CHAPTER TWO

Confronting the Creationists: The First Darwinian Revolution

A NEW DISCOVERY IN SCIENCE, such as the double-helix structure of DNA, is usually accepted almost immediately. If the assumed discovery turns out to be based on an error or a misinterpretation, it quickly disappears from the literature. By contrast, resistance to the introduction of new theories, particularly those that are based on new concepts, is much stronger and broader-based. Isaac Newton's theory that gravitation is responsible for the motion of the planets required some eighty years before it was universally accepted. Alfred Wegener's theory of continental drift was published in 1912 but was generally adopted only fifty years later, after the acceptance of the theory of plate tectonics.

Theories that either implied or overtly assumed organic evolution had been proposed from Buffon (1749) on, most explicitly by Lamarck (1809), but were largely ignored or actively resisted. When Charles Darwin first began to think about such problems, in his Cambridge days and on the *Beagle,* all of his teachers and friends firmly believed that species do not change. They held this belief in large part because of their religious views. The two teachers in Cambridge to whom Darwin was closest, Henslow and Sedgwick, were both orthodox Christians and accepted the dogma of the Bible literally, including the story of creation. Even the geologist Charles Lyell, whose work profoundly influenced Darwin's thinking—although Darwin did not meet him personally until after he returned from the *Beagle* voyage—was a theist who believed that species were created by God's hand. In all the writings of the naturalists, geologists, and philosophers of the period, God played a dominant role. They saw nothing peculiar in explaining otherwise puzzling phenomena as being caused by God, and that included the question of how species originate.

The Argument against Creationism

When Darwin decided in 1827 to study for the ministry, he too was an orthodox Christian. As he said in his autobiography (1958:57), "As I did not then in the least doubt the strict and literal truth of every word in the Bible," he neither questioned the occurrence of miracles nor any other supernatural phenomena. When he sailed on the *Beagle,* he reports, "I was quite orthodox, and I remember being heartily laughed at by several of the officers for quoting the Bible as an unanswerable authority on some point of morality" (1958:85). And yet it is evident that many of the experiences he had during the five years of his voyage raised the first doubts in his mind about his religious beliefs. How could a wise and good Creator permit the unspeakable cruelty and sufferings of slavery? How could he instigate earthquakes and volcanic eruptions that killed thousands or tens of thousands of innocent people? Yet Darwin was far too busy with his work to become obsessed by such disturbing thoughts. After his return from the *Beagle* Darwin was more strongly influenced by his family's beliefs than by his Cambridge friends. As Ruse (1979:181) has observed: "His grandfather Erasmus was at best a weak deist, quite able to believe in evolution . . . his father Robert, who had an overwhelming influence on Darwin, was an unbeliever; his uncle Josiah Wedgwood was a unitarian; and most important of all, Charles's older brother Erasmus had become an unbeliever by the time Charles returned from the Beagle voyage."

But a more important influence on his changing beliefs than his intellectual environment was Darwin's own scientific findings. Almost everything he learned in his natural-history studies was more or less in conflict with Christian dogma. Every species had numerous adaptations, from species-specific songs or courtships to specialized food and specific enemies. According to the philosophy of natural theology, which was widely accepted in England at that time, God had designed and looked after all of these numberless details. They could not possibly be controlled by physical laws, for these details were far too specific. Laws can control the physical world, where adaptation was absent, but the specificities and adaptations of the organic world required that God personally look after every detail relating to thousands or, as we now know, millions of species. Darwin could not accept this explanation of the enormous diversity and adaptation he observed, and he found himself more and more inclined toward natural mechanisms.

Darwin's observations were also in conflict with the natural theologians' belief in a perfect world. What the naturalist finds instead are numerous imperfections. How could all the species of former periods have become extinct if they had been perfect? As Hull (1973:126) has said rightly, "The god implied by . . . a realistic appraisal of the organic world was capricious, cruel, arbitrary, wasteful, careless, and totally unconcerned with the welfare of his creations." Such considerations as these gradually drove Darwin to the decision to try to explain the world without invoking God or any kind of supernatural forces.

As we will see in more detail below, Darwin adopted natural selection in the fall of 1838, which would suggest that he had decided to reject supernatural explanations prior to that date. But this conclusion has been vigorously denied by several authors, whose views are seemingly well supported by Darwin's own statements in the *Origin* and elsewhere. There is now in the Darwin literature an extreme spread of opinions, ranging from the conclusion that Darwin was already an agnostic in 1837 when he began to write his *Notebooks*, to the notion that he was still a theist in 1859 and became an agnostic only late in life. How could such a wide divergence of interpretation develop in view of the massive material relating to the issue in Darwin's own notes, letters, and publications? The answer is Darwin's own ambiguity. This has been splendidly analyzed by Kohn (1989). Additional light on changes in Darwin's thinking has been provided by Moore (1989). Reading these accounts (as well as earlier ones by Ospovat, Greene, Gillespie, Moore, Manier, and Richards) leads me to the conclusions that follow. However, Kohn has rightly said, every interpreter of Darwin's religiosity has tended to read into Darwin what he wanted to find, and presumably I am not escaping this weakness either.

It is quite evident that prior to the end of July 1838 Darwin had made quite a few notebook entries that were thoroughly "materialistic" (= agnostic). But July 29–31, 1838, Darwin visited the Wedgwoods at Maer in Staffordshire, and the courtship of Charles and his cousin Emma began with that visit. Emma was an orthodox Christian and, as has often been pointed out, it became clear to Darwin that it would destroy their marriage if he was not cautious in the expression of his religious views. More than that, as Kohn has said quite rightly, "Emma became Darwin's model of the conventional Victorian reader" (1989:226). She clearly had an effect on "the contruction of Darwin's texts. To me this means one crucial thing, not a word of the ambiguous God-talk of the *Origin* can be taken at face value" (Kohn 1989:226). To be sure, it seems that Darwin himself was still wavering. "Atheism both attracted and frightened him" (p. 227). He was aware of the great unknown, and it would have been a comfort to him to believe in a supreme being. But all the phenomena of nature he encountered were consistent with a straightforward scientific explanation that did not invoke any supernatural agencies.

Thirteen years later, in 1851, an event occurred in Darwin's life that thoroughly affected him. He lost his beloved ten-year-old daughter Annie, a child seemingly perfect in her goodness. As Moore (1989) describes, this "cruel" event seems to have extinguished the last traces of theism in Darwin.

Whether one wants to call him a deist, an agnostic, or an atheist, this much is clear, that in the *Origin* Darwin no longer required God as an explanatory factor. Creation as described in the Bible was contradicted for Darwin by almost every aspect of the natural world. Furthermore, creation simply could not explain the fossil record, nor the hierarchy in types of organisms that had been proposed by the taxonomist Carl Linnaeus, nor many of the other findings of science. Yet almost all of Darwin's peers still believed in some form of creation, and many of Darwin's contemporaries accepted Bishop Ussher's calculation that creation had occurred as recently as 4004 years B.C.

By contrast, the geologists had long been aware of the immense age of the earth, which would have allowed plenty of time for abundant organic evolution. Another discovery of geology that was most important and most disturbing for the creationist was the discovery of abundant extinction. Already in the eighteenth century the German naturalist Johann Friedrich Blumenbach and others had accepted extinction of formerly existing types like ammonites, belemnites, and trilobites, and of entire faunas, but it was not until Cuvier worked out the extinction of a whole sequence of mammalian faunas in the Tertiary of the Paris Basin that the acceptance of extinction became inevitable. The ultimate proof for it was the discovery of fossil mastodons and mammoths, animals so huge that any living survivors could not possibly have remained undiscovered in some remote part of the globe.

Three explanations for extinction were offered. According to Lamarck, no organism ever became extinct; there simply was such drastic transformation that formerly existing types had changed beyond recognition. According to another school, one to which Louis Agassiz belonged, each former fauna had become extinct as a whole through some catastrophe and was replaced by a newly created, more progressive fauna. This had happened, according to Agassiz, fifty times since the earth was formed. Such catastrophism was unpalatable to Lyell, who produced a third theory consistent with his uniformitarianism. He believed that individual species became extinct one by one as conditions changed and that the gaps thus created in nature were filled by the introduction of new species through some presumably supernatural means. Lyell's theory was an attempt at a reconciliation between those who recognized a changing world of long duration and those who supported the tenets of creationism.

The question of precisely how these new species were introduced was left unanswered by Lyell. He bequeathed this problem to Darwin, who in due time made it his most important research program. Darwin thus approached the problem of evolution in an entirely different manner from Lamarck. For Lamarck, evolution was a strictly vertical phenomenon, proceeding in a single dimension, that of time. Evolution for him was a movement from less perfect to more perfect, from the most primitive infusorians up to the mammals and man. Lamarck's *Philosophie Zoologique* was the paradigm of vertical evolutionism. Species played no role in Lamarck's thinking. New species originated all the time by spontaneous generation from inanimate matter, but this produced only the simplest infusorians. Each newly established evolutionary line gradually moved up to ever greater perfection, as organisms adapted to their environment and passed along to their offspring these newly acquired traits.

Darwin was unable to build on this foundation but rather started from the fundamental question that Lyell had bequeathed to him, namely, how do new species originate? Although Lyell had appealed to "intermediate causes" as the source of the new species, the process was nevertheless a form of special creation. "Species may have been created in succession at such times and at such places as to enable them to multiply and endure for an appointed period and occupy an appointed space on the globe" (Lyell 1835, 3:99–100). For Lyell, each creation was a carefully planned event. The reason why Lyell, like Henslow, Sedgwick, and all the others of Darwin's scientific friends and correspondents in the middle of the 1830s, accepted the unalterable constancy of species was ultimately a philosophical one. The constancy of species—that is, the inability of a species, once created, to change—was the one piece of the old dogma of a created world that remained inviolate after the concepts of the recency and constancy of the physical world had been abandoned.

Evidence for the Gradual Evolution and Multiplication of Species

No genuine and testable theory of evolution could develop until the possibility was recognized that species have the capacity to change, to become transformed into new species, and to multiply into several species. For Darwin to accept this possibility required a fundamental break with Lyell's thinking. The question which we must ask ourselves is how Darwin was able to emancipate himself from Lyell's thinking, and what observations or conceptual changes permitted Darwin to adopt the theory of a transforming capacity of species.

As Darwin tells us in his autobiography, he encountered many phenomena during his visit to South America on the *Beagle* that any modern biologist would unhesitatingly explain as clear evidence for evolution. Yet even when sorting his collections on the homeward voyage, and realizing that the "varieties" he observed "would undermine the stability of species," Darwin at that date (approximately July 1836) had not yet consciously abandoned the concept of constant species (Barlow 1963). This Darwin apparently did in two stages. The discovery of a second, smaller species of rhea (South American ostrich) led him to the theory that an existing species could give rise to a new species, by a sudden leap or saltation. Such an origin of new species had been postulated scores of times before, from the Greeks to Robinet and Maupertuis (Osborn 1894). Sudden new origins, however, are not evolution. The diagnostic criterion of evolutionary transformation is gradualness.

The concept of gradualism, the second step in Darwin's conversion, was apparently first adopted by Darwin when the ornithologist John Gould, who prepared the scientific report on Darwin's bird collections, pointed out to him that there were three different endemic species of mockingbirds on three different islands in the Galapagos. Darwin had thought they were only varieties (Sulloway 1982b). The mockingbird episode was of particular importance to Darwin for two reasons. The Galapagos endemics were quite similar to a species of mockingbirds on the South American mainland and clearly derived from it. Thus, the Galapagos birds were not the result of a single saltation, as Darwin had postulated for the new species of rhea in Patagonia, but had gradually evolved into three separate but similar species on three different islands. This fact helped to convert Darwin to the concept of gradual evolution (see Chapter 3). Even more important was the fact that these three different species had branched off from a single parental species, the mainland mockingbird—an observation that gave Darwin a solution to the problem of speciation—that is, how and why species multiply.

For a believer in saltational evolution, speciation meant the sudden change of a species into a different one. For a believer in transformational evolution, speciation meant the gradual change of a species into a different one in a phyletic lineage. But neither of these two theories explained the origin of the enormous organic diversity Darwin saw around him. There are at least ten million species of animals and almost two million species of plants on the Earth today, not to mention the countless kinds of fungi, protists, and prokaryotes. Even though in Darwin's day only a fraction of this number was known, the question why there are so many species and how they originated was already being asked. Lamarck had ignored the possibility of a multiplication of species in his *Philosophie Zoologique* (1809). For him, diversity was produced by differences in rates of adaptation, and new evolutionary lines originated by spontaneous generation, he thought. In Lyell's steady-state world, species number was constant, and new species were introduced to replace those that had become extinct. Any thought of the splitting of a species into several daughter species was absent among these earlier authors.

A solution to the problem of species diversification required an entirely new approach, and only the naturalists were in the position to find it. Leopold von Buch in the Canary Islands, Darwin in the Galapagos, Moritz Wagner in North Africa, and A. R. Wallace in Amazonia and the Malay Archipelago were the pioneers in this endeavor. They each discovered numerous populations that were in all conceivable intermediate stages of species formation. The sharp discontinuity between species that had so impressed John Ray, Carl Linnaeus, and others was now called into question by a continuity among species.

The problem of how these new species and incipient species come into being was clarified for Darwin by the Galapagos mockingbirds. These specimens showed that new species can originate by what we now call geographical (or allopatric) speciation. This theory of speciation says that new species may originate by the gradual genetic transformation of isolated populations. These isolated populations become in the course of time geographic races or subspecies, and Darwin realized that they may become new species, if isolated sufficiently long. By this thought Darwin founded a branch of evolutionism which, for short, we might designate as horizontal evolutionism, in contrast with the strictly vertical evolutionism of Lamarck. The two terms deal with two entirely different aspects of evolution, even though the processes responsible for these aspects proceed simultaneously. Vertical evolutionism deals with adaptive changes in the time dimension, while horizontal evolutionism deals with the origin of new diversity in the space dimension, that is, with the origin of incipient species and new species as populations move into new environmental niches. These species enrich the diversity of the organic world and are the potential founders of new higher taxa and of new evolutionary departures that will occupy new adaptive zones.

From 1837 on, when Darwin first recognized and solved the problem of the origin of diversity, this vertical/horizontal duality of the evolutionary process has been with us. Unfortunately, only a few authors have had the breadth of thought and experience of Darwin that would allow them to deal simultaneously with both aspects of evolution. Instead, paleontologists and geneticists have concentrated on vertical evolution, while the majority of naturalists have studied the origin of diversity as reflected in the horizontal process of the multiplication of species and the origin of higher taxa.

For Darwin, horizontal thinking about speciation permitted the solution of three important evolutionary problems: (1) why and how species multiply; (2) why there are discontinuities between major groups of organisms in nature, when the concept of gradual evolution would seem to imply countless subtle gradations between all groups; and (3) how higher taxa could evolve. But perhaps the most decisive consequence of the discovery of geographic speciation was that it led Darwin automatically to a branching concept of evolution. This is why branching entered Darwin's notebooks at such an early stage (see below).

Despite these insights of Darwin and the naturalists, the deep significance of the concept of speciation has been clarified only very slowly. As we will see in more detail in Chapter 3, in the decades after the publication of the *Origin of Species* Darwin himself vacillated in his understanding of how species multiply, and he continued to struggle with problems surrounding the origin of diversity for the rest of his life. Nevertheless, his realization that any evolutionary theory must somehow account for the multiplication of species was a pillar of Darwin's evolutionary thought from 1837 onward.

The Theory of Common Descent

The case of the species of Galapagos mockingbirds provided Darwin with an additional important new insight. The three species had clearly descended from a single ancestral species on the South American continent. From here it was only a small step to postulate that all mockingbirds were derived from a common ancestor—indeed, that every group of organisms descended from an ancestral species. This is Darwin's theory of common descent. By contrast, for those who accepted the concept of the *scala naturae* (scale of nature, or Great Chain of Being)—and in the eighteenth century this included most naturalists to a lesser or greater extent—all organisms were part of a single linear scale of ever-growing perfection. Lamarck still adhered, in principle, to this concept even though he allowed for some branching in his classification of the major phyla. Peter Simon Pallas and others had also published branching diagrams, but it required the categorical rejection of the *scala naturae* by Cuvier in the first and second decades of the nineteenth century before the need for a new way to represent organic diversity became crucial.

A group known as quinarians experimented with indicating relationship by osculating circles, but their diagrams did not fit reality at all well. The archetypes of Richard Owen and the *Naturphilosophen* strengthened the recognition of discrete groups in nature, but their use of the term "affinity" in relation to these groups remained meaningless prior to the acceptance of the theory of evolution. For Agassiz and Henri Milne-Edwards, branching reflected a divergence in ontogeny, so that the adult forms were far more different than the earlier embryonic stages. From all these examples it is evident that the static branching diagrams of nonevolutionists are no more indications of evolutionary thinking than branching flow charts in business or branching diagrams in administrative hierarchies.

Apparently very soon after Darwin understood that a single species of South American mockingbird had given rise to three daughter species in the Galapagos Islands, he seemed to realize that such a process of multiplication of species, combined with their continuing divergence, could in due time give rise to different genera and still higher categories. The members of a higher taxon then would be united by descent from a common ancestor. The best way to represent such a common descent would be a branching diagram. Already in the summer of 1837 Darwin clearly stated that "organized beings represent an irregularly branched tree" (*Notebook B*:21), and he drew several tree diagrams in which he even distinguished living and extinct species by different symbols.

By the time Darwin wrote the *Origin,* the theory of common descent had become the backbone of his evolutionary theory, not surprisingly so because it had extraordinary explanatory powers. Indeed, the manifestations of common descent as revealed by comparative anatomy, comparative embryology, systematics (in its search for "the natural system"), and biogeography became the main evidence for the occurrence of evolution in the years after 1859. Reciprocally, these biological disciplines, which up to 1859 had been primarily descriptive, now became causal sciences, with common descent providing an explanation for nearly everything that had previously been puzzling.

The concept of common descent was not entirely original with Darwin, however. Buffon had already considered it for close relatives such as horses and asses; but not accepting evolution, he had not extended this thought systematically. There are occasional suggestions of common descent in a number of other pre-Darwinian writers, but historians so far have not made a careful search for early adherents of common ancestry. The theory was definitely not upheld by Lamarck, who, although he proposed the occasional splitting of "masses" (higher taxa), never thought in terms of a splitting of species and regular branching. For him descent was linear descent within each phyletic line, and the concept of common descent was alien to him.

The theory of common descent, once proposed, is so simple and so obvious that it is hard to believe Darwin was the first to have adopted it consistently. Its importance was not only that it had such great explanatory powers but also that it provided a unity for the living world that had been previously missing. Up to 1859 people had been impressed primarily by the enormous diversity of life, from the lowest plants to the highest vertebrates, but this diversity took on an entirely different complexion when it was realized that it all could be traced back to a common origin. The final proof of this, of course, was not supplied until our time, when it was demonstrated that even bacteria have the same genetic code as animals and plants.

None of Darwin's theories was accepted as enthusiastically as common descent. Everything that had seemed to be arbitrary or chaotic in natural history up to that point now began to make sense. The archetypes of Owen and of the comparative anatomists could now be explained as the heritage from a common ancestor. The entire Linnaean hierarchy suddenly became quite logical, because it was now apparent that each higher taxon consisted of the descendants of a still more remote ancestor. Patterns of distribution that previously had seemed capricious could now be explained in terms of the dispersal of ancestors. Virtually all the proofs for evolution listed by Darwin in the *Origin* actually consist of evidence for common descent. To establish the line of descent of isolated or aberrant types became the most popular research program of the post-*Origin* period, and has largely remained the research program of comparative anatomists and paleontologists almost up to the present day. To shed light on common ancestors also became the program of comparative embryology. Even those who did not believe that ontogeny recapitulates phylogeny often discovered similarities in embryos that were obliterated in the adults. These similarities, such as the chorda in tunicates and vertebrates, or the gill arches in fishes and terrestrial tetrapods, had been totally mystifying until they were interpreted as vestiges of a common past. Though there are still a number of connections among higher taxa to be established, particularly among the phyla of plants and invertebrates, there is probably no biologist left today who would question that all organisms now found on the earth have descended from a single origin of life. This Darwin anticipated when he suggested that "all our plants and animals [have descended] from some one form, into which life was first breathed" (1859:484).

