactions to the structure and development of individual organisms, selection remains cen-

tral to Darwin's argument. Once we have set aside the idea of "design" as the result of divine fiat, adaptation can be explained only through natural selection, and imperfections in adaptive design are also a result of selection. One of the most important principles of morphology is the linkage of species through "homologous" structures. "What can be more curious than that the hand of a man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should all be constructed on the same pattern, and should include the same bones, in the same relative positions?" (in this volume, p. 364). This singularity or curiosity of the natural world cannot be explained through design or even merely through a form of descent like that envisioned by Lamarck. But it can be explained "on the theory of the natural selection of successive slight modifications" (in this volume, pp. 364-65), and such modifications can be organized in adaptively functional ways only by natural selection. So also with embryology. Embryos share an initial phylogenetic commonality, and only in the course of ontogenetic development do they progressively differentiate into the characteristics of some one distinct species. At certain points in the phylogenetic history of all organisms, selection has activated morphological change for adaptive purposes, and those changes appear at specific points in the ontogenetic sequence of each organism (in this volume, pp. 367-74).

In all of these major fields of evidence, then—in systematics, geographical distribution, ecology, morphology, and embryology—selection is central to Darwin's explanation of descent with modification. The field of variation and heredity was of course not yet established as "genetics," and it was the most mysterious and obscure part of Darwin's subject, but even in this field the logic of natural selection shed light for Darwin. It explained, for instance, why it is that "*a part developed in any species in an extraordinary degree or manner ... tends to be highly variable*" (in this volume, p. 189). Darwin's solution for this conundrum is that "an extraordinary amount of modification implies an unusually large and long-continued amount of variability, which has continually been accumulated by natural selection for the benefit of the species" (in this volume, p. 191) and that this recent variability has remained active.

Darwin understood the integrity of his own argument, and he understood further, as most of his successors did not, the constraining force of that argument. The total logic of the argument pointed decisively to the necessity or inevitability of the existence of mechanisms of inheritance of a sort that were in fact eventually recognized in the synthesis of Mendelian genetics and the theory of natural selection. It can reasonably be said that Darwin's theory *predicts* some such set of mechanisms. If the theory is true, those mechanisms must exist, and the weight of all the *other* evidence that

Darwin himself marshaled, in all the fields that he brought into play, should have given presumptive credibility to that prediction. Darwin was rationally confident of this outcome, but generations of biologists who came after him became absorbed in the details, the puzzles of inheritance, and because of these puzzles, they lost confidence in the larger argument that had nonetheless radically and permanently altered their convictions about the reality of descent with modification.

In this respect, the history of evolutionary theory from about 1860 to about 1920 turns Kuhn's model on its head. Darwin's theory did not provide a paradigm within which scientists busily and almost mechanically went about solving technical "puzzles"—relatively trivial details entailed by the theory. Instead, many of them abandoned the theory and became absorbed in working out the details as an empirical and technical enterprise. The situation in this case bears a fairly close parallel to the developments in geology from the last decade of the eighteenth century through the third decade of the nineteenth. Geologists had become disgusted with the grand theoretical debates between the Wernerian Neptunists—proponents of a universal flood that precipitated the continents—and the Huttonian Vulcanists who identified cataclysmic volcanic activity as the main constructive force in geology. Turning away from large-scale theories, geologists preoccupied themselves instead with the practical work of identifying the total stratigraphic column, an immense and absorbing empirical enterprise. Lyell's *Principles of Geology* constituted something very like a "modern synthesis" between Hutton's large-scale theory of a homeostatic equilibrium and this relatively theory-free empirical research.

Looked at in a negative light, one might say that between the time of Darwin and the Modern Synthesis, geneticists were like the Israelites who had left Egypt and had not yet entered the promised land—they spent decades wandering lost in the wilderness. In a more positive light, one can say that the geneticists constructed their discipline from the ground up, working out the technical structure in empirical, experimental research, and then discovered, to their own surprise, that the structures they had defined fit neatly as mechanisms within a larger logic that united their own discipline once again with all the interconnected fields of evolutionary biology.

10. Recommendations for Further Reading

Useful collections of excerpts from Darwin's own writings include *The Darwin Reader*, edited by Ridley, and *Darwin on Evolution*, edited by Glick and Kohn. Darwin's *Life and Letters*, edited by his son Francis, is indispensable for further study, but the version of the *Autobiography* included in that work is the bowdlerized version sanctioned by Darwin's wife and daughter.