But perhaps the most important consequence of the theory of common descent was the change in the position of man. For theologians and philosophers alike, man was a creature apart from the rest of life. Aristotle, Descartes, and Kant agreed in this, no matter how much they disagreed in other aspects of their philosophies. Darwin, in the *Origin,* confined himself to the cautiously cryptic remark, "Light will be thrown on the origin of Man and his history" (p. 488). But Ernst Haeckel, T. H. Huxley, and in 1871 Darwin himself demonstrated conclusively that humans must have evolved from an ape-like ancestor, thus putting them right into the phylogenetic tree of the animal kingdom. This was the end of the traditional anthropocentrism of the Bible and of the philosophers. This application of the theory of common descent to humans, however, encountered vigorous opposition. To judge from contemporary cartoons, no Darwinian idea was less acceptable to the Victorians than the derivation of man from a primate ancestor. Yet today this derivation is not only remarkably well substantiated by the fossil record, but the biochemical and chromosomal similarity of man and the African apes is so great that it is puzzling why they are so relatively different in morphology and brain development. The primate origin of man, as first suggested by Darwin, immediately raised questions about the origin of mind and consciousness that are controversial to this day.

The Fate of Darwin's First Revolution

Darwin's theory of evolution as such (together with the nonconstancy of species), his theory of common descent, and his theory that species multiply were victorious within a remarkably short time. The victory of these three theories is the first Darwinian revolution. Within fifteen years of the publication of the *Origin* hardly a qualified biologist was left who had not become an evolutionist. The evolutionary origin of man was still unacceptable to some with religious commitments but was taken as firmly established by the anthropological profession.

Even though a theory of the multiplication of species is now taken for granted as an essential component of evolutionary theory, it is still controversial how this multiplication comes about. That much, if not most, speciation is geographical is generally accepted, but what other forms of speciation may also exist, and how frequent they are, is still an unsettled problem, as we will see in the next chapter.

CHAPTER THREE

How Species Originate

FROM THE SUMMER OF 1837 ON, Darwin collected notes on the great book he was going to write, and he referred to it in his notes and in his correspondence always as "the species book." When finally published in 1859, it was called by him *On the Origin of Species*. Darwin was fully conscious of the fact that the change from one species into another one was the most fundamental problem of evolution. Indeed, evolution was, almost by definition, a change from one species into another one. The belief in constant, unchangeable species was the fortress of antievolutionism to be stormed and destroyed. Once this was accomplished, it would not be difficult to adduce other evidence in favor of evolution.

In view of this central position of the problem of species and speciation in Darwin's life work, one would expect to find in the *Origin* a satisfactory and indeed authoritative treatment of the subject. This, curiously, one does not find. Indeed, the longer Darwin struggled with these concepts, the more he seemed to become confused. In the end, the *Origin* was a superb treatment of the theory of common descent and a great plea for the efficacy of natural selection, but it was vague and contradictory both on the nature of species and the mode of speciation.

What Is a Species?

After his crucial conversation with John Gould about the Galapagos mockingbirds in 1837, Darwin continued to struggle with the problem of how to define a species; but for that matter, so did virtually all other naturalists during the ensuing 150 years. It will help to understand Darwin's problem if I give a short overview of the four major species concepts that developed during this period.

THE TYPOLOGICAL SPECIES CONCEPT

A typological species is an entity that differs from other species by constant diagnostic characteristics. This was the species concept of Linnaeus and Lyell and was supported by those philosophers from Plato to modern times who consider species to be "natural kinds" or "classes." The concept was entirely consistent with the belief in creationism ("that which was separately created by God") and with the philosophy of essentialism ("that which has an essence of its own"; see Chapter 4). However, this species concept has three major practical weaknesses, which is the reason why it has been largely given up in recent times. First, it forces its adherents to consider as species even different variants within a population. Second, the invalidity of this concept is demonstrated by the high frequency of so-called sibling species—species which are indistinguishable on the basis of their appearance but which do not interbreed in nature. These species cannot be discriminated under the typological species concept. And third, it forces us to recognize as full species many local populations that differ by one diagnostic character from other populations of the species.

THE NOMINALIST SPECIES CONCEPT

According to this concept, only individual objects exist in nature. Similar objects or organisms are bracketed together by a name, and this subjective action of the classifier determines which objects are combined into one species. Species, therefore, are merely arbitrary mental constructs. That species have no reality in nature has been the claim of the nominalists from the Middle Ages right up to the writings of some recent philosophers. By contrast, the reality of species has been supported consistently by naturalists up to the present day. There is no more devastating refutation of the nominalistic claim than the fact that primitive natives in New Guinea, with a Stone Age culture, recognize as species exactly the same entities of nature as Western taxonomists. If species were something purely arbitrary, it would be totally improbable for representatives of two drastically different cultures to arrive at identical species delimitations.

THE EVOLUTIONARY SPECIES CONCEPT

Paleontologists who study species distributed in the time dimension have always been rather dissatisfied with a species definition derived from the nondimensional species concept of the local naturalist. What paleontologists were looking for was a species concept that would be particularly suitable for the discrimination of fossil species. This need eventually led the naturalist G. G. Simpson (1961:153) to this species definition: "An evolutionary species is a lineage (an ancestral–descendent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." Wiley (1980, 1981) and Willmann (1985) have proposed slightly modified versions of Simpson's definition.

An evolutionary definition of species has not been widely accepted because it is only applicable to monotypic species, since all isolates that "evolve separately" would also have to be recognized as species. Furthermore, how is one to describe and determine the "unitary evolutionary role and tendencies" of a population or taxon? The main objective of the evolutionary species definition was to permit a clear delimitation of a species in the time dimension, but this hope turned out to be illusory in all cases of gradual species transformation. The exact determination of the origin of a new species can be made only in cases of instantaneous speciation (as in polyploidy), and the exact endpoint of a species can only be determined in the case of extinction. The biological species definition, as we will see, is equally qualified to determine these two points, and has other advantages going for it as well.

THE BIOLOGICAL SPECIES CONCEPT

This species concept is based on the observation of local naturalists that at a given locality, populations of different species coexist but do not interbreed with each other. This I articulated in the definition: "Species are groups of interbreeding natural populations that are reproductively isolated from other such groups." Statements in Darwin's notebooks show that by 1837 he had given up the typological species concept and had developed a species concept based on reproductive isolation. For instance, "My definition of species has nothing to do with hybridity, is simply an instinctive impulse to keep separate, which will no doubt be overcome [or else no hybrids would ever be produced], but until it is, these animals are distinct species" (C:161). There are repeated references in the notebooks to mutual "repugnance" of species to intercrossing. "The dislike of two species to each other is evidently an instinct; and this prevents breeding" (B:197). "Definition of species: one that remains at large with constant characters, together with other beings of very near structure" (B:213). For Darwin, species status had little if anything to do with degree of difference: "Hence species may be good ones and differ scarcely in any external character" (B:213).

Darwin adhered to this biological species concept for about the next fifteen years. But then he became rather confused, particularly after he tried to apply his zoological findings to plants. As we shall see, he considered the *variety* (which in animals is a subspecies) to be an incipient species, and he encountered no difficulties with this concept as long as he dealt with animals. However, when through Hooker and other botanical friends Darwin came to study varieties of plants, he did not realize that the botanical terminology was rather different from that of zoology. Plant varieties very often were individual variants within a local population, and to consider them incipient species not only caused problems for the explanation of speciation but also for the delimitation of species against varieties, and of species against one another. There were a number of other developments in these years which induced Darwin to give up his biological species concept and return to a more or less typological species definition (Sulloway 1979). The twenty-five pages on species and speciation in his unfinished big book manuscript (Darwin 1975:250–274) contain so many contradictions that they are almost embarrassing to read.

The species concept at which Darwin finally arrived is clearly described in the *Origin*. There is nothing left of the biological criteria of the notebooks, and his characterization of the species now is a mixture of the typological and nominalist species definitions.

> Systematists . . . will not be incessantly haunted by the shadowy doubt whether this or that form be in essence a species. This I feel sure . . . will be no slight relief . . . Systematists will have only to decide . . . whether any form be sufficiently constant and distinct from other forms, to be capable of definition; and, if definable, whether the differences be sufficiently important to deserve a specific name . . . The only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations . . . In short, we shall have to take species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species" (1859:484–485).

The example set by Darwin was followed by just about every taxonomist and evolutionist in the nineteenth century except for a few enlightened field naturalists. It clearly was the species concept of the Mendelians. The counter movement in the twentieth century, initiated by Jordan, Poulton, Stresemann, and other progressive workers, ultimately resulted in the biological species concept's being widely accepted.

However, each of the three major species concepts (typological, evolutionary, and biological) has a certain legitimacy in some areas of biological research, even today. Which of them one adopts may depend on the type of research one does. The museum taxonomist, as well as the stratigrapher, may find the typological species concept most useful, never mind how clearly it is refuted by the existence of sibling species and strikingly different variants (phena). But anyone working with living populations, restricted to one place and time, finds any species concept other than the biological one to be unsatisfactory. Finally, the paleontologist, part of whose endeavor it is to delimit fossil species taxa in the vertical sequence of strata, cannot help but pay attention to the time dimension.

Modern biologists are almost unanimously agreed that there are real discontinuities in organic nature, which delimit natural entities that are designated as species. Therefore, the species is one of the basic foundations of almost all biological disciplines. Each species has different biological characteristics, and the analysis and comparison of these differences is a prerequisite for all other research in ecology, behavioral biology, comparative morphology and physiology, molecular biology, and indeed all branches of biology. Whether he realizes it or not, every biologist works with species.

What Is Speciation?

Paleontologists, conditioned to vertical thinking, considered speciation to be the change of a phyletic lineage over time. But since there is a steady extinction of species, where do the new species come from? This has been the problem from Lamarck and Lyell on. The answer which Darwin found was that species not only evolve in time but also multiply. Speciation, since Darwin, has come to mean the production of new, reproductively isolated populations.

That the multiplication of species was a major evolutionary phenomenon became clear to Darwin as soon as he followed up the consequences of his new understanding of the taxonomy of the Galapagos mockingbirds. But it was really not until the coming of the new systematics and the evolutionary synthesis (see Chapter 9) that speciation became the focal point of evolutionary research at the species level.

Considering Darwin's uncertainties about the nature of species, it is perhaps not surprising that he vacillated about the mode of speciation. It must be remembered that at first Darwin believed in Lyell's sudden, saltational "introduction" of new species. It was John Gould's pronouncement in March 1837 that each of the three populations of mockingbirds in the Galapagos Islands was a separate species that started Darwin along an entirely new path of thinking about the origin of diversity. Obviously, the different mockingbirds on the three islands in the Galapagos had all descended from colonists of the South American mainland species; but the three populations had evolved in a slightly different manner on each of the three islands. This led Darwin to adopt the theory of speciation by the gradual modification of populations that were geographically isolated from their parent species. And this was Darwin's theory of speciation until the early 1850s. It was not a new theory, because a similar one had previously been proposed by von Buch (1825). Later, Wagner (1841) and Wallace (1855) also independently arrived at the same conclusion.

Darwin considered isolation on islands as the principal speciation mechanism, and he seems to have had difficulties in explaining speciation on continents. At one time, to account for the rich species diversity in South Africa, he postulated large-scale geological changes—up and down movements of the crust—during which South Africa was temporarily converted into an archipelago, setting the stage for abundant geographical speciation.

Just as Darwin's botanical researches induced him to change his species concept, so did these researches, at least in part, induce Darwin to accept, in addition to geographic speciation, a process we now call sympatric speciation. The exact reasoning by which Darwin arrived at this new explanation is still not fully explored (Sulloway 1979; Mayr 1982; Kohn 1985). Owing to the prevailing typological thinking, geographic races of animals were called varieties in Darwin's time. In plants, however, as mentioned above, the term variety had a dual meaning. It was applied not only to geographic races (subspecies) but also to individual variants (phena) within a single population. Darwin, on the basis of his zoological studies, had concluded that varieties of animals were incipient species. When he transferred this concept of the role of varieties in speciation to plants, he was induced to consider also individual variants within a population as incipient species. Darwin concluded, therefore, that in addition to geographic speciation there is also a process of sympatric speciation, which he defined as the origin of a new species by ecological specialization within the range of the parental species. The survival and flourishing of the new sympatric species, it was said, was made possible by its shift into a new niche, thus removing it from competition with the parental species. Natural selection would lead to an ever greater difference (character divergence) of the two competing new species. Darwin developed this concept of sympatric speciation by character divergence in the years 1854 to 1858 (Kohn 1985) and continued to support it even though once in a while he would concede that maybe geographic isolation was nearly always necessary.

It was this claim of sympatric speciation that involved Darwin in a bitter controversy with the explorer and naturalist Moritz Wagner (1868, 1889), who insisted that geographic isolation was absolutely indispensible for speciation. Unfortunately Wagner beclouded the issue by also insisting that natural selection could not operate unless the population was isolated. What we now know about speciation indicates that Wagner's arguments on the whole were more valid than Darwin's. Nevertheless, Darwin's insistence on the frequency of sympatric speciation prevailed, and prior to the evolutionary synthesis sympatric speciation was considered a frequent and, as far as the entomological literature is concerned, perhaps the prevailing mode of speciation.

In his early notebook statements on species (B:197, 213; C:161), Darwin clearly saw species as reproductively isolated entities. By the 1850s, however, his attention concentrated on species as adapted entities. He would describe how they became adapted to a new niche, but he failed to account for their reproductive isolation from the parental species. His reasoning was aggravated by a return from populational to typological thinking (see Chapter 4). "If a variety were to flourish so as to exceed in number the parent species, it would then rank as the species and the species as the variety, or it might come to supplant and exterminate the parent species, or both might coexist, and both rank as independent species" (1859:52). How could the new variety coexist as an independent species unless it had acquired reproductive isolation? This question is particularly troublesome, given that Darwin, in an argument about the origin of isolating mechanisms among species, definitely rejected the capacity of natural selection to establish a reproductive barrier (Mayr 1959b; Sulloway 1979).

Looking over all of Darwin's writings on species and speciation, one cannot escape the impression that he was rather confused about the issues and that he not infrequently contradicted himself. A major reason for his confusion can be traced to his puzzlement over the origin of genetic variation. The clear statements about mechanisms of speciation that we now can make more than 125 years later are based on our understanding (as far as it goes) of genetics. Despite his failure to reach a definitive conclusion about species and speciation, Darwin deserves credit for having pointed out the problems and for having clearly stated various alternative solutions.

CHAPTER FOUR

Ideological Opposition to Darwin's Five Theories

IN BOTH SCHOLARLY and popular literature one frequently finds references to "Darwin's theory of evolution," as though it were a unitary entity. In reality, Darwin's "theory" of evolution was a whole bundle of theories, and it is impossible to discuss Darwin's evolutionary thought constructively if one does not distinguish its various components. The current literature can easily leave one perplexed over the disagreements and outright contradictions among Darwin specialists, until one realizes that to a large extent these differences of opinion are due to a failure of some of these students of Darwin to appreciate the complexity of his paradigm.

The term "Darwinism," as we will see in Chapter 7, has numerous meanings depending on who has used the term and at what period. A better understanding of the meaning of this term is only one reason to call attention to the composite nature of Darwin's evolutionary thought. Another reason is that one cannot answer the question correctly of how and when "Darwinism" was accepted in different countries throughout the world unless one focuses on the various Darwinian theories separately. What Darwin presented in 1859 in the *Origin* was a compound theory, whose five subtheories had very different fates in the eighty years after Darwin.

One particularly cogent reason why Darwinism cannot be a single monolithic theory is that organic evolution consists of two essentially independent processes, as we have seen: transformation in time and diversification in ecological and geographical space. The two processes require a minimum of two entirely independent and very different theories. That writers on Darwin have nevertheless almost invariably spoken of the combination of these various theories as "Darwin's theory" in the singular is in part Darwin's own doing. He not only referred to the theory of evolution by common descent as "my theory," but he also called the theory of evolution by natural selection "my theory," as if common descent and natural selection were a single theory.

Discrimination among his various theories has not been helped by the fact that Darwin treated speciation under natural selection in chapter 4 of the *Origin* and that he ascribed many phenomena, particularly those of geographic distribution, to natural selection when they were really the consequences of common descent. Under the circumstances I consider it necessary to dissect Darwin's conceptual framework of evolution into a number of major theories that formed the basis of his evolutionary thinking. For the sake of convenience I have partitioned Darwin's evolutionary paradigm into five theories, but of course others might prefer a different division. The selected theories are by no means all of Darwin's evolutionary theories; others were, for instance, sexual selection, pangenesis, effect of use and disuse, and character divergence. However, when later authors referred to Darwin's theory they invariably had a combination of some of the following five theories in mind:

(1) *Evolution as such.* This is the theory that the world is not constant nor recently created nor perpetually cycling but rather is steadily changing and that organisms are transformed in time.
(2) *Common descent.* This is the theory that every group of organisms descended from a common ancestor and that all groups of organisms, including animals, plants, and microorganisms, ultimately go back to a single origin of life on earth.
(3) *Multiplication of species.* This theory explains the origin of the enormous organic diversity. It postulates that species multiply, either by splitting into daughter species or by "budding," that is, by the establishment of geographically isolated founder populations that evolve into new species.

(4) *Gradualism.* According to this theory, evolutionary change takes place through the gradual change of populations and not by the sudden (saltational) production of new individuals that represent a new type.

(5) *Natural selection.* According to this theory, evolutionary change comes about through the abundant production of genetic variation in every generation. The relatively few individuals who survive, owing to a particularly well-adapted combination of inheritable characters, give rise to the next generation.

For Darwin himself these five theories were apparently a unity, and someone might claim that indeed these five theories are a logically inseparable package and that Darwin was quite correct in treating them as such. This claim, however, is refuted by the fact, as demonstrated in Table 1, that most evolutionists in the immediate post-1859 period—that is, authors who had accepted the first theory—rejected one or several of Darwin's other four theories. This shows that the five theories are not one indivisible whole.

There are several reasons why Darwin's five theories had such different fates. One reason is that abundant evidence was already available to support some of them. This was true, for example,

TABLE 1

The composition of the evolutionary theories of various evolutionists. All these authors accepted a fifth component, that of evolution as opposed to a constant, unchanging world.

	Common descent	Multiplication of species	Gradualism	Natural selection
Lamarck	No	No	Yes	No
Darwin	Yes	Yes	Yes	Yes
Haeckel	Yes	?	Yes	In part
Neo-Lamarckians	Yes	Yes	Yes	No
T. H. Huxley	Yes	No	No	(No)[a]
de Vries	Yes	No	No	No
T. H. Morgan	Yes	No	(No)[a]	Unimportant

a. Parentheses indicate ambivalence or contradiction.

for the theory of common descent. In the case of the theory of natural selection, however, the evidence for or against was contradictory, and it required generations of research time before the controversial points could be settled. A more important reason, however, for the delay in the acceptance of some of Darwin's theories was that they were in conflict with certain ideologies dominant at Darwin's time.

During the three centuries preceding the publication of the *Origin,* Europe had been in the throes of a continuous intellectual upheaval, punctuated by the Scientific Revolution of the sixteenth and seventeenth centuries and the Enlightenment of the eighteenth century. Why did it take so long for evolution to be seriously proposed? And why did Darwinism face such an uphill battle after it was proposed? The reason is that Darwin challenged some of the basic beliefs of his age. Four of them were pillars of Christian dogma:

(1) *A belief in a constant world.* In spite of Lamarck and the *Naturphilosophen,* it was still widely, if not almost universally, accepted in 1859 that except for minor perturbations (floods, volcanism, mountain building) the world had not changed materially since creation. And in spite of Buffon, Kant, Hutton, Lyell, and the ice age theory, the prevailing opinion was still that the world had been created rather recently.

(2) *A belief in a created world.* Species and other taxa were believed to be unchanging, and therefore the existing diversity of the living world could only be due to an act of creation. This was a single creation as believed by the orthodox Christians or repeated creations, either of whole biota as believed by the so-called progressionists (for example, Agassiz), or of individual species as proposed by Lyell.

(3) *A belief in a world designed by a wise and benign Creator.* Even though the world had its imperfections, it was the best of the *possible* worlds, according to Leibniz. The adaptation of organisms to their physical and living environment was perfect because it had been designed by an omnipotent Creator.

(4) *A belief in the unique position of man in the creation.* The world was anthropocentric in the eyes of the Christian religion as well as in

the view of the foremost philosophers. Man had a soul, something animals did not have. There was no possible transition from animal to man.

In addition to these four religious beliefs, there were three secular philosophies that were also in conflict with certain of Darwin's theories. These secular beliefs were:

(5) *A belief in the philosophy of essentialism* (see below).

(6) *A belief in an interpretation of the causal processes of nature as they had been elaborated by the physicists* (see Chapter 5).

(7) *A belief in "final causes" or teleology* (see Chapter 5).

The theories of evolution proposed by Darwin challenged all seven of these traditional and well-entrenched views, though not every one of Darwin's five theories was in conflict with all of them.

External Factors in Scientific Revolutions

For the last sixty years there has been a good deal of controversy in the history of science over the question whether scientific revolutions or, indeed, any conceptual changes in science are due to discoveries and new observations made within the field ("internalism") or are the result of outside influences ("externalism"). The Marxist thesis, first promoted by Hessen (1931), that the socioeconomic milieu is decisive in initiating conceptual changes in science was particularly actively debated during part of this period.

Researches during this period have made it clear that one must distinguish between two sets of external factors: socioeconomic and ideological ones. It has also become quite clear that these two sets of factors differ fundamentally in their impact on science. Socioeconomic factors, it would seem, have very little influence on the acceptance or rejection of scientific ideas, as was shown by Mayr (1982:4–5) and by many other historians. If the industrial revolution and the socioeconomic situation had been responsible for the theory of natural selection, this theory should have been most palatable to the British public of the mid-nineteenth century. But this was not the case at all. On the contrary, the theory of natural selection, as we shall see, was almost unanimously rejected by Darwin's contemporaries. It was evidently not a reflection of the socioeconomic situation.

The other set of external factors—ideological ones—by contrast, had a powerful effect on the acceptance of Darwin's theories. What is remarkable and rarely sufficiently emphasized is that it was not the prevailing ideologies almost universally adopted in Britain (and much of the rest of the world) in the first half of the nineteenth century that inspired Darwin and gave him his new theories. On the contrary, the prevailing *Zeitgeist* was utterly opposed to Darwin's thought and prevented a universal acceptance of some of his new ideas for more than a hundred years. Indeed, as shown by the many recently published books and papers that still attempt to refute Darwinism, many Darwinian ideas are still not yet full accepted, owing to the continuing power of the opposing ideologies.

From Essentialism to Population Thinking

Of the seven ideologies challenged by Darwin's theories, none was more deeply entrenched than the philosophy of essentialism. Essentialism had dominated Western thinking for more than 2000 years, going back to the geometric thinking of the Pythagoreans. They pointed out that a triangle, regardless of the combination of angles, always has the form of a triangle. It is discontinuously different from a quadrangle or any other kind of polygon. The triangle is one of the limited number of possible forms of a polygon. In an analogous manner, all the variable phenomena of nature, according to this thinking, are a reflection of a limited number of constant and sharply delimited *eide* or essences. Essentialism, as a definite philosophy, is usually credited to Plato, even though he was not as dogmatic about it as some of his later followers, for instance the Thomists. Plato's cave allegory of the world is well known: What we see of the phenomena of the world corresponds to the shadows of the real objects cast on the cave wall by a fire. We can never see the real essences. Variation is the manifestation of imperfect reflections of the underlying constant essences.

All of Darwin's teachers and friends were, more or less, essentialists. For Lyell, all nature consisted of constant types, each created at a definite time. "There are fixed limits beyond which the descendants from common parents can never deviate from a certain type." And he added emphatically: "It is idle . . . to dispute about the abstract possibility of the conversion of one species into another, when there are known causes, so much more active in their nature, which must always intervene and prevent the actual accomplishment of such conversions" (Lyell 1835:162). For an essentialist there can be no evolution: there can only be a sudden origin of a new essence by a major mutation or saltation.

Virtually all philosophers up to Darwin's time were essentialists. Whether they were realists or idealists, materialists or nominalists, they all saw species of organisms with the eyes of an essentialist. They considered species as "natural kinds," defined by constant characteristics and sharply separated from one another by bridgeless gaps. The essentialist philosopher William Whewell stated categorically, "Species have a real existence in nature, and a transition from one to another does not exist" (1840, 3:626). For John Stuart Mill, species of organisms are natural kinds, just as inanimate objects are, and "kinds are classes between which there is an impassable barrier."

Essentialism's influence was great in part because its principle is anchored in our language, in our use of a single noun in the singular to designate highly variable phenomena of our environment, such as mountain, home, water, horse, or honesty. Even though there is great variety in kinds of mountain and kinds of home, and even though the kinds do not stand in direct relation to one another (as do the members of a species), the simple noun defines the class of objects. Essentialistic thinking has been highly successful, indeed absolutely necessary, in mathematics, physics, and logic. The observation of nature seemed to give powerful support to the essentialists' claims. Wherever one looked, one saw discontinuities—between species, between genera, between orders and all higher taxa. Such gaps as between birds and mammals, or beetles and butterflies, were mentioned often by Darwin's critics.

In daily life we largely proceed essentialistically (typologically) and become aware of variation only when we compare individuals. He who speaks of "the Prussian," "the Jew," "the intellectual" reveals essentialistic thinking. Such language ignores the fact that every human is unique; no other individual is identical to him.

It was Darwin's genius to see that this uniqueness of each individual is not limited to the human species but is equally true for every sexually reproducing species of animal and plant. Indeed, the discovery of the importance of the individual became the cornerstone of Darwin's theory of natural selection. It eventually resulted in the replacement of essentialism by population thinking, which emphasized the uniqueness of the individual and the critical role of individuality in evolution. Darwin no longer asked, as had Agassiz, Lyell, and the philosophers, "What is good for the species?" but "What is good for the individual?" (Ghiselin 1969). And variation, which had been irrelevant and accidental for the essentialist, now became one of the crucial phenomena of living nature.

From Saltationism to Gradualism

Many of Darwin's contemporaries who accepted the fact of evolution nevertheless were incapable of population thinking, owing to their ideological commitment to essentialism. As we have seen, they accepted instead a concept of evolution based on the sudden production of new species through saltations. Saltational evolution is a necessary consequence of essentialism: if one believes in evolution and in constant types, only the sudden production of a new type can lead to evolutionary change. That such saltations can occur and indeed that their occurrence is a necessity are old beliefs. Almost all theories of evolution described by Osborn in his history of evolution, *From the Greeks to Darwin* (1894), were saltational theories, that is, theories of the sudden origin of new kinds. After the publication of the *Origin,* many biologists who accepted evolution as such (Darwin's first theory) nevertheless, because they were essentialists, turned to saltational theories to explain the process of evolution.

One can distinguish three kinds of saltationist theories: (1) extinct species are replaced by newly created ones that are more or less at the same level as those that they replace (Lyell 1830–1833); (2) extinct species are replaced by new creations at a higher level of organization (progressionists, such as William Buckland, Sedgwick, Hugh Miller, Agassiz); (3) new species originate through saltations of pre-existing species (E. Geoffroy Saint-Hilaire, Darwin in Patagonia, Galton, Goldschmidt).

Saltational evolution is best called "transmutation," because the production of new species or new types is discontinuous, owing to the sudden creation of a new essence. But transmutation should not be confused with another concept of evolution known as transformational evolution. According to this concept, evolution consists of the gradual transformation of a thing from one condition to another. Lamarck's concept of evolution was transformational, designating a completely gradual process, a change due to a trend toward perfection or adjustment to the environment. To the best of my knowledge Lamarck was the first author to propose a consistent theory of gradual transformation. After 1800, but before 1859, the idea of gradual evolution was accepted by a considerable number of authors on the Continent, but in a vague manner and unsupported by adequate evidence.

As Lewontin (1983) has pointed out, Darwin, by contrast, introduced a new concept of evolution that was entirely different from saltational evolution or transformational evolution. According to Darwin's concept, which we can designate as "variational evolution," variations are produced in every generation, and evolution takes place because only a small number of variants survive to reproduce. No longer is a concrete object transformed, as in transformational evolution, but a new beginning is made in every generation. Indeed, evolution is a two-step phenomenon, the first step in each generation being responsible for the production of variation, which is then sorted in the second step, selection proper (see Chapter 6). Thus, strictly speaking, Darwinian evolution is discontinuous because a new start is made in every generation when a new set of individuals is produced. That evolution nevertheless appears to be totally gradual is because it is populational and depends on sexual reproduction among the members of the population. Such evolution is not necessarily progressive; it is an opportunistic response to the moment; hence, it is unpredictable.

Darwin's Growing Commitment to Gradualism

The concept of the gradual transformation of a population was not entirely new with Darwin. The occurrence of continuity had been stressed by some authors as far back as Aristotle, with his principle of plenitude (Lovejoy 1936). It was reflected in the concept of the *scala naturae,* and even such an arch-essentialist as Linnaeus stated that the orders of plants were touching each other like countries on a map. Lamarck was the first person to apply the principle of gradualism to the origin of the hierarchy of life, but there is no evidence that Darwin derived his gradualistic thinking from Lamarck.

Then how did Darwin arrive at the concept of gradual evolution? References to gradual changes are scattered through Darwin's notebooks from early on (Kohn 1980). For instance, Darwin considered the changes of organisms either to be produced directly by the environment or to be at least an answer to the changes in the environment. Hence, "The changes in species must be very slow, owing to physical changes slow" (*Notebook C:*17). Gradualness was also favored by Darwin's conclusion that changes in habit or behavior may precede changes in structure (*Notebook C:*57, 199). At that time Darwin still believed in a principle called Yarrell's Law (named after William Yarrell, a naturalist and animal breeder), according to which it takes many generations for the effects of the environment or of use and disuse to become strongly hereditary. As Darwin stated, "Variety when long in blood, gets stronger and stronger" (*Notebook C*:136). Various other sources for Darwin's gradualist thinking have been suggested in the recent literature, such as the writings of J. B. Sumner (Gruber 1974:125), or Leibniz's principle of plenitude (Stanley 1981). But to me it seems more likely that Darwin arrived at his gradualism owing to two major influences. One was Lyell's uniformitarianism, which Darwin extended from geology to the organic world. The other influence consisted of his own empirical researches.

At least three observations may have been influential: (1) the slightness of the differences among the mockingbird populations on the three Galapagos islands and the South American mainland, as well as a similarly slight difference among many varieties and species of animals; (2) the barnacle researches, where Darwin complained incessantly about the extent to which species and varieties were intergrading; (3) Darwin's work with races of domestic pigeons, where he convinced himself that even the most extreme races (which, if found in nature, would be unhesitatingly placed by taxonomists in different genera) were nevertheless the product of painstaking, long-continued, gradual, artificial selection. In his *Essay* of 1844 Darwin argues in favor of gradual evolution by analogy with what is found in domesticated animals and plants. And he postulates that "there must have existed intermediate forms between all the species of the same group, not differing more than recognized varieties differ" (p. 157).

Finally, Darwin had didactic reasons for insisting on the slow accumulation of rather small steps. He answered the argument of his opponents that one should be able to "observe" evolutionary change owing to natural selection by saying: "As natural selection acts solely by accumulating slight successive favorable variations, it can produce no great or sudden modifications; it can act only by very short and slow steps" (1859:471).

Thus, Darwin's rejection of essentialism and the general emergence of population thinking strengthened his adherence to gradualism and led him to totally reject saltations. As soon as one adopts the concept that species evolve as populations and are transformed, owing to the differential reproductive success of unique individuals over generations—and this is what Darwin increasingly believed—one is automatically forced also to believe that evolution must be gradual. Gradualism and population thinking probably were originally independent strands in Darwin's conceptual framework, but eventually they reinforced each other powerfully, just as essentialism and saltationism reinforced one another in the thinking of many of Darwin's opponents.

Darwin's totally gradualist theory of evolution—that not only species but also higher taxa arise through gradual transformation—immediately encountered strong opposition. Even some of Darwin's closest friends were unhappy about it. T. H. Huxley wrote to Darwin on the day before the publication of the *Origin:* "You have loaded yourself with an unnecessary difficulty in adopting *Natura non facit saltum* [Nature makes no jumps] so unreservedly" (Huxley 1900 2:27). In spite of the urgings of Huxley, Galton, Kölliker, and other contemporaries, Darwin insisted on the gradualness of evolution, even though he was fully aware of the controversial nature of this concept. Furthermore, Darwin's adherence to gradualism became stronger with time; eventually (after the 1867 critique by F. Jenkin) he minimized even more the evolutionary role of drastic variations ("sports").

But essentialism and saltationism continued to be widely adopted. After Darwin's death the concept of gradualism became even less popular than it had been in Darwin's own time. This began with William Bateson's 1894 book and reached a climax with the mutationist theories of the Mendelians (see Chapter 9). Both Bateson and de Vries missed no opportunity to make fun of Darwin's belief in gradual evolution and upheld instead evolution by macromutations (Mayr and Provine 1980). A mild popularity of saltationist theories continued right through the evolutionary synthesis (Goldschmidt 1940; Willis 1940; Schindewolf 1950). The naturalists were the main supporters of gradual evolution, which they encountered everywhere in the form of geographic variation. Eventually, geneticists arrived at the same conclusion through the discovery of ever slighter mutations.

Defining gradualism as populational evolution—and this is what Darwin basically had in mind—permits us to say that in spite of all the opposition to him, Darwin ultimately prevailed even with his fourth evolutionary theory. The only exceptions to gradualism that are clearly established are cases of stabilized hybrids that can reproduce without crossing.

Nothing is said in the theory of gradualism about the precise rate at which the change may occur. Darwin was aware of the fact that evolution could sometimes progress rapidly, but, as Andrew Huxley (1981) has pointed out, evolution could also contain periods of complete stasis "during which these same species remained without undergoing any change." In a well-known diagram in the *Origin*, Darwin lets one species (F) continue unchanged through 14,000 generations or even through a whole series of geological strata. Understanding the independence of gradualness and evolutionary rate is important for evaluating the theory of punctuated equilibria put forth in 1972 by Stephen J. Gould and Niles Eldredge (see Chapter 10).

CHAPTER FIVE

The Struggle against Physicists and Philosophers

ESSENTIALISM WAS NOT the only ideology Darwin had to overcome. A concept of science had developed since the seventeenth century that was completely dominated by physics and mathematics. The philosophers from Bacon and Descartes to Locke and Kant entirely agreed with the physical scientists from Galileo and Newton to Lavoisier and Laplace that the ideal of science should be to establish mathematically formed theories that were based on universal laws. The possibility of proof and of exact prediction were the tests for the goodness of a scientific explanation. Newton's physics was the shining example of good science. Every British scientist and philosopher, at the time when Darwin was developing his ideas on evolution, agreed in this concept of science, and there are indications that Darwin did his best, particularly after reading and rereading John Herschel's *Discourse,* to live up to his ideal (Ruse 1979).

In spite of all these efforts, Darwin's empirical researches led to results that were in conflict with most of the basic assumptions of physicalism. The physicalists were essentialists, a philosophy that Darwin totally rejected. Instead, Darwin developed population thinking, a mode of thinking utterly alien to the physicalists. The physicists at that time were strict determinists; prediction was not only possible but was the very test of the validity of theories. Evolutionary processes, by contrast, involved a considerable chance element: they were probabilistic, and hence they did not permit absolute prediction. All evolutionary phenomena could be explained only by inferring past historical events, a consideration absent (at that period) in the physical sciences. The probabilistic nature of the evolutionary process was so alien to the thinking of the physicists that Herschel referred to natural selection as the theory of the "higgledy-piggledy" (F. Darwin 1888, 2:240).

Darwin's findings completely undermined the physicalist concept of laws. The order and harmony of the created universe made the physical scientists search for laws, for wise regulations in the running of the universe installed by the Creator. To serve his Creator best a physicist studied His laws and their working. In this tradition Darwin refers in the *Origin of Species* no fewer than 106 times in 490 pages to laws controlling certain biological processes. But Darwin's "laws" were not the laws of the deists but were either simple facts or regular processes. No longer relying on universal laws, Darwin had no problem in accepting statistical generalizations. It was a complete rejection of Cartesian-Newtonian determinism.

The role Darwin assigned to chance has never been properly analyzed. The deterministic spirit of science at his time was in complete conflict with Darwin's findings, which showed how strong a role in evolution was played by chance. In the case of variations, he distinguished between those being accidental as far as their "purpose" or selective value is concerned, and others that are "accidental as to their cause of origin" (F. Darwin 1888 I:314). A similar train of thought is expressed in the *Variation of Animals and Plants* (1868 2:431). It is evident that Darwin accepted the strict working of what he called natural laws at the physiological level but was aware of chance (stochastic) processes at the organismic level.

The realization that neither essentialism nor determinism nor any other aspect of physicalism was a valid ideology was of the utmost importance for the further development of Darwin's thought. Darwin could have never adopted natural selection as a major theory, even after he had arrived at the principle on a largely empirical basis, if he had not rejected essentialism and physicalism. But there was one other impeding ideology Darwin had to refute in order to be able to adopt natural selection, and that was the finalistic or teleological worldview.

Final Causes

Again and again the statement has been made that "Darwin was no philosopher," even by an otherwise so perceptive author as G. G. Simpson (1964:50). In fact, Darwin was keenly interested in philosophy and, as we have seen, attempted to follow in his own writings the best advice of the philosophers of science of his day. Admittedly, he never published an essay or volume explicitly devoted to an exposition of his philosophical ideas, but in his scientific works he systematically demolished one after the other of the basic philosophical concepts of his time and replaced them with revolutionary new concepts.

In retrospect it is rather surprising to what an extent the contemporary philosophers who were involved with scientific ideas ignored Darwin or at least failed either to incorporate his concepts into their own systems or at least to try seriously to refute him adequately. This is as true for the British philosophers Herschel, Whewell, Mill, and Jevons, as well as for the various German philosophers and philosophical biologists, the followers of Kant, the later *Naturphilosophen,* the mechanoteleologists (Lenoir 1982), and the mechanists (DuBois-Reymond, Helmholtz, Sachs, Ludwig, Loeb). To a large extent these philosophers failed to recognize the importance of Darwin's ideas because of their commitment to the philosophies of essentialism and finalism.

From the days of the earliest philosophers it was widely believed that the world must have a purpose because, as Aristotle had said, "Nature does nothing in vain," and neither, a Christian would say, does God. Any change in this world, they would say, is due to final causes that move the particular object or phenomenon toward an ultimate goal. The development of an organism from the fertilized egg to the adult stage was frequently cited, from Aristotle on, as an illustration of this striving toward a goal.

It was almost universally believed that everything in nature, particularly all directional processes, moved in an analogous manner toward a predetermined end. Those who adhered to this view have been designated teleologists, or "finalists."

The thinkers of the Scientific Revolution in the sixteenth and seventeenth centuries were fascinated by motion. They worked out the laws of falling bodies and the motion of the planets around the sun; for them, the world was a world of motion controlled by eternal laws. God had instituted these laws at the time of creation, but from that point on laws kept the world moving. God was the final cause of everything, but He ruled the world through His laws and not by continuous intervention. René Descartes was one of the chief spokesmen for this strictly physicalist or mechanistic worldview, which was primarily that of the physicists. It was, however, more or less adopted even by the naturalist Buffon and carried to the most extreme consequences by Baron Holbach. Even those who adopted this concept of a mechanized world had certain misgivings about applying it to the living world. Buffon, for instance, was fully aware of the conflict between the mechanized world picture and many phenomena encountered in the study of organisms. Yet any alternative view was unacceptable to him.

Those who were dissatisfied with a strictly mechanistic world, entirely run by laws, developed a different explanatory framework. They credited God with a much larger role in designing the world down to the last detail and in effecting the changes that had taken place since creation. It was distasteful to them to remove God from the running of His world and to replace Him by the efficient causes of His laws. Not only that, but they also found it inconceivable that the observed harmony of nature and all the mutual adaptations of organisms to one another could be due simply to efficient causes. Their answer was to stress the elaborateness of the original design of the world to a far greater degree than had been done by the mechanists. No matter where you looked in nature, they claimed, you would find evidence for the infinite wisdom of the Creator. Anyone who would study His work (nature) was as legitimate a theologian as he who would study His word (the Bible). Beginning with John Ray (1691) and William Derham (1713), the study of nature became physicotheology or natural theology. It became the study of design.