The version edited by his granddaughter Nora Barlow restores the mutilated passages and is now the standard text. The volumes of Darwin's collected correspondence continue to appear, but most scholarly works still make frequent reference to the letters contained in *More Letters of Charles Darwin* (a title the inelegance of which has become softened by time and usage). The Notebooks have been made available in an annotated scholarly format, edited by Barrett et al., under the title *Charles Darwin's Notebooks, 1836-1844*. Darwin's manuscripts on the species question, written in 1842 and 1844, along with Wallace's Linnean Society paper of 1858, are available in *Evolution by Natural Selection*, with a foreword by de Beer. The *Voyage of the Beagle* is available in various editions, some using the first edition, and some the revised edition of 1844, which is significantly different, especially with respect to the evolutionary implications of the Galapagos. For specialized scholarly study of the *Origin* itself, Morse Peckham's splendid variorum edition is the indispensable tool. The full text of the first edition of the *Descent of Man* is available in a fine facsimile edition edited by Bonner and May.

Among the more prominent biographies of Darwin, Browne's *Voyaging* can be recommended for the density of its well-digested detail on the contemporary scientific context of Darwin's work. Bowlby's *Charles Darwin: A New Life* succeeds better than any other biography in evoking Darwin's personal qualities. Ghiselin's *The Triumph of the Darwinian Method* remains the single most successful effort to comprehend the coherence and strength of Darwin's whole body of thought. In their lengthy biography, *Darwin*, Desmond and Moore offer a Marxist commentary on the social background of Darwin's work. This biography has been widely criticized for the use of intentionally misleading techniques of quotation and documentation, but it has also established itself as a centerpiece in the currently fashionable approach to science as a reflex of social conditions. Eiseley's *Darwin's Century* gives a still useful account of Darwin's predecessors, but it is strangely mean-spirited and distorted in its treatment of Darwin himself. Alan Moorehead's *Darwin and the Beagle* offers an instance of attractive science journalism undermined by poor historical scholarship. One would do better to consult Sulloway's articles on the inception of Darwin's theory. Irving Stone's peculiar technique of novelized biography is of course academically beyond the pale, and one hesitates even to mention *The Origin: A Biographical Novel of Charles Darwin*. Stone presents passages from letters and books as actual dialogue and internal monologue, and he interweaves these passages with purely fictional thoughts and comments that are freely attributed to the "characters"—Darwin, his wife Emma, Hooker, Lyell, and the rest. Stone's account of the development and structure of Darwin's theory is unreliable, but he effectively evokes both the social quality of Darwin's scientific community and the general character of Darwin's vision.

On the historical background to Darwin, Toulmin and Goodfield, in *The Discovery of Time*, offer an insightful overview marred by an inaccurate account of Cuvier's theory of special creation. The essays in *Forerunners of Darwin: 1745-1859*, edited by Glass, Temkin, and Strauss, are still useful, as is Gillispie's *Genesis and Geology*. On the history of paleontology, see Rudwick's *The Meaning of Fossils: Episodes in the History of Paleontology*. To get a feel for the wildly speculative or fanciful character of geological thought up to the middle of the eighteenth century, one might look at the descriptions of the cosmogonies of Burnet and Buffon in Eiseley's *Darwin's Century* and in Albritton's *The Abyss of Time*. The first five chapters in Lyell's *Principles of Geology* provide an illuminating though partisan account of the history of geology prior to his own work. Hallam's *Great Geological Controversies* offers an informative commentary on the conflict between the Neptunists and the Vulcanists. Winchester's biography *The Map That Changed the World: William Smith and the Birth of Modern Geology* offers an appealing introduction to the development of stratigraphy. Oldroyd's *Thinking About the Earth* reflects intelligently on the history of geology from a modern perspective.

Among the several general histories of evolutionary thought, Young's *Evolution* is one of the most attractive and accessible—sumptuously illustrated and written with a clear and generous appreciation for the cumulative efforts that contributed to the developing structure of scientific knowledge. Bowler's *Evolution: The History of an Idea* contains much information. In *Science as a Way of Knowing: The Foundations of Modern Biology*, Moore offers solid parallel histories of evolutionary biology, genetics, and embryology. Mayr's *The Growth of Biological Thought: Diversity, Evolution, and Inheritance* is magisterial in its scope and precise in its detail. His *One Long Argument: Charles Darwin and the Genesis of Modern Evolutionary Thought*, focusing on Darwin and the subsequent developments of evolutionary thought, is much shorter and full of good things. Mayr's historical accounts are occasionally somewhat biased and distorted by his preoccupations as a major participant in the living history of the Modern Synthesis.