Two further developments strengthened the belief in final causes. One was the increasingly strong belief that God had created the world for the sake of man. This was foreshadowed by Aristotle's statement (*Politics* 1, 8, 1256a, b), "Now if nature makes nothing incomplete and nothing in vain, the inference must be that she has made all animals for the sake of man." It was made legitimate by corresponding statements in Genesis. The other reinforcement of the belief in final causes came from manifold observations indicating ongoing changes in the world. This led to a new concept of creation. Creation was no longer seen as something that had happened instantaneously (or in six days), but as a gradual and slow process, directed by final causes, culminating in the production of man. Consistent with this modified concept of creation, G. W. Leibniz and J. G. Herder temporalized the *scala naturae,* which more and more was considered a scale of perfection. One of the foremost objectives of the writings of the physicotheologians was to demonstrate how perfectly everything in the world was designed. Since God could not have created anything that was not perfect, the world was considered the "best of all possible worlds." This was a dominant theme of that vast literature from Ray and Derham to William Paley and the Bridgewater Treatises. It dominated even Darwin's early thinking and certainly that of most of his contemporaries. Until evolution was accepted, there was no conceivable alternative to chance but "necessity," that is, God's design.

Much of the literature of natural theology is quite admirable. R. Boyle (1688), for instance, understood perfectly well that the explanation of the mechanical workings of a structure is an entirely independent endeavor from the explanation of the reason why the organ exists and what its role in the life of the organism is. Thus, he made quite clearly a distinction between proximate or immediate causations and ultimate causations. For instance, the proximate cause of sexual dimorphism in the plumage of birds is hormonal difference; the ultimate causation is sexual selection. Proximate causations could be explained mechanistically, by physical laws, but one could not explain ultimate causations without postulating a final goal or purpose (Lennox 1983).

Though the beginnings of natural theology go back to the Greeks and even the Egyptians, its period of true dominance, at least in England, lasted from the last quarter of the seventeenth century to 1859. It made little difference whether an author believed that everything in the world was governed by laws or was specifically regulated by God, because in either case God was either directly or indirectly responsible. He was the final cause of everything.

A belief in cosmic teleology fit well into the thinking of the seventeenth and eighteenth centuries. This was a period of increasing optimism, of emancipation from social and legal burdens, of conviction that better times were coming, possibly a millennium. Progress was preached not only by utopians and reformers but became the theme of philosophies, particularly of the historical-idealistic schools from Herder and Schelling to Hegel and Marx (Toulmin 1982). Nowhere else did teleology have as great an influence as in Germany. Almost all German philosophers, from Leibniz, Herder, and Kant to modern times, were teleologists to a greater or lesser extent. Kant, whose thought dominated German philosophy throughout the nineteenth century, was a teleologist (Löw 1980). As far as inanimate nature was concerned, he was a strict mechanist, but he considered all phenomena of living nature to be the product of teleological forces. Under Kant's influence, German biology in the first half of the nineteenth century was permeated with teleological thinking (Lenoir 1982). K. E. von Baer's comprehensive critique of Darwin was largely based on teleology, and so was that of the philosopher Eduard von Hartmann (1876). And the post-Darwinian teleological theory of orthogenesis had nowhere as many followers as in Germany.

Teleological thinking was strongly reinforced by the studies of the geologists and particularly by the discovery of successions of fossil faunas culminating in strata containing mammals and eventually man (Bowler 1976). It fit well with Lamarck's theory of gradual evolutionary change, this being the first genuine theory of evolution (1809). Not all progressionism in geology led to the acceptance of evolution; in fact, the majority of paleontologists from Cuvier to Agassiz thought, rather, in terms of catastrophes and subsequent more progressive new creations. Fewer and fewer authors continued to insist on the constancy of the world; most of them saw continuous change and indeed a trend toward perfection. This can be perceived in the writings of almost all authors between 1809 and 1859, even though it was expressed in various ways by authors like Meckel, Chambers, Owen, Bronn, von Baer, and Agassiz.

The general optimism of the eighteenth century received a severe jolt through the disastrous Lisbon earthquake of November 1, 1755. It induced Voltaire to satirize the Panglossian thinking of Alexander Pope and Leibniz in his *Candide*. David Hume also ridiculed claims of a harmony of nature: "Inspect a little more narrowly these living existences, the only beings worth regarding. How hostile and destructive; how insufficient all of them for their own happiness! How contemptible or odious to the spectator! The whole presents nothing but the idea of a blind nature." Kant likewise refuted the claims of natural theology. The unhappy consequences of the French Revolution contributed to the spreading of a deep pessimism. It is reflected in the thinking of Malthus and other demographers. No longer was the growth of human populations seen as one of the benefits bestowed on man by God. Rather, it was claimed that owing to limits imposed by the environment, such growth would inevitably lead to poverty, disaster, and death.

The more the studies of the naturalists progressed, the more often phenomena were found that contradicted the excellence of design. Not every organism could have been exclusively designed for its role in nature: how would this account for the existence of a limited number of well-defined types, such as mammals, birds, snakes, beetles, and so on? Rather, it was said, at the beginning relatively few archetypes were created and the laws of nature gave rise to the subsequent diversity, everything, however, had been contained in the plan of creation. Thus, indirectly, even in this thinking, diversity and adaptation were due to design (Bowler 1977).

But this revision of the design argument could not silence criticism. One asked: What is so wonderful about a parasite that tortures its victims and leads to their eventual death? Even worse, how could design be perfect if it leads to such widespread extinction, as documented by the fossil record? If the harmony of the living world, as described by natural theologians, is reflected by the mutual adaptation of organisms to one another and to their environment, and if these adaptations must be adjusted continuously to cope with the changes of the earth and with the restructuring of the faunas owing to extinction, what final causes could there be to govern all these ad hoc changes? If the environment changes, the organism has to readjust to it. But there is no necessary direction, no thought of necessary progress, and no reaching of any final goals. After evolutionary thinking had begun to spread, Matthias Schleiden (1842:61) insisted that although one can observe simple as well as complicated organisms, "it would be a totally misleading language if we would use for them the words imperfect and perfect, or lower and higher."

Natural theology, with its emphasis on design, had been virtually abandoned on the Continent by about 1800. But it continued to be strong in England, and all of Darwin's teachers and peers, particularly Sedgwick, Henslow, and Lyell, were confirmed natural theologians. This was Darwin's conceptual framework when he began to think about adaptation and the origin of species.

From Natural Theology to Natural Selection

There are many indications that when Darwin returned from the *Beagle* voyage he shared the beliefs of the natural theologians. He had wholly abandoned them, twenty-three years later, when he published the *Origin*. There is, however, not yet complete consensus in the Darwin literature under what influences and in what stages Darwin revised his interpretations. It was a peculiar period, since the British philosophers of science—Herschel, Whewell, and Mill—emphasized a rigorous scientific methodology and yet all firmly believed in final causes. They believed in laws, but God's guiding hand was needed because unguided laws would lead to random disorder (Ruse 1975b; 1979).

To what did the young Darwin attribute adaptation? Prior to 1838 his ideas on this point were rather vague. He seems to have attributed adaptation to certain laws, particularly the influence of the environment on the generative system. He still thought in terms of the design of the world. In his *Transmutation Notebooks* of this period, the most clearly teleological statement refers to dispersal: "When I show that islands would have no plants were it not for seeds being floated about,—I must state that the mechanism by which seeds are adapted for long transportation, seems to imply knowledge of whole world—if so doubtless part of system of great harmony" (*D:*74). Darwin's pre-1838 interpretation of evolutionary change depended on God's planning and was thus clearly a finalistic interpretation. For the Darwin of the *Transmutation Notebooks* (before September 1838), the seeming path of progression toward perfection was simply the result of certain laws that made such a development possible. All organic change, he thought, was an adaptive response to changes, however slight, in external conditions. These environmental influences induced the generative system to produce appropriate responses. This implied that God was directly involved in adaptation because only God could have made the generative system in such a way that changes in the environment would induce it to come up with an adequate response.

Yet, as Darwin's studies proceeded he discovered one phenomenon after the other that cast doubt on the perfection of adaptations (Ospovat 1981). First, he discovered all sorts of evidence for descent (called "propagation" or progression in Darwin's earlier notes), which served as a definite constraint on the absoluteness of adaptation. Then came the consideration of rudimentary or vestigial organs, which also contradicted perfect adaptation, as did the widespread occurrence of extinction. Those natural theologians, and there were others beside Darwin, who saw such inconsistencies and seeming incompatibilities with the concept of a total harmony of nature ascribed the deviations from perfect adaptation to a conflict between various laws instituted by the Creator. Organisms, said these authors, were only as perfect as is possible within the limits set by the necessity of conforming to these laws. There are, for instance, different laws required to explain the facts of structure, distribution, and succession.

Somehow such a direct reliance on eternal God-given laws for the explanation of natural phenomena must have been unsatisfactory to Darwin and in conflict with some part of his major philosophical framework. This must be the reason why he abandoned this type of thinking so speedily after he read Malthus and formulated his theory of natural selection on September 18, 1838. Natural selection gave him a purely mechanistic explanation for adaptation and for evolutionary progression. As Darwin stated in his *Autobiography* (1958:87): "The old argument of design in nature, as given by Paley, which formerly seemed to me so conclusive, fails, now that the law of natural selection has been discovered. We can no longer argue that, for instance, the beautiful hinge of bivalve shell must have been made by an intelligent being, like the hinge of a door by man. There seems to be no more design in the variability of organic beings and in the action of natural selection, than in the course which the wind blows."

After 1838 Darwin at first remained enough of a natural theologian to believe that natural selection could give him perfect adaptation. But, he abandoned this belief by the 1850s, and the *Origin* is remarkably free of any teleological language (Ospovat 1981). To be sure, the word "progress" is used ten times in this volume but almost always as a term to describe a passing of time. Only in connection with the replacement of fossil faunas of which each one seems to be "higher" than the one it has replaced does Darwin speak of a process of improvement; but he adds, "I can see no way of testing this sort of progress" (1859: 337). However, Darwin points out that there are differences in competitive ability even among living faunas. British faunal elements introduced to New Zealand are highly successful, while he doubts the reverse would be true. "Under this point of view," says Darwin, "the productions of Great Britain may be said to be higher than those of New Zealand." Yet this is not a teleological argument. The greater competitive ability of the faunal elements of Great Britain was not due to any built-in drive or final cause but simply due to the fact that the British fauna had passed through a more severe struggle for existence.

Nevertheless, the concepts of "perfect" and "perfection" continued to be popular with Darwin. In the *Origin* he used the word "perfect" 77 times, "perfected" 19 times, and "perfection" 27 times. What is remarkable, however, in these uses is how carefully Darwin makes a distinction between the product of selection and the process of perfecting. We look to his explanations in vain for a drive or tendency toward perfection. Invariably Darwin emphasizes that selection carries the evolutionary line to ever-greater perfection. This is particularly well-stated in the section of Chapter 6 with the heading "Organs of Extreme Perfection and Complication" (p. 186) which, among others, contains Darwin's well-known discussion of the evolution of eyes through natural selection. Since natural selection is not a finalistic process, Darwin now sees quite clearly that "natural selection will not necessarily produce absolute perfection; nor as far as we can judge from our limited faculties, can absolute perfection be everywhere found" (p. 206). Complete perfection, of course, is not needed, because "natural selection tends only to make each organic being as perfect as, or slightly more perfect than, the other inhabitants of the same country with which it has to struggle for existence. And we see that this is the degree of perfection attained under nature" (p. 201). There is not even a trace of a suggestion of any final cause, because perfection is simply the product of the *a posterior* process of natural selection. With the world and its biota constantly changing, perfect creation in the beginning would have been futile. "Almost every part of every organic being is so beautifully related to its complex condition of life that it seems as improbable that any part should have been suddenly produced perfect, as that a complex machine should have been invented by man in a perfect state" (*Origin,* 6th ed., pp. 58–59).

Darwin's subsequent correspondence with the American botanist Asa Gray permits us to analyze his thought even a little further. Gray, even though a rather strict creationist, accepted the importance and guiding capacity of natural selection. However, "Natural selection is not the wind which propels the vessel, but the rudder which, by friction, now on this side and now on that shapes the course" (Moore 1979:316). Variation—the wind in Gray's metaphor—was guided for Asa Gray by a divine hand. This possibility was emphatically rejected by Darwin and induced him to state his ideas, rather evidently as a direct answer to Gray, in *The Variation of Animals and Plants* (1868 II:432). Gray, however, failed to understand Darwin's argument and went even so far as to praise "Darwin's great service to natural science in bringing back to it teleology" (Gray 1876:237).

In his later years, particularly in letters to his numerous correspondents, Darwin was sometimes rather careless in his language. For instance, he referred to "the extreme difficulty or rather impossibility of conceiving this immense and wonderful universe, including man with his capacity of looking far backwards and far into futurity, as the result of blind chance or necessity." How could he have said this when the theory of natural selection had given him exactly the means to escape from the alternatives chance *or* necessity? On another occasion he said, "The mind refuses to look at this universe, being what it is, without having been designed." It is not surprising therefore that Darwin was misclassified by a number of authors who did not understand the working of natural selection. Kölliker, for instance, accused Darwin of being "in the fullest sense of the word a teleologist." And even T. H. Huxley when defending Darwin was driven to distinguish between "the teleology of Paley and the teleology of evolution" (Moore 1979:264).

Darwin was not totally alone in his rejection of finalism. Ernst

Haeckel declared emphatically that "the causes of all phenomena of nature . . . are purely mechanically acting causes, never final, the goal-directed causes" (1866 2:150). The most articulate among Darwin's supporters was August Weismann, who took up the battle for natural selection again and again and refuted the theories of Darwin's opponents (see Chapter 8). The voices of Haeckel, Weismann, F. Müller, and Darwin's naturalist friends were, however, merely cries in the wilderness, for the opposition to the mechanistic process of natural selection was almost universal. But none of his opponents truly understood natural selection, and this misunderstanding was to a large extent due to a long-standing ideological commitment to finalism. The opposition to natural selection continued up to the evolutionary synthesis and with it an open or unspoken support of finalism. For example, the geneticist T. H. Morgan, who showed his lack of understanding of natural selection even in his last book on evolution in 1932, claimed in 1910 that finalism had entered biology through natural selection because "by picking out the new variation . . . purpose enters in as a factor, for selection had an end in view," completely ignoring the randomness of variation and the statistical nature of the selection process.

Finalism as an Alternative to Natural Selection

Numerous attempts were made in the years after 1859 to replace Darwin's theory of natural selection with a superior way of achieving adaptation. The best-known of these theories are usually classified under the headings neo-Lamarckism (inheritance of acquired characters), orthogenesis (an intrinsic perfecting principle), and saltation. They all incorporated some finalistic components to a lesser or greater extent. It is not easy to report on these theories for a number of reasons. Not only are the descriptions of the postulated mechanism by which the changes are achieved usually quite vague, but the same author may support first one and then the other of these theories, or a mixture of them (Kellogg 1907; Bowler 1983, 1988). Even after the Paleyan concept of an ad hoc design of every—even the slightest—adaptation had lost all credibility, there remained a concept of a universal design of organic progression, an evolutionary reinterpretation of the temporalized scale of nature (Bowler 1977). Such a concept seemed, at first, to have a sound observational foundation. Considering that variation is random, as Darwin postulated, and considering that the number of environmental constellations is quite unlimited, one would expect a totally chaotic network of evolutionary phenomena. What one actually finds is the existence of a limited number of well-defined lineages and the possibility of arranging organisms into progressive series. This was described not only by paleontologists but also by students of living organisms, be they butterflies (Theodor Eimer) or birds (Charles O. Whitman). Variation evidently was not random but followed well-defined pathways of change. Such evolutionary trends were ascribed to an intrinsic, direction-giving force, called orthogenesis. It was described as a perfecting principle or (in German) *Vervollkommnungstrieb*.

The intrinsic nature of this force seemed to be confirmed by the fact that it was possible to establish rectilinear series not only for characters that might have been advanced by natural selection, such as increasing precision of mimicry patterns or phyletic increases in body size, but also for nonutilitarian or seemingly deleterious characters. This was an argument made particularly emphatically by Eimer (Bowler 1979). Most proposals of orthogenesis were made in strict opposition to and as alternatives to natural selection.

However, there was a group of Christian Darwinians for whom natural selection was "evidence of a directing agency and of a presiding mind" (Moore 1979). They either thought that variation as such was directive, supplying just the right material to selection, or they considered the selecting process as purposive. Clearly for them natural selection was a teleological process.

Even such an ultra-mechanist as Julius Sachs (1894) adopted Carl Naegeli's perfecting principle as the agent of all major evolutionary developments, with natural selection merely being able to improve fine-grained adaptation. Kölliker (1864) was another adherent to an autogenetic theory ascribing all evolutionary progress to "intrinsic causes," and like Naegeli he stimulated Weismann to a reply.

Evolutionary Progress without Final Causes

For some Darwinians the concept of evolutionary progress seems to have raised some embarrassing questions. How can a strictly opportunistic competitive struggle lead to progress? Darwin himself occasionally seems to have had such doubts, and they are reflected in his comment, "Never use the words higher or lower," written on the margin of his copy of the *Vestiges*. Others who also questioned progress pointed to the continued existence of the archaebacteria and other prokaryotes, to the great flourishing of the protists and lower fungi up to the present, to the parasites, and to the inhabitants of caves. None of these can be called progressive, in the sense of "higher," and yet they continue to exist and flourish. So, it was said, evolution is simply a process of specialization. And yet, who can deny that overall there is an advance from the prokaryotes that dominated the living world more than three billion years ago to the eukaryotes, with their well-organized nucleus and chromosomes as well as cytoplasmic organelles; from the single-celled eukaryotes to plants and animals with a strict division of labor among their highly specialized organ systems; and, within the animals, from ectotherms that are at the mercy of climate to the warm-blooded endotherms; and, within the endotherms, from types with a small brain and low social organization to those with a very large central nervous system, highly developed parental care, and the capacity to transmit information from generation to generation?

Attempts to define progress have been many. For Lamarck, for instance, and for many nineteenth-century authors man was clearly the most perfect organism, and all forms of life were arranged in a single column on the basis of their assumed progress toward manhood. Now we know that diversification is the most characteristic attribute of evolution and that life not only very early split within the prokaryotes into eubacteria and archaebacteria, but the eukaryotes after their origin quickly gave rise to the protists, and to the kingdoms of fungi, plants, and animals. Literally thousands of distinct phyletic lines developed within each of these kingdoms, most of them not in the slightest tending toward the characteristics of man. Neither can the dominance of a group on earth be considered the criterion of progress. On that basis the vascular plants would have to be considered more dominant than man and even the insects. And man's ancestors until less than ten thousand years ago were anything but dominant on earth.

Structural complexity is sometimes mentioned as a sign of progress, but trilobites and placoderms would seem to have been more complex in structure and perhaps more specialized than modern man. Huxley (1942) considered emancipation from the environment an important index of progressiveness, and in that criterion man certainly ranks higher than any other organism. However, is independence from the environment truly an index of progressiveness?

When discussing evolutionary progress one seems to be quite unable, since one is a member of the human species, to get away from criteria that would give man supremacy. However, there are two criteria of progressiveness that would seem to have a considerable amount of objective validity. One of these is parental care (promoted by internal fertilization), which provides the potential for transferring information nongenetically from one generation to the next. And the possession of such information is of course of considerable value in the struggle for existence. This information transfer generates at the same time a selection pressure in favor of an improved storage system for such remembered information, that is, an enlarged central nervous system. And, of course, the combination of postnatal care and an enlarged central nervous system is the basis of culture, which together with speech, sets humans quite aside from all other living organisms. However, even if we would designate the acquisition of these capacities as evidence for evolutionary progress, it would not strengthen the case for final causes, since these developments were clearly achieved through natural selection.