Among historical accounts that focus on Darwin's development in relation to his predecessors and contemporaries, two nearly contemporaneous books, Ruse's *The Darwinian Revolution: Science Red in Tooth and Claw* and Oldroyd's *Darwinian Impacts: An Introduction to the Darwinian Revolution*, can both be commended for sensible circumspection. Oldroyd also describes some modern developments in Darwinism. The second edition of Ruse's book contains an updated bibliographic essay. Ruse also has a helpful bibliographic essay appended to his anthology *Philosophy of Biology* and yet another in a review essay in *Victorian Studies*: "The Darwin Industry: A Guide." In another work that concentrates on situating Darwin within his contemporary scientific context, *The Development of Darwin's Theory: Natur-*

al History, Natural Theology, and Natural Selection, 1838-1859, Dov Ospovat argues that the mature development of Darwin's ideas in the *Origin* depended on assimilating and explaining the various fields of natural history that occupy the later chapters of the *Origin*. This is an important argument, but in Ospovat's handling it tends toward the misleading implication that Darwin's theory merely provides a conduit for the convergence of prevailing paradigms in specialist areas. Ospovat attributes these paradigms largely to metaphysical and ideological presuppositions, and in reflecting on Darwin's assimilation of his sources, he draws the false and gratuitous inference that Darwin's theory provides an insight not into nature itself but only into "socially constructed conceptions of nature" (229). Marxist historians have of course responded warmly to such contentions. For Darwin's interaction with his critics after 1859, see Hull's *Darwin and His Critics*, which contains both primary documents and scholarly commentaries on them. *The Darwinian Heritage*, edited by Kohn, contains essays by specialist historical scholars on the background to Darwin's work, on Darwin's own development, and on the subsequent fortunes of his theory.

For a classic exposition of Lamarck's place in intellectual history, see Lovejoy's *The Great Chain of Being*. On Spencer's relation to Lamarck, and Darwin's relation to both Lamarck and Spencer, the best single study is still Freeman's article "The Evolutionary Theories of Charles Darwin and Herbert Spencer." Mayr gives a succinct and incisive comparison of Spencer and Darwin in *One Long Argument* (102). On social Spencerism or Spencer's place within the misnamed field of "social Darwinism," see Hawkins' *Social Darwinism in European and American Thought, 1860-1945* and Taylor's *Men Versus the State: Herbert Spencer and Late Victorian Individualism*.

On the history of evolutionary theory in the period between Darwin's death and the completion of the new synthesis, see Provine in *The Darwinian Heritage*, edited by Kohn, *The Evolutionary Synthesis*, edited by Mayr and Provine, Bowler's *The Eclipse of Darwinism*, and Hull's *Science as a Process* (chapter 2). Accessible texts from the formative period of the Modern Synthesis include Dobzhansky's *Genetics and the Origin of Species*, Julian Huxley's *Evolution: The Modern Synthesis*, Simpson's *The Meaning of Evolution: A Study of the History of Life and of Its Significance for Man*, and Mayr's *Systematics and the Origin of Species*. More recent works by main contributors to the Modern Synthesis include *Evolution*, by Dobzhansky, Ayala, Stebbins, and Valentine, *Evolution After Darwin* (3 vols.), edited by Sol Tax, Haldane's essay "Natural Selection" in *Darwin's Biological Works*, edited by P.R. Bell (Haldane also has several collections of superb popular essays), Stebbins' *Darwin to DNA, Molecules to Humanity*, and Mayr's *Animal Species and Evolution and Evolution and the Diversity of Life*.

On the nature of scientific revolutions, Kuhn remains the central point

of reference, if not the central authority. For an astute critique of Kuhn's model, in addition to those given by Popper, Mayr, and Ghiselin (cited in the section "The Nature of the Darwinian Revolution"), see Weinberg, *Facing Up: Science and Its Cultural Adversaries* (chapters 13, 17 and 18). For a summary of conflicting views on the degree to which Kuhn is himself responsible for the most radically constructivist interpretations of his theories, see Carroll's *Evolution and Literary Theory* (p. 463, note 16).