Whether one is looking at the highest mammals and birds, the social insects, the orchids, or giant trees, it has seemed inconceivable to some students of evolution that the slow struggle for existence among individuals of a species could account for the enormous evolutionary progress observed in so many phyletic lines. To see all evolution simply as the result of competition among the individuals in a population is indeed simplistic, because superimposed on this individual selection is a process traditionally referred to as species selection, although perhaps a better term would be species replacement or species succession. An individual organism competes not only with members of its own species but struggles for existence also against members of other species. And this process is probably the greatest source of evolutionary progress. Each newly formed species, if it is evolutionarily successful, must represent, in some way, evolutionary progress. Darwin explained this as follows: "But in one particular sense the more recent forms must, on my theory, be higher than the more ancient; for each new species is formed [that is, has become successful] by having had some advantage in the struggle for life over other and preceding forms" (1859: 337). When the competition among individuals of different species leads to or at least contributes to the extinction of one of the competing species, it is a case of species replacement. That competition among species could lead to the extinction of one of the competitors was of course already known to Lyell and other pre-evolutionary authors.

A new species will be successful in the struggle for existence over a previously existing species only if it has made some, even the smallest, evolutionary invention. This might be an improvement in its digestive physiology or its nervous system or its life-style or any other of the countless ways by which the so-called "higher" organisms differ from the lower ones. Thus, the Darwinian mechanisms of variation and selection, of speciation and extinction, are fully capable of explaining all macroevolutionary developments, whether specializations, improvements, or other innovations. And none of this requires any finalistic agent.

Close study of evolutionary progress shows that its characteristics are not compatible with what one would expect from a process guided by final causes. Progressive changes in the history of life are neither predictable nor goal-directed. The observed advances are haphazard and highly diverse. It is always uncertain whether newly acquired adaptations are of permanent value. Who at the beginning of the Cretaceous would have predicted the total extinction by the end of the period of that flourishing taxon the dinosaurs? Episodes of stasis alternate with episodes of precipitous evolutionary change. Evolutionary trends are rarely rectilinear for any length of time, and when such rectilinearity occurs it can usually be shown to be due to built-in constraints.

All the evolutionary phenomena and aspects of evolutionary progress that were considered as irrefutable proof of teleology by earlier generations can now be shown to be entirely consistent with natural selection. Phenomena that are due to a chain of historical events cannot be ascribed to simple laws and can therefore not be proven in the same way as can phenomena studied in the physical sciences. However, they can be shown to be consistent with the findings of genetics and with the theory of natural selection in its modern sophisticated form. No one has refuted the finalistic thesis of evolution more convincingly than Simpson (1949; 1974). He pointed out that each evolutionary line goes its own way, and evolutionary progress can be defined only in terms of that particular lineage. Nothing seemed more progressive in the geological past than the ammonites and the dinosaurs, and yet both taxa became extinct. On the other hand many evolutionary lines have displayed no evidence of progress in hundreds or thousands of millions of years, and yet they have survived to the present day, as the archaebacteria and other prokaryotes. Progress thus is not at all a universal aspect of evolution, as it ought to be if evolution were generated by final causes.

The Decline, if not Demise, of Finalism

By the time of the evolutionary synthesis of the 1940s (see Chapter 9), virtually no evolutionary biologist, in fact no competent biologist, was left who still believed in any final causation of evolution. The few biologists who still did so either had theological commitments, like Teilhard de Chardin, or were unaware of the developments of biology in the twentieth century, like Comte de Nouy.

Final causes, however, are far more plausible and pleasing to a layperson than the haphazard and opportunistic process of natural selection. For this reason, a belief in final causes has had a far greater hold outside of than within biology. Almost all philosophers, for instance, who wrote on evolutionary change in the one hundred years after 1859 were confirmed finalists, from Whewell, Herschel, and Mill to Henri Bergson in France, who postulated a metaphysical force, *élan vital,* which, even though he disclaimed its finalistic nature, could not have been anything except a final cause, considering its effects. Whitehead, Polanyi, and many lesser philosophers were also finalistic. Throughout this period there have been exceptions, the most noteworthy perhaps being the German philosopher Sigwart, who as early as 1881 provided a remarkably modern treatment of the problems of teleology.

Modern philosophers—that is, those who have published since the evolutionary synthesis—have, on the whole, refrained from invoking final causes when discussing evolutionary progress. Apparently they fully accept the explanation provided by the evolutionary synthesis. When they do discuss teleology, like Morton Beckner or Ernest Nagel, they deal with adaptation and with "teleological systems." Finalism is no longer part of any respectable philosophy. One last vigorous attack on finalism was Monod's book *Chance and Necessity* (1970). But Monod failed to understand the explanatory power of natural selection and opted for pure chance as having been responsible for the phenomena of nature. Such Epicureanism, however, is only rarely encountered in modern times.

The reason why the controversy about the validity of teleological thinking has been so indecisive has finally become evident in recent years: the designation "teleological" has been applied to four quite different natural phenomena. Three of these can be explained by science, while the fourth one, an explanatory postulate for certain phenomena, has not been substantiated.

(1) Many seemingly end-directed processes or movements in inorganic nature are the simple consequences of natural laws. The falling of a stone (due to gravity) or the cooling of heated pieces of metal (owing to the second law of thermodynamics) are examples of such *teleomatic* processes, as such law-directed processes are called.

(2) Processes in living organisms—as well as their behavior—that owe their goal-directedness to the operation of an inborn or acquired program are called *teleonomic*. This includes all changes in ontogenetic development as well as end-directed behavioral activities. Such processes can be analyzed strictly scientifically, since the end-point or goal is already contained in the program.

(3) Adapted systems, like the heart, which pumps blood, or the kidneys, which eliminate by-products of protein metabolism, and which seem to work toward a goal have also been called teleological. An organism has hundreds, if not thousands, of such adapted systems, from the molecular level up to the organism as a whole, all of them acquired during the evolution of its ancestors and continuously fine-tuned by natural selection. These systems have the capacity for teleonomic behavior, but, being stationary, are not themselves goal-seeking.

(4) From the Greeks on, there was a widespread belief that everything in nature and its processes has a purpose, a predetermined goal. And these processes would lead the world to ever-greater perfection. Such a teleological worldview was held by many of the great philosophers. Modern science, however, has been unable to substantiate the existence of such a *cosmic teleology*. Nor have any mechanisms or laws been found that would permit the functioning of such a teleology. The conclusion of science has been that final causes of this type do not exist.

CHAPTER SIX

Darwin's Path to the Theory of Natural Selection

WHEN WE SPEAK of Darwinism today, we mean evolution by natural selection. The meaning of natural selection, its limits, and the processes by which it achieves its effects are now the most active areas of evolutionary research.

The fifth one of Darwin's great evolutionary theories was his most daring, most novel. It dealt with the *mechanism* of evolutionary change and, more particularly, how this mechanism could account for the seeming harmony and adaptation of the organic world. It attempted to provide a natural explanation in place of the supernatural one of natural theology. In that respect Darwin's theory was unique; there was nothing like it in the whole philosophical literature from the pre-Socratics to Descartes, Leibniz, or Kant. It replaced teleology in nature with an essentially mechanical explanation.

To judge from his writings, Darwin had a much simpler concept of natural selection than the modern evolutionist does. For him there was a steady production of individuals, generation after generation, some of whom were "superior" in having a reproductive advantage. For Darwin selection was essentially a single-step process, the conveying of reproductive success. The modern evolutionist agrees with Darwin that the individual is the target of selection; but we now also realize that natural selection is actually a two-step process, the first one consisting of the production of genetically different individuals (variation), while the survival and reproductive success of these individuals is determined in the second step, the actual selection process. Although I have called the theory of natural selection Darwin's fifth theory, it is actually itself a small package of theories. This includes the theory of the perpetual existence of a reproductive surplus, the theory of a continuing availability of great genetic variability, the theory of the heritability of individual differences, the theory that mere reproductive superiority is selected for (sexual selection), and several others.

The question concerning the conceptual sources of Darwin's theory of natural selection is still highly controversial. A favorite interpretation among historians has always been that it was a manifestation of the thinking of upper-class England in the first half of the nineteenth century (consistent with empiricism, mercantilism, industrial revolution, poor laws, and so forth). Darwin's admission that reading Malthus had given him the crucial insight seemed to provide a powerful confirmation of this "external causation." The evolutionists, by contrast, have favored an interpretation based on "internal causation," relying on Darwin's insistence that his familiarity with the practices of the animal breeders had provided him with the decisive evidence. The rediscovery of Darwin's notebooks covering the one and a half years prior to the date of his "conversion" has provided us with a great amount of new information, but—although narrowing down our options—it still permits conflicting interpretations. What I present here is anything but the last word in a still-ongoing controversy. It will require further research before the remaining disagreements can be removed (Hodge and Kohn 1985).

Darwin had returned to England from the voyage of the *Beagle* in October 1836. While working on his bird collections, and particularly through discussions with the ornithologist John Gould, Darwin became an evolutionist, apparently in March 1837 (Sulloway 1982b). Certainly by July 1837 he had firmly accepted evolution by common descent. His new interpretation of the world consisted not only in replacing a static or steady-state world by an evolving one but also, and more important, in depriving man of his unique position in the universe and placing him into the stream of animal evolution. Darwin, after this date, never questioned the fact of evolution, even though he continued for another twenty years to collect supporting evidence. Yet, the causes of evolution were at first a complete mystery to him.

For a year and a half Darwin speculated incessantly, developing and then again rejecting one theory after the other (Kohn 1975), until he finally had a decisive illumination on September 28, 1838. In his autobiography he describes it as follows (Darwin 1958: 120):

> Fifteen months after I had begun my systematic enquiry, I happened to read for amusement Malthus on Population, and being well prepared to appreciate the struggle for existence which everywhere goes on, from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favorable variations would tend to be preserved, and unfavorable ones to be destroyed. The result of this would be the formation of new species. Here, then, I had at last got a theory by which to work.

It was the theory later called by Darwin the theory of natural selection. It was a most daring innovation, since it proposed to explain by natural causes, mechanically, all the wonderful adaptations of living nature hitherto attributed to "design."

Darwin makes it sound as though the concept of natural selection was simplicity itself. But his memory deceived him. His autobiography was written almost forty years later (in 1876), largely for the benefit of his grandchildren, and was replete with characteristically Victorian self-denigrations. Darwin had forgotten what a complex shift in four or five major concepts had been required to arrive at the new theory. He probably never fully realized himself how unprecedented his new concept was and how totally opposed to many traditional assumptions.

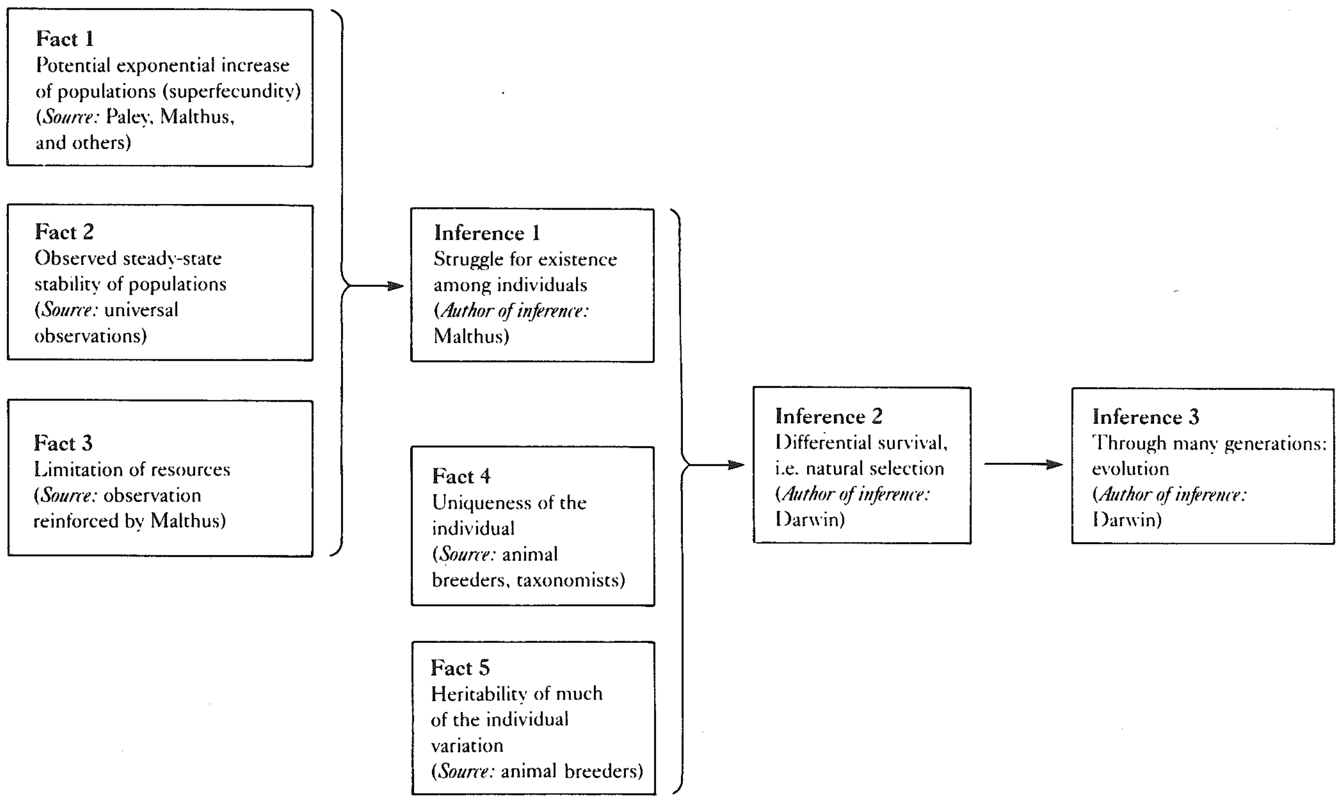
Indeed, the concept of natural selection was so strange to Darwin's contemporaries when he proposed it in the *Origin of Species* that only a handful adopted it. Nearly three generations passed before it became universally accepted even among biologists. Among nonbiologists the idea is still unpopular, and even those who pay lip service to it often reveal by their comments that they do not fully understand the working of natural selection. Only when one is aware of the complete unorthodoxy of this idea can one appreciate Darwin's revolutionary intellectual achievement. And this poses a powerful riddle: How could Darwin have arrived at an idea which not only was totally at variance with the thinking of his own time but was so complex that even now, one and a half centuries later, it is widely misunderstood in spite of our vastly greater understanding of the processes of variation and inheritance?

Darwin's own version (in his autobiography) was that contemplation of the success of animal breeders in producing new breeds had provided him with the clue for the mechanism of evolution and was thus the basis for his theory of natural selection. We know that this is a vast oversimplification—a revision of our thinking which we owe to the rediscovery of Darwin's notebooks. In July 1837 he had started to write down all the facts as well as his own thoughts and speculations "which bore in any way on the variation of animals and plants under domestication and [in] nature." Even though he later cut out occasional pages, to use them for his book manuscripts, Darwin never discarded these notebooks, and they were rediscovered in the 1950s among the Darwin papers at the Cambridge University Library (Barrett et al. 1987). Darwin's day-by-day records throw an entirely new light on the development and the changes in his thought during the period from July 1873 to September 28, 1838, when the theory of natural selection was conceived.

One fact, the importance of which has not been reduced by the recent discoveries, is the impact of Darwin's reading of Malthus. The interpretation of the Malthus episode, however, has become the subject of considerable controversy among the Darwin scholars. According to some of them—de Beer (1961) and S. Smith (1960), and, to a lesser extent, Gruber (1974) and myself—it was merely the culmination in the gradual development of Darwin's thinking, a little nudge that pushed Darwin across a threshold he had already reached. According to others—Limoges (1970) and

FIGURE I

Darwin's Explanatory Model of Evolution through Natural Selection



Kohn (1980), for example—it constituted a rather drastic break, almost equivalent to a religious conversion. Which of these two interpretations is nearer to the truth?

There are essentially two methods by which we can try to find an answer. Either we can attempt to analyze all the entries in the notebooks, in a chronological sequence, or we can try to reconstruct Darwin's explanatory model of natural selection and then study separately the history of each of its individual components. My own choice is in favor of the second method, placed in a chronological framework, although both methods are necessary for a full understanding. The first method attempts to reconstruct the trials and errors of Darwin's gradual approach, as reflected in successive entries in the notebooks. It also examines tentative ideas that he later rejected. Gruber, Kohn, and, in part, Limoges have favored this method.

Darwin's Explanatory Model

What were the components of Darwin's explanatory model? For my analysis I have found it most convenient to recognize five facts and three inferences (see Figure 1). I shall attempt to determine, first, at what time Darwin became aware of these five facts, then at what time he made the three inferences, and whether or not these inferences had already been made previously and could be found in the literature.

The five facts were already widely known before the Malthus episode, not only to Darwin but to his contemporaries, only a single one of whom, A. R. Wallace, used them in exactly the same way as Darwin. Merely having these facts obviously was not enough. They had to be related to one another in a meaningful manner; that is, they had to be placed in an appropriate conceptual background. In other words, Darwin had to be intellectually prepared to see the connections among these facts.

This leads us to the most interesting but also the most difficult question: What had been going on in Darwin's mind in the one and a half years prior to the Malthus episode? All the indications are that it was a period of unprecedented intellectual activity in Darwin's life. Precisely what the changes in Darwin's thinking were and how they were connected with one another has not yet been investigated nearly as fully as it deserves. Gruber and Kohn have examined this problem more carefully than anyone else, but the Darwin correspondence of that period and other manuscript materials that have not yet been thoroughly analyzed are bound to provide new insights. My own tentative conclusions may, therefore, turn out to be incorrect. However, my reading suggests to me that Darwin's beliefs changed moderately or drastically in four areas, which I shall simply list here and then discuss in the context of Darwin's model.

(1) The gradual replacement of the assumption that all individuals of a species are essentially alike by the concept of the uniqueness of every individual. As discussed previously, the belief that the observed variability of phenomena reflects a limited number of constant, discontinuous essences was gradually replaced by population thinking, a belief in the reality of variation within a population and in the importance of these individual differences. Most of Darwin's earlier statements on species and varieties were strictly typological. It is my impression that they became more populational as Darwin delved deeper into the literature of the animal breeders and also later as a result of his work on the barnacles (Ghiselin 1969).

(2) A shift from soft toward hard inheritance. In his earlier statements Darwin seemed to assume that most, if not all, inheritance was "soft." He assumed that the material basis of inheritance is not unchangeably constant but can be modified by use and disuse, by physiological activities of the body, by a direct influence of the environment on the genetic material, or by an inherent tendency to progress toward perfection, and that these environmentally induced changes could be passed along to the next generation. This theory is called the inheritance of acquired characters. The growth of his population thinking, with its increasing stress on genetic differences among individuals, indicates a growing awareness of the need to postulate "hard" inheritance—that

is, inheritance that is not affected directly by environmental factors.

(3) A changing attitude toward the balance of nature. Darwin began to believe that the balance of nature is dynamic rather than static, and he began to ask whether the balance is maintained by benign adjustments or by constant war.

(4) A gradual loss of his Christian faith. Darwin lost his faith in the years 1836–1839, much of it clearly prior to the reading of Malthus. In order not to hurt the feelings of his friends and of his wife, Darwin often used deistic language in his publications, but much in his notebooks indicates that by this time he had become a "materialist" (more or less equivalent to an atheist; see Chapter 2).

These four changes in Darwin's thinking are to some extent interconnected. Since they were largely unconscious, they are usually reflected in Darwin's notebooks only in subtle changes of wording, and there is considerable leeway in possible interpretation. However, keeping these four points in mind will sharpen our awareness of possible changes in Darwin's thinking in the years prior to reading Malthus, while we make a point-by-point analysis of Darwin's explanatory model.

The Struggle for Existence

When recording his reaction to reading Malthus, Darwin makes it quite clear that it was not Malthus's general attitude that had acted as a catalyst on his thoughts but one particular sentence, for he says that "yet until the one sentence of Malthus no-one clearly perceived the great check amongst men" (D:135). De Beer (1963:99) succeeded in determining what Malthus's crucial sentence was: "It may safely be pronounced, therefore, that the population, when unchecked, goes on doubling itself every twenty-five years, or increases in a geometrical ratio." From then on, Darwin stressed that it was Malthus's demonstration of the exponential increase of populations that was decisive in his discovery of the importance of natural selection (Fact I).