For contributions to modern sociobiology and evolutionary psychology, see Wilson's *On Human Nature*, Alexander's *Darwinism and Human Affairs*, Symons' *The Evolution of Human Sexuality*, Daly's and Wilson's *Sex, Evolution, and Behavior*, Brown's *Human Universals*, Tooby's and Cosmides' "The Psychological Foundations of Culture" (in *The Adapted Mind*, edited by Barkow, Cosmides, and Tooby), Mithen's *The Prehistory of the Mind: The Cognitive Origins of Art, Religion, and Science*, Pinker's *How the Mind Works*, and Buss's textbook *Evolutionary Psychology*. For the history of modern anthropology in its antagonistic relation to Darwinian naturalism, see Degler's *In Search of Human Nature* and Fox's *The Search for Society: Quest for a Biosocial Science and Morality* (chapters 3 and 4). Shorter accounts of this history are also given in Brown and in Tooby and Cosmides, cited above, and in Freeman's article "Paradigms in Collision."

For efforts to extend evolutionary psychology to the humanities, see Carroll's *Evolution and Literary Theory*, Dissanayake's *Homo Aestheticus and Art and Intimacy*, Storey's *Mimesis and the Human Animal*, Miller's *The Mating Mind: How Sexual Selection Shaped The Evolution of Human Nature*, Wilson's *Consilience: The Unity of Knowledge* (chapter 10), Cooke's *Human Nature in Utopia: Zamyatin's We*, and special issues of the journals *Human Nature* (6:2 [1995]) and *Philosophy and Literature* (25:2 [2001]). For efforts by poststructuralist literary scholars to assimilate Darwin to Derridean and Foucauldian irrationalism and indeterminacy, see Beer's *Darwin's Plots* and Levine's *Darwin Among the Novelists*.

For commentary on the debates over sociobiology and the anti-adaptationist campaigns of Stephen Jay Gould and others, see Gould's "Darwinian Fundamentalism," Mayr's "How To Carry Out the Adaptationist Program?"; Maynard Smith's *Did Darwin Get It Right?: Essays on Games, Sex, and Evolution* (part 3), and Maynard Smith's "Genes, Memes, and Minds," Hull's *Science as a Process: An Evolutionary Account of the Social and Conceptual Development of Science* (chapter 6), Dennett's *Darwin's Dangerous Idea: Evolution and the Meanings of Life* (chapter 10), Conway Morris' *Crucible of Creation*, Dawkins' *Unweaving the Rainbow: Science, Delusion, and the Appetite for Wonder*, Segerstråle's *Defenders of the Truth: The Battle for Science in the Sociobiology Debate and Beyond*, Pinker's "Evolutionary Psychology: An Exchange," Alcock's "Unpunctuated Equilibrium" and *The Triumph of Sociobiology*,

Ruse's *The Evolution Wars: A Guide to the Debates*, Brown's *The Darwin Wars: How Stupid Genes Became Selfish Gods*, and Sterelny's *Dawkins vs. Gould: The Survival of the Fittest*.

For comprehensive presentations of evolutionary theory as it is currently conceived, see Maynard Smith's *Theory of Evolution*, Maynard Smith's and Szathmáry's *The Origins of Life*, Ridley's *The Problems of Evolution* and his textbook *Evolution*, and Mayr's *This Is Biology*. Dawkins' *The Blind Watchmaker* offers a more narrowly focused theoretical meditation on natural selection and the problem of design. Ridley's anthology *Evolution* usefully collates a sequence of classic and contemporary passages on a variety of standard topics. Williams' *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought* (1966) gives an account of the criteria for adaptationist explanation that has attained canonical status. In *Natural Selection: Domains, Levels, and Challenges* (1992), Williams revisits the topics of his earlier work. For introductions to the philosophy of biology, in addition to Ruse's anthology *Philosophy of Biology*, mentioned above, one might also consult *Conceptual Issues in Evolutionary Biology*, edited by Sober, and *The Philosophy of Biology*, edited by Hull and Ruse. A survey of the field by Sterelny and Griffiths, *Sex and Death: An Introduction to Philosophy of Biology*, is written in an exceptionally turgid style, but it is solidly researched and has useful guides to further reading appended to each chapter. *Keywords in Evolutionary Biology*, edited by Keller and Lloyd, contains concise introductory essays on a variety of standard theoretical topics by a well-chosen set of expert commentators.

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