Yet there is a puzzling difficulty. Why did it take Darwin so long to recognize the evolutionary significance of the Malthusian principle? The prodigious fertility of animals and plants had been pointed out by many of Darwin's favorite and most frequently read authors, like Erasmus Darwin, Charles Lyell, Alexander von Humboldt, and William Paley. Furthermore, Malthus's principle was widely discussed in the essay literature of the period. Why then did this suddenly impress Darwin so profoundly on September 28, 1838?

Four reasons might be suggested—the first one being, as pointed out by Gruber (1974), that Darwin had learned on the three preceding days (between September 25 and 27) of the unbelievable fertility of protozoans by reading Ehrenberg's work on the subject. This quite likely primed Darwin's receptivity for Malthus's thesis. The second reason is that when Malthus applied the principle to man, a species with relatively few offspring, Darwin suddenly realized that a potentially exponential increase of a population was entirely independent of the actual number of offspring of a given pair. The third reason is that the Malthus episode came at a time when population thinking had begun to mature in Darwin's mind. The fourth reason, suggested by Ruse (1979: 175), is that the numerical formulation suggested by Malthus seemed to satisfy the mathematical requirements of such Newtonians as Herschel.

The second fact in Figure 1—population stability—was not in the slightest bit controversial. No one questioned that the number of species and, aside from temporary fluctuations, the number of individuals in every species maintained a steady-state stability. This is implicit in the concept of plenitude of the Leibnizians and in the harmony-of-nature concept of the natural theologians. If there is an extinction, it is balanced by speciation, and if there is high fertility it must be counterbalanced by mortality. In the end everything adds up to a steady-state stability.

The third fact—limitation of resources—again was not at all controversial, being very much part of the balance-of-nature concept of natural theology, so dominant in England in the first half of the nineteenth century.

Darwin's first great inference, derived from these three facts, was that exponential population growth combined with a fixed amount of resources would result in a fierce struggle for existence. We must ask if this inference was original with Darwin, and if so, what part of it did he owe to Malthus? This is perhaps the most controversial question raised by the analysis of the selection theory. The main difficulty is that the term "struggle for existence" and similar synonymous terms were used in different senses by different authors.

Before we can analyze them, we must deal with one other concept, the idea of a perfect balance of nature, an idea prevalent in the eighteenth century: nothing in nature is too much, nothing too little, everything is designed to fit with everything else. Rabbits and hares have lots of young because food must be available for foxes and other carnivores. The whole economy of nature forms a harmonious whole that can in no way be disturbed. This is why Lamarck, who was very much an adherent of this concept, could not conceive of extinction. Cuvier likewise had adopted the idea of perfect balance, as shown in correspondence with his friend Pfaff. He transferred the same concept to the structure of an organism, which he visualized as a "harmonious type" in which nothing could be changed. Everything in such a complex system is so perfect that any change would lead to deterioration.

This type of thinking was still dominant in Darwin's day, not only among the natural theologians of England but also on the Continent. Indeed, one can find a number of entries in Darwin's notebooks that seem to reflect this kind of thinking. But was Darwin still a wholehearted supporter of the concept of a harmonious balance of a benign nature? This is a very important question because it affects the interpretation of what Darwin understood under the term "struggle for existence."

For us moderns the term means a fierce fight with no holds barred. But for the natural theologians the struggle for existence was a beneficial feedback device, the function of which was to maintain the balance of nature. It is, as Herder (1784) called it, "the balance of forces which brings peace to the creation." Linnaeus (1781) devoted an entire essay to the "Police of Nature" and emphasized that "those laws of nature by which the number of species in the natural kingdoms is preserved undestroyed, and their relative proportions kept in proper bounds are objects extremely worthy of our attentive pursuit and researches." Lamarck expressed similar sentiments.

Was this benign interpretation of the struggle for existence unanimous? Unfortunately, even today we have no reliable analysis that would give us an answer to this question. My impression is, however, that as the interaction of predators and prey, of parasites and their victims, the frequency of extinction, and the struggles of competing species became better known, the struggle for existence was more and more recognized as a "war" or fight, a struggle for survival, "red in tooth and claw" as Tennyson later expressed it. Bonnet (1781) and de Candolle (1820) emphasized that this war among species consisted not merely of predator–prey relationships but of competition for any and all resources. However, it was not at all appreciated how fierce this struggle is, and Darwin admits that "even the energetic language of de Candolle does not convey the warring of the species as [convincingly as does the] inference from Malthus."

Nevertheless, it is highly probable that Darwin had been gradually conditioned by his reading to a far less benign interpretation of the struggle for existence than that held by the natural theologians. The mere fact that Darwin had adopted evolution must have made him aware of the frequency of extinction and of the unbalances and adaptational lags caused by evolutionary changes. From Aristotle to the natural theologians it was considered axiomatic that a belief in a harmonious universe and perfect adaptation in nature, or in a Creator continuously active in correcting imperfections and imbalances, was incompatible with a belief in evolution. By necessity, accepting evolutionary thinking undermined a continued adherence to a belief in a harmonious universe.

Struggle among Species or Individuals?

Of far greater importance is a second question: Between whom does the struggle for existence take place? This question allows two drastically different answers. In the entire essentialistic literature the struggle is considered to take place among species. The balance of nature is maintained by this struggle, even if it occasionally causes the extinction of a species. This is the interpretation of the struggle for existence in the literature of natural theology, up to de Candolle and Lyell, and is the major emphasis of Darwin's notebooks up to the Malthus reading. The main function of this struggle is to correct disturbances in the balance of nature, but it can never lead to changes; on the contrary, it is a device to preserve a steady-state condition. As such it continued even after 1838 to be an important component of Darwin's thinking, particularly in his biogeographic discussions (such as determination of species borders).

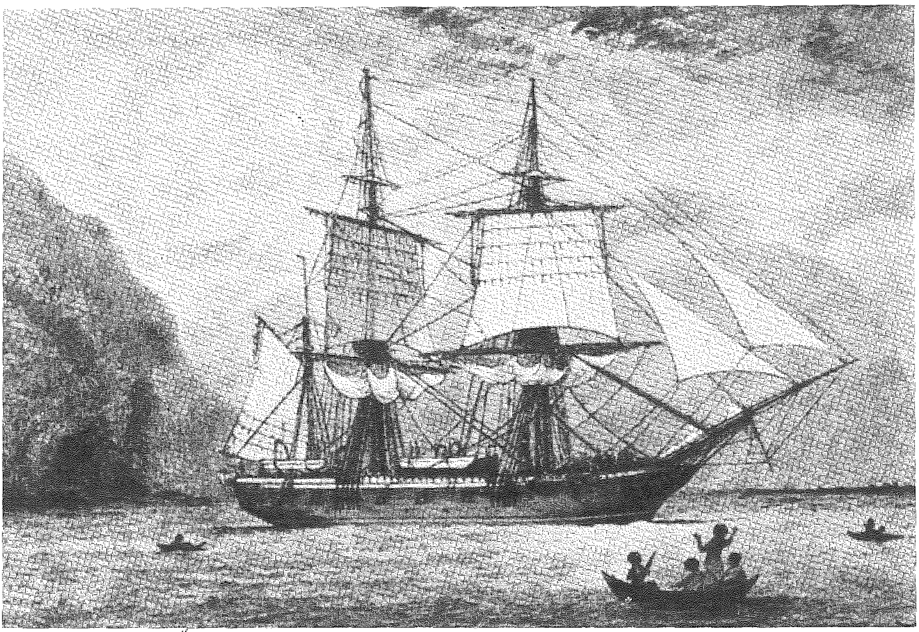
Only when one applies population thinking to the struggle for existence can one make the crucial conceptual shift to recognizing a struggle for existence among individuals of a single population. This, as Herbert (1971) was the first to recognize clearly, was Darwin's decisive new insight resulting from his reading of Malthus, although Mayr (1959b) and Ghiselin (1969) had previously pointed out the populational nature of selection. If most individuals of every species are unsuccessful in every generation, then there must be a colossal competitive struggle for existence among them. It was this conclusion that made Darwin think at once of various other facts that had been slumbering in his subconscious but for which, up to that moment, he had had no use.

Darwin's reading of Malthus was dramatic and climactic, and it does not matter whether one interprets it as a complete reversal of Darwin's thinking or whether one believes that "the evidence suggests that the change in choice of unit was a protracted process, stretched over a year or more, and linked to other aspects of his thought" (Gruber 1974). I myself hold with the latter view, because the capacity to be able to interpret the Malthus statement on exponential growth of populations and to apply it to individuals requires population thinking, and this Darwin had been gradually acquiring during the preceding year and a half. That everything came to a dramatic climax on September 28, 1838, however, is beyond question.

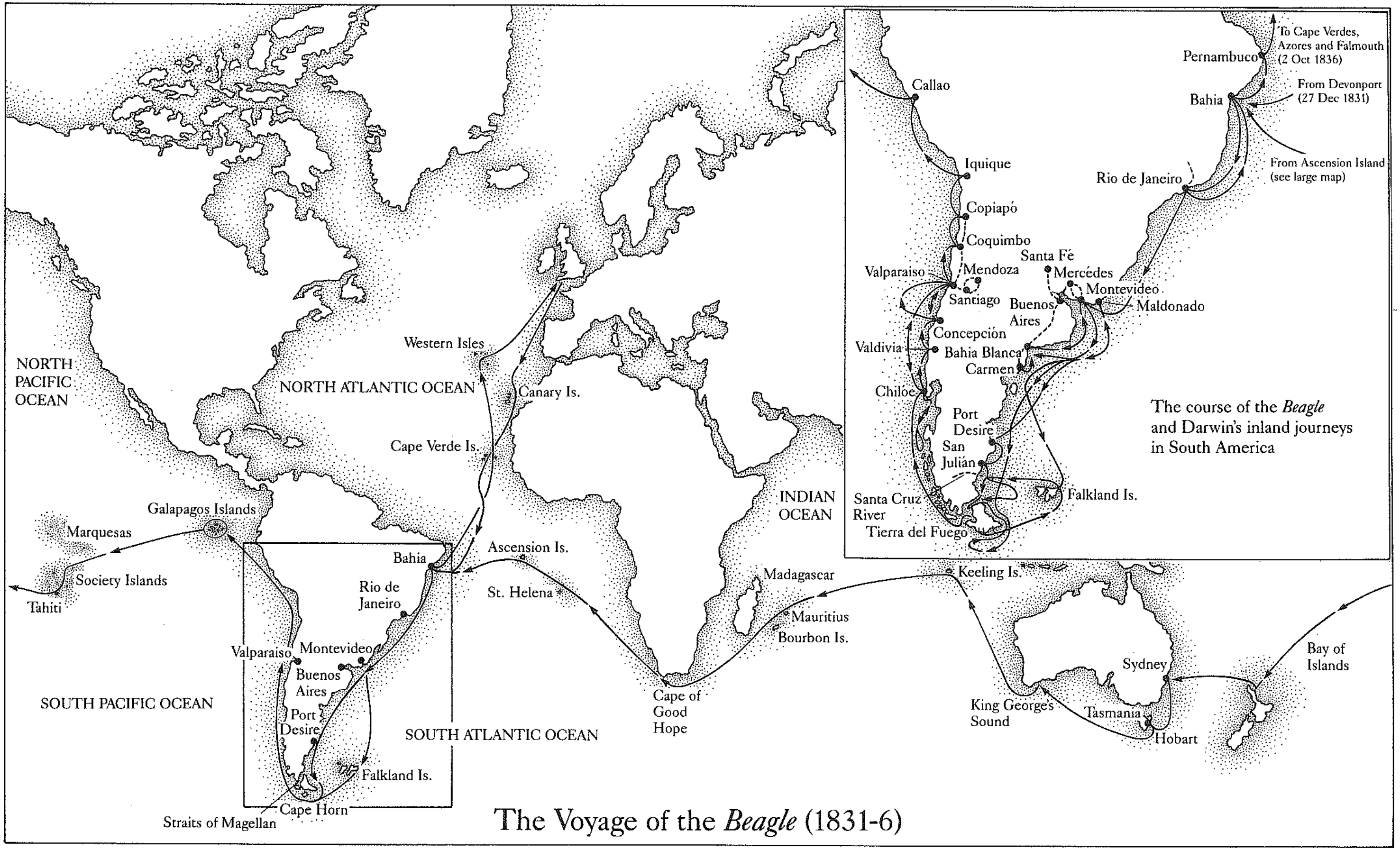
The whole concept of competition among individuals would be irrelevant if all these individuals were typologically identical—if they all had the same essence. Competition does not become meaningful in an evolutionary sense until a concept has developed that allows for variability among the individuals of the same population. Each individual may differ in the ability to tolerate climate, to find food and a place in which to live, to find a mate, and to raise young successfully. The recognition of the uniqueness of every individual and the role of individuality in evolution is not only of the utmost importance for an understanding of the history of biology, but it is one of the most drastic conceptual revolutions in Western thought (Fact 4).

There is little doubt that this concept—which we call "population thinking"—received an enormous boost in Darwin's mind through his reading Malthus at that right moment. Yet, curiously, when we go through Malthus's writings we find no trace of population thinking. There is nothing whatsoever even faintly relating to the subject in those early chapters of Malthus that gave Darwin the idea of exponential growth. There is a reference to animal breeding in chapter 9, but there the subject is introduced to prove exactly the opposite point. After referring to the claims of the animal breeders, Malthus states, "I am told that it is a maxim among the improvers of cattle that you may breed to any degree of nicety you please, and they found this maxim upon another, which is, that some of the offspring will possess the desirable qualities of the parents in a greater degree." He then pro-

J. S. Henslow (1796–1861), Darwin's botany professor at Cambridge University, who procured for Darwin the invitation to join the *Beagle* voyage



The *H.M.S. Beagle*, in the Straits of Magellan, 1833



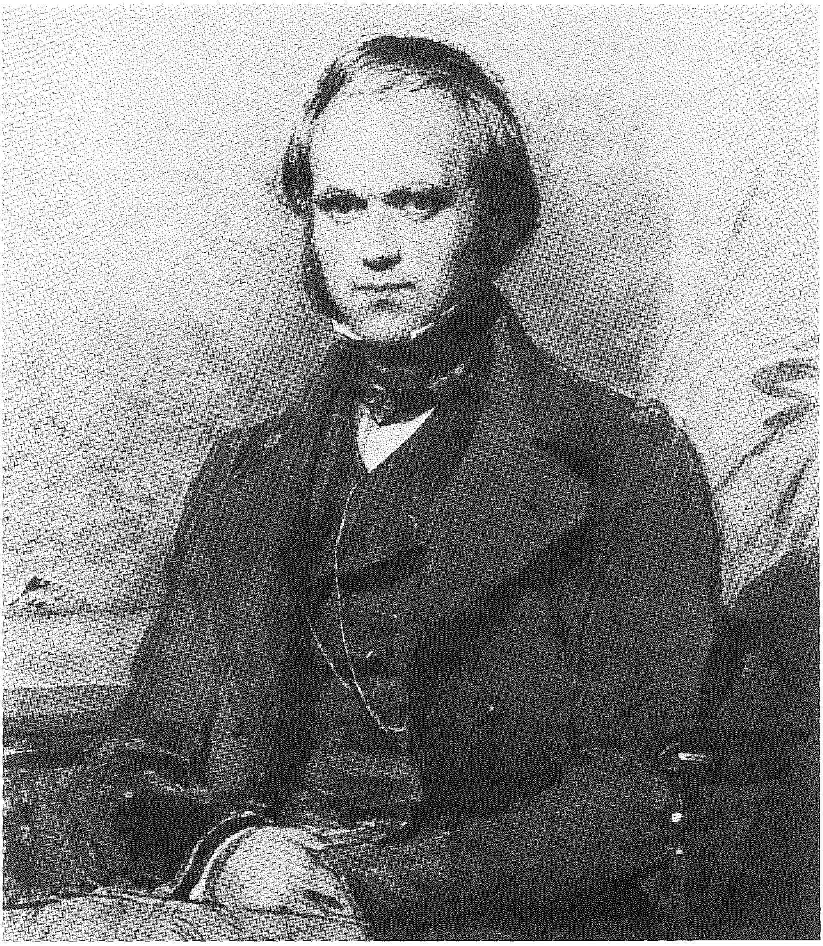
The route of the voyage of the *Beagle*, 1831–1836

The naturalist Jean Baptiste Lamarck (1744–1829), the first person to adopt a consistent theory of gradual evolutionary change

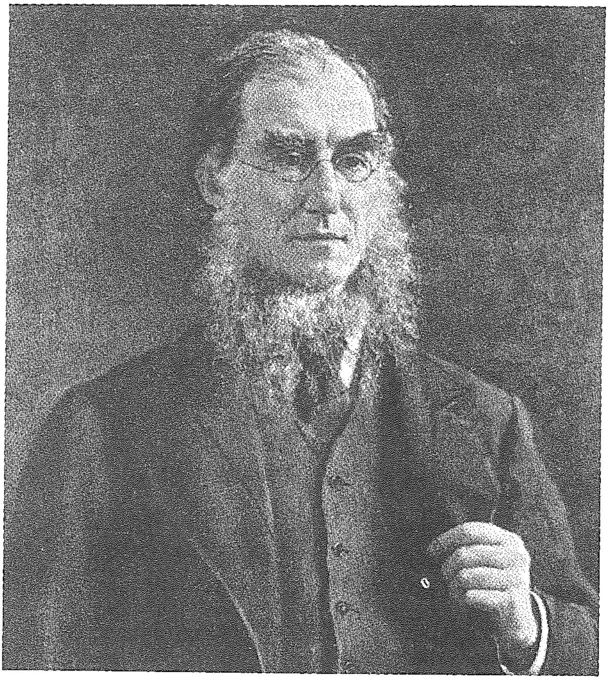
Charles Lyell (1797–1875), geologist, to whose theory of uniformitarianism Darwin owed much of his thinking about evolutionary change

The ornithologist John Gould (1804–1881), who informed Darwin in March 1837 that the specimens of mockingbirds he had collected on three islands in the Galapagos were three distinct species

Emma Wedgwood Darwin (1808–1896) in 1840, Charles Darwin's wife and first cousin, and daughter of the famous potter Josiah Wedgwood II



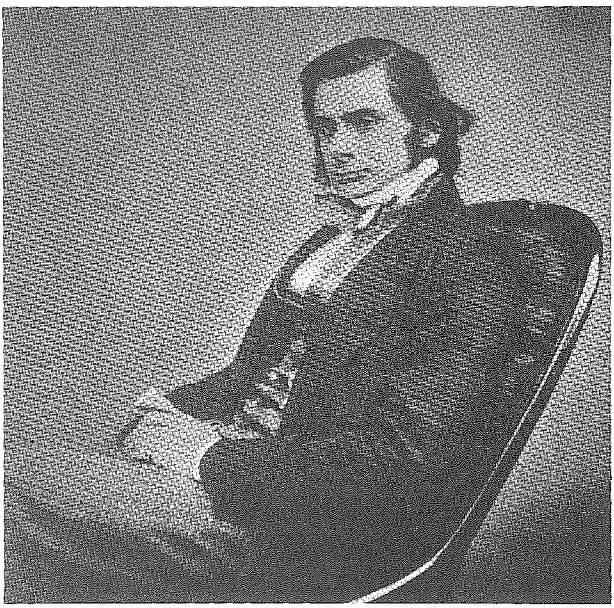
Charles Darwin in 1840



The botanist Joseph Dalton Hooker (1817–1911), Darwin's friend and supporter, who in 1858, with Lyell, presented Darwin's and Wallace's findings to the Linnean Society of London

The morphologist and paleontologist Richard Owen (1804–1892), once Darwin's friend, who viciously attacked the *Origin* and whose statements Huxley attacked with equal vigor

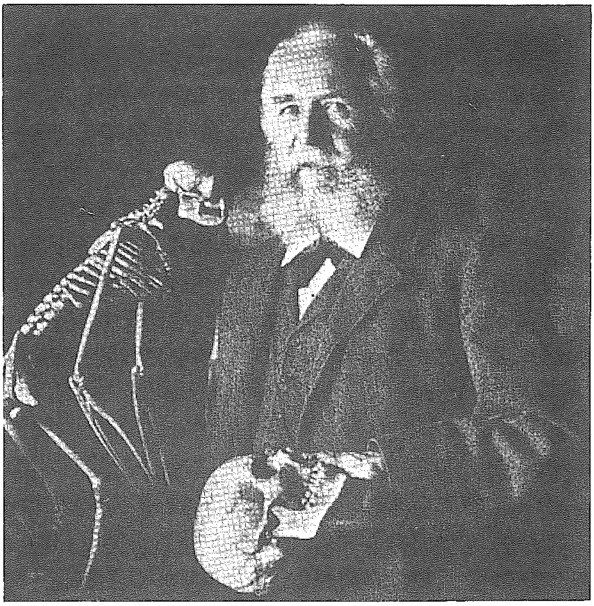
Alfred Russel Wallace (1823–1913), co-discoverer with Darwin of the theory of evolution through natural selection and opponent, with Weismann, of the theory of the inheritance of acquired characters

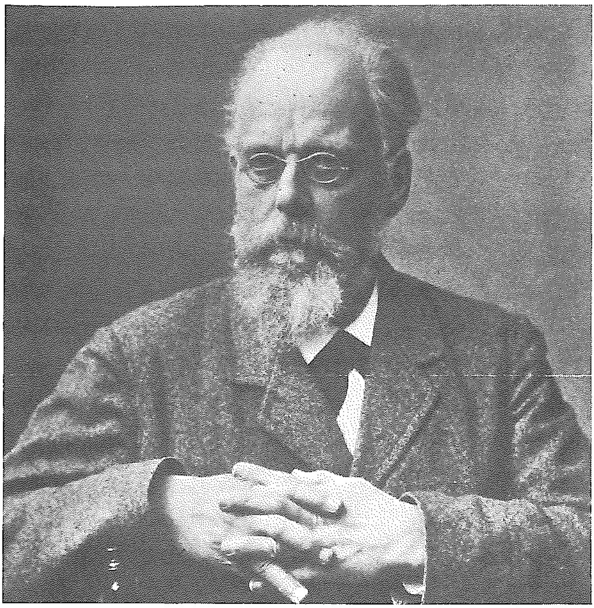


The morphologist, physiologist, and embryologist Thomas Henry Huxley (1825–1895), self-anointed as "Darwin's bulldog" for his energetic defense of Darwin and the theory of descent

Above: The botanist Asa Gray (1810–1888), Darwin's most important supporter in America and a devout Christian who succeeded in reconciling natural selection with a belief in a personal god

Below: The Swiss-born naturalist Louis Agassiz (1809–1873), an outstanding ichthyologist and specialist of other groups of organisms, who played a prominent role in the spread of natural history studies in America; a devout creationist, Agassiz characterized the *Origin* as "a scientific mistake, untrue in its facts, unscientific in its method, and mischievous in its tendencies"





Above: The biologist Ernst Haeckel (1834–1919), an enthusiastic supporter and popularizer of Darwinism in Germany, who specially emphasized the study of phylogeny

Below: August Weismann (1834–1914), the nineteenth century's greatest evolutionist after Darwin and a staunch supporter of natural selection; he was responsible for the demise of the theory of acquired characters and laid the foundations of genetics

Charles Darwin on the veranda at Down House duces all sorts of facts and reasons why this cannot possibly be the case, leading him to the conclusion that "it cannot be true, therefore, that among animals, some of the offspring will possess the desirable qualities of the parents in a greater degree; or that animals are indefinitely affectable" (Malthus 1798:163).

Where, then, did Darwin get his population thinking, since he evidently did not get it from Malthus? In his autobiography and in various letters Darwin emphasized again and again that he had been mentally prepared for the Malthus principle by studying the literature of animal breeding. Recent commentators such as Limoges and Herbert have insisted that this must be a lapse of Darwin's memory because there is very little about animal breeding in Darwin's notebooks until about three months after the Malthus reading. For myself, I am convinced that Darwin's own presentation is nevertheless essentially correct.

If we ask ourselves what Darwin would be likely to enter in his notebooks, we would certainly say new facts or new ideas. Hence, since it was not a new subject, animal breeding surely would not qualify. Darwin's best friends at Cambridge University were the sons of country squires and of owners of estates. They were the "horsy set," riding or hunting with dogs on every occasion (Himmelfarb 1959). All of them to a greater or lesser degree were interested in animal breeding. They must have argued a great deal among themselves about Bakewell and Sebright and the best methods of breeding and improving dogs, horses, and livestock.

How else—other than that it had a great interest for him—can one explain that Darwin, in the excessively busy period after the return of the *Beagle,* devoted so much of his time to studying the literature of the animal breeders? To be sure, Darwin's primary interest was in the origin of variation, but in the course of his reading Darwin could not help absorbing the important lesson from the breeders—that every individual in the herd was different from every other one and that extreme care had to be used in selecting the sires and dams from which to breed the next generation. I am quite convinced that it is no coincidence that Darwin studied the literature of the animal breeders so assiduously exactly during the six months before reading Malthus (Ruse 1975a).

It was not the process of selection but the fact of the differences among individuals that Darwin remembered when suddenly becoming aware of the competition among individuals, of the struggle for existence among individuals. Here we have the fortuitous coming together of two important concepts—excessive fertility and individuality—which jointly provide the basis for an entirely new conceptualization.

Variation can be of evolutionary significance—that is, it can be selected—only if at least part of it is heritable (Fact 5). Like the animal breeders from whom he got so much of his information, Darwin took this heritability of characters completely for granted. And this assumption can be held quite independently of one's assumptions concerning the nature of the genetic material and of the origin of new genetic factors. Darwin's ideas on these subjects were quite confused, but he did know a number of things by observation. He knew that in asexual reproduction the offspring are identical with the parent, while in sexual reproduction offspring are different from the parent and from one another. Furthermore, he knew that each offspring had a mixture of the characters of both parents. On the whole Darwin treated genetic variation as a "black box." As a naturalist and reader of the animal breeding literature, he knew that variation was always present, and this is all he *had* to know. He was also convinced that the supply of variation was renewed in every generation and thus was always abundantly available as raw material for natural selection. In other words, a correct theory of genetics was *not* a prerequisite for the theory of natural selection.

The Path to Discovery

The next question we have to answer is how Darwin arrived at the actual concept of natural selection on the basis of the stated five facts and his first inference. In his autobiography (1958: 118–

120) Darwin stressed that he "collected facts on a wholesale scale, more especially with respect to domesticated productions, by printed enquiries, by conversation with skillful breeders and gardeners, and by reading . . . I soon perceived that selection was the key-stone of man's success in making useful races of animals and plants. But how selection could be applied to organisms living in a state of nature remained for some time a mystery to me." In 1859 he wrote to Wallace, "I came to the conclusion that selection was the principle of change from the study of domestic productions; and then, reading Malthus, I saw at once how to apply this principle." To Lyell he wrote, with reference to Wallace's theory, "We differ only [in] that I was led to my views from what artificial selection had done for domestic animals." Traditionally, these statements were accepted by Darwin students as a correct representation of the facts.

This interpretation of Darwin's path to the concept of natural selection has been challenged in recent years in the wake of the discovery of Darwin's notebooks, for the same reason that researchers have come to doubt the sources of Darwin's population thinking. Limoges and Herbert point out that in the first three notebooks Darwin nowhere refers to selection or to the selective activities of animal breeders, particularly in the production of new domestic races. They claim that Darwin was interested in domestic animals only because he hoped to find evidence concerning the occurrence of variations and the mechanisms of their production, matters that are difficult to study in wild populations.

It is true that the term "selection" does not occur in Darwin's notebooks; it is first found in his 1842 sketch in the words "natural means of selection" (F. Darwin 1909:17). Darwin here refers to artificial selection by the term "human selection." Actually, in the notebooks Darwin not infrequently refers to the process of selecting, but he uses a different term—"picking."

I am willing to grant to the recent critics that there is no evidence in the notebooks of a simple application to the evolutionary process of the analogy between selection by man and selection by nature. This is quite evident when one reads the crucial entry in the notebooks on September 28, 1838 (here reproduced in the original telegraph style):

> Take Europe on an average every species must have same number killed year with year by hawks, by cold etc.—even one species of hawk decreasing in number must affect instantaneously all the rest.—The final cause of all this wedging, must be to sort out proper structure, and adapt it to changes—to do that for form, which Malthus shows is the final effect (by means however of volition) of this populousness on the energy of man. One may say there is a force like a hundred thousand wedges trying [to] force every kind of adapted structure into the gaps in the economy of nature, or rather forming gaps by thrusting out the weaker ones.

The metaphor here is "wedging," not "selecting." Thus it appears that the arguments of the critics have considerable validity. However, the analogy between artificial selection and natural selection is not necessary for Darwin's conclusions. Inference 1 and Fact 4 automatically result in Inference 2 (natural selection). It is quite likely that Darwin did not see the obvious analogy between artificial and natural selection until some time after the Malthus reading. Yet, I have little doubt that the copious reading Darwin had done in the field of animal breeding had prepared his mind to appreciate the role of the individual and its heritable qualities. Indeed, I am convinced, with Ruse, that the many years during which Darwin had been exposed to the ideas of the animal breeders had preconditioned his mind to appreciate the importance of the Malthus principle. This dormant knowledge was actualized under the impact of reading Malthus.

The natural selection of individuals with particular heritable qualities, continued over many generations, automatically leads to evolution, as in Inference 3. In fact, this process is sometimes used as the definition of evolution. In this connection it must be emphasized once more that Darwin's inference is exactly the opposite of that of Malthus, who had denied that "some of the offspring will possess the desirable qualities of the parents in a greater degree." Indeed, Malthus used his entire argument as a refutation of the thesis of Condorcet and Godwin of human perfectibility. The Malthusian principle, dealing with populations of essentialistically identical individuals, causes only quantitative, not qualitative, changes in populations (Limoges 1970). The frequently upheld thesis that it was the social-sciences message of Malthus that was responsible for Darwin's new insight has been convincingly refuted by Gordon (1989).

How Great Was Darwin's Debt to Malthus?

That the Malthus reading acted as a catalyst in Darwin's mind in producing the theory of natural selection cannot be disputed and was emphasized by Darwin himself again and again. However, when we analyze the components of the theory, as we have just done, we find that it is primarily the insight that competition is among individuals rather than species that is clearly a Malthusian contribution. To be sure, this in turn led Darwin to a reevaluation of other phenomena, such as the nature of the struggle for existence, but only as second-order consequences. I agree with those who think that the Malthusian thesis of exponential growth was the capstone of Darwin's theory. "The one sentence of Malthus" acted like a crystal dropped into a supercooled fluid.

There is, however, also a second and more subtle Malthusian impact. The world of the natural theologians was an optimistic world: everything that was happening was for the common good and helped to maintain the perfect harmony of the world. The world of Malthus was a pessimistic world: there are ever-repeated catastrophes, an unending, fierce struggle for existence, yet the world essentially remains the same. However much Darwin might have begun to question the benign nature of the struggle for existence, he clearly did not appreciate the fierceness of this struggle before reading Malthus. And it permitted him to combine the best elements of Malthus and of natural theology: it brought him to the belief that the struggle for existence is not a hopeless steady-state condition, as Malthus believed, but the very means by which the harmony of the world is achieved and maintained. Adaptation is the result of the struggle for existence.

The events of September 28, 1838, are of great interest to students of theory formation. Given the extent to which Darwin was in possession of all the other pieces of his theory prior to this date, it becomes clear that in the case of a complexly structured theory it is not sufficient to have most of the pieces; one must have them all. Even a small deficiency, like defining the word "variety" typologically instead of populationally, might be sufficient to prevent the correct piecing together of the components. Equally important is the general ideological attitude of the theory-builder. A person like Edward Blyth might have had in his possession the very same components of the theory as Darwin but would have been unable to piece them together correctly owing to incompatible ideological commitments. Nothing illustrates better how important the general attitude and conceptual framework of the maker of a theory is than the simultaneous, independent proposal of the theory of natural selection by A. R. Wallace. He was one of the few people, perhaps the only one, who had had a similar set of past experiences: a life dedicated to natural history, years of collecting on tropical islands, and the experience of reading Malthus.

What Is Natural Selection?

Darwin's choice of the word "selection" was not particularly fortunate. It suggests some agent in nature who, being able to predict the future, selects "the best." This, of course, is not what natural selection does. The term simply refers to the fact that only a few (on the average, two) of all the offspring of a set of parents survive long enough to reproduce. There is no particular selective force in nature, nor a definite selecting agent. There are many possible causes for the success of the few survivors. Some survival, perhaps a lot of it, is due to stochastic processes, that is, luck. Most of it, though, is due to a superior working of the physiology of the surviving individual, which permits it to cope with the vicissitudes of the environment better than other members of the population. Selection cannot be dissected into an internal and an external portion. What determines the success of an individual is precisely the ability of the internal machinery of the organism's body (including its immune system) to cope with the challenges of the environment. It is not the environment that selects, but the organism that copes with the environment more or less successfully. There is no external selection force.

A few examples may illustrate this. Let us take, for instance, resistance against pathogens. Bacteria and other pathogens represent the environment; an animal's defense against them consists of intracellular selection processes. Likewise, adaptation to the temperature of the environment is controlled by balanced physiological mechanisms, regulated by feedback mechanisms. The success of an organism depends to a great deal on its normal development from the fertilized egg to adulthood. Almost all departures from normalcy in development will be selected against.

Considering that for many people the term "selection" has a teleological connotation—that is, it suggests purpose—many alternative terms have been proposed, such as "survival of the fittest," "selective retention," "biased nonelimination," and so forth. What all these terms try to make clear is that selection is an *a posteriori* phenomenon—that is, it is the survival of a few individuals who are either luckier than the other members of the population or who have certain attributes that give them superiority in the particular context. The probabilistic nature of selection cannot be stressed too strongly. It is not a deterministic process. Moreover, because selection is a very broad principle, it is probably not refutable (Tuomi 1981). However, each concrete application of the principle of natural selection to a specific situation is testable and refutable.

One must distinguish between two applications of selection. "Selection of" specifies the target of selection, and this is normally (in sexually reproducing organisms) a potentially reproducing individual, as represented by its phenotype (body). For this reason it is confusing to say that the gene is the unit of selection. "Selection for" specifies the particular phenotypic attribute and corresponding component of the genotype (DNA) that is responsible for the success of the selected individual. The now-obsolete concept that evolution is the interplay between genetic mutation and selection was part of the saltationist thinking of the Mendelians, as we will see. The material with which selection works is not mutation but is rather the recombination of parental genes, which produces the new genotypes that direct the development of individuals which are then exposed to selection in the next generation. It must always be remembered that selection is a two-step process. The first step consists in the production (through genetic recombination) of an immense amount of new genetic variation, while the second step is the nonrandom retention (survival) of a few of the new genetic variants.

Selection at the level of the whole organism results in changes at two other levels: that of the gene, where through the selection of individuals certain genes may increase or decrease in frequency in the population, and at the level of the species, where the selective superiority of members of one species may lead to the extinction of another species. This process, as mentioned earlier, has often been called species selection but is perhaps better called species replacement or species succession, in order to avoid misinterpretations. (Nothing is ever selected "for the good of the species.")

Finally, it must be pointed out that two kinds of qualities are at a premium in selection. What Darwin called "natural selection" refers to any attribute that favors survival, such as a better use of resources, a better adaptation to weather and climate, superior resistance to diseases, and a greater ability to escape enemies. However, an individual may make a higher genetic contribution to the next generation not by having superior survival attributes but merely by being more successful in reproduction. Darwin called this kind of selection "sexual selection." He was particularly impressed by male secondary sexual characters, such as the gorgeous plumes of male birds of paradise, the gigantic size of bull elephant seals, or the impressive antlers of stags. Modern research has shown that selection favors their evolution either because they aid in competition with other males over access to females, or because females are attracted to mates with these characteristics. This latter process is known as "female choice." Selection for reproductive success affects many life history traits beyond sexual dimorphism.

The path by which the theory of evolution by natural selection was gradually clarified and modified will be described in the following chapters. Eventually the theory was universally adopted among biologists, a development I refer to as the second Darwinian revolution.

CHAPTER SEVEN

What Is Darwinism?

CHARLES DARWIN was the most talked about person of the 1860s. T. H. Huxley, always a coiner of felicitous phrases, soon referred to Darwin's ideas as "Darwinism" (1864), and in 1889 Alfred Russel Wallace published a whole volume entitled *Darwinism*. However, since the 1860s no two authors have used the word "Darwinism" in exactly the same way. As in the old story of the three blind men and the elephant, every writer on Darwinism seemed to touch upon only one of the many aspects of Darwinism, all the while thinking that he had the real essence of what this term signifies. Thus, everybody who read the *Origin* responded only to those parts of it that either supported his own preconceived ideas or were in conflict with them. What these writers failed to grasp is that Darwinism is not a monolithic theory that rises or falls depending on the validity or invalidity of a single idea.

This monolithic tradition actually started with Darwin himself, who often spoke of his "theory of descent with modification through natural selection" (1859:459) as though the theory of common descent was inseparable from that of natural selection. How separable the two theories actually were was demonstrated when almost every knowledgeable biologist adopted the theory of common descent soon after 1859 but rejected natural selection. They explained descent instead by Lamarckian, finalist, or saltational theories (Bowler 1988). A number of passages in the *Origin* indicate how confused Darwin himself was on the subject: "The fact, as we have seen, that all past and present organic beings constitute one grand natural system, with group subordinate to group, and with extinct groups often falling inbetween recent groups, is intelligible on the theory of natural selection" (1859:478). Actually, the hierarchical organization of the living world is explicable by the theory of common descent, but this tells us absolutely nothing about the mechanism by which these changes were effected.

Even in modern times far more authors speak of Darwin's theory in the singular than acknowledge the heterogeneity of Darwin's paradigm. Even authors like Kitcher (1985) and Burian (1989), who are aware of the complexity of Darwin's paradigm, continue to refer to Darwin's theory in the singular. Burian calls the synthetic theory of evolution "the current variant of Darwin's theory."

How Darwinism is seen depends to a large extent on the background and the interests of the viewer. The word has a different meaning for a theologian, a Lamarckian, a Mendelian, or a post-synthesis evolutionary biologist. Another dimension that contributes to the diversity of opinion about the meaning of Darwinism is geography: the word "Darwinism" has meant something different in England, in Germany, in Russia, and in France. From the beginning, as we have seen, Darwin's theories were in opposition to a number of ideologies such as essentialism, physicalism, natural theology, and finalism whose strength varied from one country to the next. For the supporters of one or the other of these ideologies, the word "Darwinism" stood for the opposite of their own beliefs.

An equally great diversity exists in the time dimension. Concepts differ from facts by continuing to change over time. Hull (1985) has rightly referred to "conceptual development as a genuinely temporal process in which real change occurs." What was called Darwinism in 1859 was no longer considered so thirty years later, because the term had been transferred to something very different from that which it designated at the earlier period.

This fact was well stated by Wallace in the preface to *Darwinism* (1889). Here he explained that Darwin had done such an excellent job in proving descent with modification that this theory was now universally accepted as the order of nature in the organic world. "The objections now made to Darwin's theory apply, solely, to the particular means by which the change of species has been brought about, not to the fact of that change." Alas, Wallace was way ahead of his time in his championship of natural selection.

Different components of Darwin's paradigm were particularly interesting at different periods. At each stage in the history of Darwinism a different one of Darwin's theories was referred to as Darwinism: anticreationism vs. Christian orthodoxy, gradualism vs. Mendelian saltationism, selectionism vs. Lamarckism or finalism, and so on. This continuing change of meaning poses the awkward question of what establishes the continuity among all these Darwinisms? Do these various Darwinisms have anything in common? The answer of course is that they are all based on Darwin's original paradigm, as presented in the *Origin*.

The best way to document the great variety of meanings of the term Darwinism is to present a list of different interpretations of the term, as encountered in the literature. In each case I will attempt to analyze the validity of such usage and the temporal and ideological context in which the term Darwinism was used with this meaning. This historical analysis will then permit us to ask whether any one of the suggested definitions of Darwinism can be singled out as the best one, or perhaps even the only correct one.

Darwinism as "Darwin's Theory of Evolution"

But which one is meant, since Darwin had so many theories of evolution? Should the term refer to the totality of Darwin's theories, including those of pangenes, the effect of use and disuse, blending inheritance, and the frequency of sympatric speciation?

Surely not. To call such a conglomerate Darwinism would be worse than useless; it would be utterly misleading.

Darwinism as Evolutionism

Evolutionism was a concept alien to the physicists, not only owing to its rejection of essentialism but also for its acceptance of the historical element, so conspicuously missing from the physics of the mid-nineteenth century. Historical inferences were equally alien to all philosophers coming from logic or mathematics. It was Darwin who made evolutionary thinking a respectable concept of science. Nevertheless, it would be misleading to refer to evolutionism as Darwinism. Evolutionary thinking was already widespread when Darwin published the *Origin,* particularly in linguistics and in sociology (Toulmin 1972:326). For its existence in biology one only needs to mention the names of Buffon, Lamarck, Geoffroy, Chambers, and several German authors. Clearly, Darwin was not the father of evolutionism, even though he eventually brought about its victory.

Darwinism as Anticreationism

This is the Darwinism which denied the constancy of species and, in particular, special creation, that is, the separate creation of every feature in the inanimate and living world. There were two very different groups of anticreationists. The deists maintained a belief in God but made him a rather remote lawgiver, who did not interfere with any specific happening in this world, having already arranged for everything through his laws. Whatever happened during evolution was the result of these laws. This thought made evolution palatable to a number of Christian scientists such as Charles Lyell and Asa Gray. However, only transformational evolution—the orderly change in a lineage over time, directed toward the goal of perfect adaptation—is susceptible to this deistic interpretation. Darwin's variational evolution, with its random components at the level of both genetic recombination and selection, cannot be instrumented by strict laws. The agnostic anticreationists explained all evolutionary phenomena without invoking any supernatural agents.

Immediately after 1859 the word Darwinism simply meant a rejection of special creation. If someone rejected special creation and adopted instead the inconstancy of species, common descent, and the incorporation of man into the general evolutionary stream, he was a Darwinian. Neither natural selection nor any special theory of speciation, nor even one's belief in gradual versus saltational evolution, had any relevance to whether at that time one was considered a Darwinian or not.

There were great differences between Darwin and other "Darwinians," such as Huxley, Lyell, Wallace, and Gray, on other aspects of evolutionary theory. But these differences were of minor importance in the 1860s, because the foremost meaning of Darwinism at that time was the rejection of special creation, together with the adoption of the inconstancy of species, the theory of common descent, and (excepting Wallace) the incorporation of man into the animal kingdom. When someone in the 1860s or 1870s attacked Darwinism, he did so primarily in defense of creationism or natural theology against these four Darwinian concepts.

Perhaps the best way to determine what we should consider to be the gist of Darwinism would be to determine what Darwin had in mind when he said the *Origin* was "one long argument." Gillespie (1979), in a careful analysis of this question, concluded that it was Darwin's argument against special creation. Independently of Gillespie I had come to the same conclusion when, in the process of making a new index to the *Origin,* I saw on how many pages Darwin reiterated his conclusion that a particular phenomenon could not possibly be explained by special creation. Instead Darwin argued for a materialistic—that is, natural—explanation for the diversity of the organic world and its history. What Darwin pointed out again and again was that any given phenomenon for which special creation had been invoked could be explained much better by his theory of common descent.

Biogeography was of particular importance in that connection, because no other evidence is as convincing for common descent as the distribution of species and higher taxa. For this reason Darwin devoted two whole chapters of the *Origin* to biogeography; and in these chapters he showed over and over how a particular distribution pattern could readily be explained by common descent but not by special creation. It was the theory of common descent which had the great unifying capacity about which Darwin talked so often (Kitcher 1985:171, 184–185), because it at once gave meaning to the Linnaean hierarchy, the archetypes of the idealistic morphologists, the history of biota, and many other biological phenomena.

Curiously, many modern authors have claimed that Darwin's "one long argument" was an argument in favor of natural selection (Recker 1987). There is no good evidence for this interpretation. In his correspondence Darwin referred to his manuscript always as his "species book," not his book on natural selection. Natural selection is dealt with in the first four chapters, apparently in order to satisfy the *vera causa* demand of the leading philosophers of science (Hodge 1982); in the remaining ten chapters natural selection is not featured. Instead, these chapters are almost exclusively devoted to documentations for common descent. Indeed, Darwin himself repeatedly called attention to "the later chapters" of the *Origin* as particularly convincing proof of his theory. The facts confirm Darwin's claim. It was the reading of these chapters that converted Darwin's contemporaries to a belief in the inconstancy of species and the validity of common descent, hence in evolution. Neither these chapters nor the first four chapters, however, produced many adherents to his theory of natural selection, a theory not adopted even by some of Darwin's closest friends and followers, such as Huxley and Lyell. This is not so surprising once one realizes that the *Origin* is not one long argument in favor of natural selection.

The adoption of evolution by natural selection necessitated a complete ideological upheaval. The "hand of God" was replaced by the working of natural processes. God was "dethroned," as one of Darwin's critics formulated it. Indeed, God did not play any role in Darwin's explanatory schemes.

By what did Darwin replace him? What were the forces that played the same role in Darwin's explanations that God played in Christian dogma? Some physicalists, as well as historians and philosophers adopting physicalist explanations, suggested that Darwin had adopted Newton's reductionist explanation—that the processes of the inanimate as well as of the living world consist of "a lawbound system of matter in motion" (Greene 1987). This wording fails to reflect Darwin's thinking. The biological explanations adopted by Darwin are a long way from the Newtonian explanation, and one looks in the *Origin* in vain for any reference to "matter in motion."

Darwinism as Anti-ideology

Not only natural selection but also many other aspects of Darwin's paradigm were in complete opposition to many of the dominant ideologies of the mid-nineteenth century, as we have seen. In addition to the belief in special creation and the design argument of natural theology, other ideologies that were in total opposition to Darwin's thinking were essentialism (typology), physicalism (reductionism), and finalism (teleology). The adherents of these creeds saw in Darwin's work their most formidable opposition, and whatever the *Origin* said or implied that was dangerous to their own position was designated by them as Darwinism. But one by one these three ideologies were defeated, and with their demise the concepts of determinism, predictability, progress, and perfectability in the living world were weakened.

One of the by-products of the total refutation of all finalistic aspects of organic evolution was the inevitable reinterpretation of evolution as a historical process subject to temporary contingencies. This led to the stress on opportunism in selection and on the tinkering aspects of evolution. Such a concept of evolution is totally different from all simple transformational changes in the inanimate world, which, though also affected by chance, are primarily controlled by natural laws and thus permit rather strict predictions. A closer approach is provided by complex inanimate systems, such as the weather systems, ocean currents (greatly affected by turbulence), and the interaction of continental plates (resulting in earthquakes and volcanic eruptions), where the multitude of interacting factors and the frequency of stochastic processes defy prediction.

Darwinism as Selectionism

Almost any modern biologist, when asked what the term Darwinism stands for, will answer that it stands for a belief in the importance of natural selection in evolution. This interpretation of Darwinism is so widely accepted today that it is sometimes forgotten how relatively new this modern version is. Natural selection as the mechanism of evolutionary change was not universally adopted by biologists until the period of the evolutionary synthesis (1930s–40s); however, natural selection always was the key theory in Darwin's total research program for at least some evolutionists. The first one of whom we know that this was true was August Weismann (see Chapter 8), but he was enthusiastically followed by A. R. Wallace, who named his book on Darwinian evolution *Darwinism* because, as he said, "my work tends forceably to illustrate the overwhelming importance of natural selection over all agencies in the production of new species." However, it took another fifty years and the refutation of the major anti-Darwinian theories before this insight was generally adopted.

Darwinism as Variational Evolution

Darwin's concept of evolution was radically different from the transformational and the saltational concepts of evolution that had previously been proposed (see Chapter 4). Although it should have been obvious from the very beginning how different Darwin's concept was, this difference was not fully appreciated until very modern times. Darwin's variational evolution was based on entirely new philosophical concepts, and the neglect of these concepts is the reason why it was usually confused with the prevailing evolutionary ideas. Kitcher's discussions indicate how far even some modern philosophers are from fully understanding the magnitude of Darwin's departure from conventional thinking. Kitcher claims, "The trouble is that the theory I have ascribed to Darwin is uncontroversial—so uncontroversial as to border on triviality" (1985:30). Kitcher claims that virtually all of Darwin's opponents accepted Darwin's statement that there is variation among the members of the species and that different organisms have different properties. However, what Kitcher fails to acknowledge is that the essentialist, as was emphasized by Lyell, Sedgwick, Herschel, and others, believes that there is a definite limit to the amount of variation possible within a species or, to put it differently, permissible to a single inherent essence. For the population thinker, variation is unlimited. Hence, there is a definite possibility of going beyond the confines of an existing species. The nature and extent of variability was the crucial difference between the population thinker Darwin and his essentialistic opponents. To call this difference uncontroversial completely ignores its revolutionary importance.

Darwinism as the Creed of the Darwinians

Thwarted by the complexity of the Darwinian paradigm in their attempts to reach a satisfactory definition of Darwinism, a number of historians and philosophers have attempted in recent years to define Darwinism as the creed of the Darwinians. Hull (1985) and Kitcher (1985), in particular, have adopted this approach. This choice of defining Darwinism is more often favored by philosophers and historians than by biologists. It seems that a philosopher, particularly if he or she is coming from the background of logic or mathematics, feels on safer ground discussing a sociological phenomenon like the Darwinians than a conceptual framework like Darwinism, which requires a thorough knowledge of evolutionary biology. They attempt to justify their approach by claiming that Darwinism can best be demarcated by the scientific community (the Darwinians) who support this system. However, Recker (1990) has pointed out how questionable this claim is. Indeed, in some respects, this approach compounds the difficulties because it is as difficult to define a Darwinian as it is to define Darwinism. For Hull, "the Darwinians formed a fairly cohesive social group." Yet, this group presumably included only Lyell, Huxley, and Hooker, because Asa Gray was in America, Wallace was in the East Indies, Fritz Müller was in South America, and Haeckel was in Germany.

Recker (1990), Hull (1985), and others have stated repeatedly that there are no Darwinian tenets that characterize all the Darwinians. Indeed, it is true that some of the leading Darwinians, like Huxley and Lyell, never believed in natural selection; neither Huxley nor, presumably, Lyell endorsed Darwin's complete gradualism; neither Wallace nor Lyell thought that human beings could be dealt with in the same way as animal species. Thus, there were drastic differences among all of these Darwinians. This disparity led Hull to state that it was not sufficient for a person to hold certain Darwinian ideas in order to be called a Darwinian. In fact, he and others implied there was not a single concept subscribed to by all of the so-called Darwinians.

This is an error. There is indeed one belief that all true original Darwinians held in common, and that was their rejection of creationism, their rejection of special creation. This was the flag around which they assembled and under which they marched. When Hull claimed that "the Darwinians did not totally agree with each other, even over essentials" (1985:785), he overlooked one essential on which all these Darwinians agreed. Nothing was more essential for them than to decide whether evolution is a natural phenomenon or something controlled by God. The conviction that the diversity of the natural world was the result of natural processes and not the work of God was the idea that brought all the so-called Darwinians together in spite of their disagreements on other of Darwin's theories, and in spite of the retention by some of them (Gray, Wallace) of other theological arguments. This situation was quite well understood in the post-*Origin* period and that is why at that time, for Darwin's opponents, Darwinism simply meant denying special creation and replacing it with the theory of evolution and in particular the theory of common descent.

The theory of evolution by natural means was powerfully supported by the explanatory power of the theory of common descent. Indeed, it was this theory which eventually brought even the morphological idealists into the Darwinian camp when they realized that this was the only reasonable way to explain the hierarchical arrangement of morphological archetypes. To be sure, some morphologists, like Louis Agassiz, ascribed this order of nature to God's laws. But the natural explanation of common descent by Darwin and his followers was so much more convincing that Agassiz's interpretation fell on deaf ears and was no longer heard after Agassiz's death in 1873.

The criteria by which one delimits scientific communities must be ranked according to their importance. Creation or not was the overwhelmingly important consideration in 1859. And it was the adoption or rejection of Darwin's thesis of evolution by natural means that neatly separated the Darwinians from the non-Darwinians. They did not need to form a closely knit social group and might reside in Europe, South America, or the East Indies, but they were held together and easily recognizable by a single firm belief, that of evolution by natural means. And this explains what has puzzled some historians, that so many nineteenth-century evolutionists considered themselves to be Darwinians even though they had adopted explanatory mechanisms that were quite different from Darwin's natural selection. Only the beliefs they shared with Darwin were considered by them the truly crucial aspects of Darwinism.

To be sure, there were some borderline cases, like Asa Gray, who seems to have adopted all of Darwin's theories and yet still thought that God ultimately controlled everything, including the nature of variation that was available to natural selection. Richard

Owen was another borderline case because he really did believe in evolution of some sort, but he thought he needed to attack Darwin's theories uncompromisingly, in part owing to his enmity with Huxley.

Finally, there is the puzzling case of Lyell (Recker 1990). Even though a friend and mentor of Darwin and usually considered a Darwinian, he never accepted the most basic components of Darwin's research program. God, for him, was apparently always the ultimate causation; Lyell did not extend evolution to man, and he never accepted natural selection. If one wants to explain why Lyell continued to support Darwin even though he disagreed with most of Darwin's evolutionary beliefs, one must not forget that Darwin originally was a geologist—not only a geologist but very definitely a Lyellian geologist, who had strongly supported Lyell in his geological writings. It is quite possible that Lyell simply reciprocated, through his support of Darwin's ideas, for everything Darwin had done in his geological writings to support the Lyellian view. And, as Hodge has pointed out so convincingly, Darwin was a Lyellian when he began to occupy himself with biological problems, even though ultimately he rebelled against some of the most basic beliefs of his teacher. Thus, politically and socially, Lyell belonged to the Darwin party. Conceptually, he never was a real Darwinian.

Except for these borderline cases, the issue was absolutely clear-cut for Darwin's contemporaries. If someone believed that the origin of the diversity of life was due to natural causes, then he was a Darwinian. But if he believed that the living world was the product of creation, then he was an anti-Darwinian. The existence of a few deistic borderline cases is no more a refutation of this basic classification than the existence of a number of incipient species is an argument against the existence of species.

Darwinism as a New Worldview

J. C. Greene (1986) has suggested, in line with the view of other historians of ideas, that the affix *-ism* should be used only for ideologies and not for scientific theories. I agree with him that one should not dignify adherence to ordinary scientific theories with the ending *-ism*. However, there are scientific theories that have become important pillars of ideologies, as is the case in Newtonianism, and this is certainly true for Darwinism. Some of Darwin's important new concepts, like variational evolution, natural selection, the interplay of chance and necessity, the absence of supernatural agents in evolution, the position of man in the realm of life, and others, are not only scientific theories but are at the same time important philosophical concepts, and characterize worldviews that have incorporated these concepts. Thus, as far as several of Darwin's most basic scientific theories are concerned, they have a legitimate standing both in science and in philosophy.

The rejection of special creation signified the destruction of a previously ruling worldview. This is why not only scientists like Sedgwick and Agassiz, but also philosophers like Whewell and Herschel, opposed Darwin so vigorously. Was there a new worldview that took the place of creationism? If so, what was it and how could it be defined? Greene suggests that henceforth "the word Darwinism should be used to designate a world view that seems to have been arrived at more or less independently by Spencer, Darwin, Huxley, and Wallace, in the late 1850s and early 1860s." Here he refers to a Victorian worldview in which certain sociological ideas were used to develop a new social theory. It was based in part on the writings of Adam Smith, Malthus, and David Ricardo, and postulated that competition, struggle, and the increase in populations would result in progress. Darwin was familiar with these ideas, but as has been shown by various careful analyses of the writings of Darwin and the social philosophers, these ideas were not the source of Darwin's biological ideas (see Gordon 1989), as much as some political writers would want us to believe this.

In his writings Darwin never upheld such a worldview. Being unable to find any support for his claims in Darwin's writings, Greene suggests that we adopt Herbert Spencer's worldview, which, according to Greene, was very much the same as that of

Darwin. Spencer's worldview is described by Greene as follows: "As a lawbound system of matter in motion, evolutionary deism verging toward agnosticism under the influence of positivistic empiricism, the idea of organic evolution, the idea of a social science of historical development, faith in the beneficient effects of competitive struggle," to single out the most important points. Was this really Darwin's worldview?

There are indications that Darwin shared in the prevailing beliefs of many enlightened upperclass Englishmen, including (according to Greene) Spencer, Huxley, and Wallace. But looking critically at the list of these beliefs, as presented by Greene, one discovers that it does not include a single one that was original with Darwin, in fact, not even a single one original with Spencer. Indeed, most of these views go all the way back to the eighteenth century, even though some of them had changed their meaning, such as the term "struggle for existence," which already had been part of natural theology. Even though Greene adopts the term "Darwinism" for this set of ideas, he admits, "Spencer could rightfully demand that it be called Spencerianism," because it does not include a single one of Darwin's own ideas. What is worse, this Spencerian paradigm is in several respects in complete conflict with Darwin's ideas. For instance, Spencer supported transformational rather than variational evolution; second, his evolution was distinctly teleological; and finally, it was based entirely on an inheritance of acquired characters, not involving natural selection in any manner. Hence, it was not only scientifically, but also philosophically, something quite different from Darwin's set of ideas. To claim that Darwin and Spencer supported the same paradigm is a clear falsification of history. It is a popular thesis with sociologists, but biologists who have looked into this problem in recent years have been unanimous in refuting it (Freeman 1974).

How long did the "Darwinism," as defined by Greene, prevail as a worldview? According to Greene, through the 1860s, and perhaps up to about 1875, but Spencer, Wallace, and Huxley actually abandoned one plank or the other of this platform soon after the 1860s. The consequences of scientific Darwinism made the acceptance of this social theory of Darwinism quite untenable.

Greene suggests that certain modern biologists, like Julian Huxley, George Gaylord Simpson, and perhaps Edward O. Wilson, have an updated Darwinian worldview. The truth of the matter is that unless a person is still an adherent of creationism and believes in the literal truth of every word in the Bible, every modern thinker—any modern person who has a worldview—is in the last analysis a Darwinian. The rejection of special creation, the inclusion of man into the realm of the living world (the elimination of the special position of man versus the animals), and various other beliefs of every enlightened modern person are ultimately all based on the consequences of the theories contained in the *Origin of Species*. Nevertheless, to define Darwinism as the worldview supposedly held by Darwin in the 1860s would be about the most useless definition I can imagine.

Darwinism as a New Methodology

In view of the intense preoccupation of modern philosophy of science with questions of methodology, it is not surprising that several philosophers have asked themselves what Darwin's method of science was, and what was new in it. Was Darwin's method strictly hypothetico-deductive, as suggested by Ghiselin (1969), or did he follow various other schemes? There have been diverging answers to these questions (Recker 1987). Almost any modern philosopher of science has suggested a somewhat different Darwinian methodology. How inductive was Darwin? Does the semantic approach to the philosophy of science describe Darwin's approach best? These are the sorts of questions being asked.

Darwin realized that to convince his readers of the validity of his concepts he had to adopt a methodology that was rather different from that used by physicists to demonstrate the validity of universal physical laws. Darwin's method was to present the evidence on which he based his inferences, and he used these inferences to support his conjectures. The greater the number and the variety of pieces of evidence he could cite, the more convincing the inferences became (Ghiselin 1969). Kitcher (1985) belittled Darwin's massive citing of supporting facts, not understanding that these facts were of little interest as such but only as evidence and documentation for the inferences that Darwin was making. These inferences not only served to support his conjectures, but they also reveal some of Darwin's basic underlying ideas.

One of the reasons why different authors were able to claim that Darwin had used different methodologies is that Darwin was rather pluralistic, methodologically. In some arguments he did indeed follow the hypothetico-deductive method; in others he was proceeding in an inductive manner. I think that any claim that Darwin consistently applied only a single method could easily be refuted. And what is more important, the ultimate validation of most of Darwin's theories did not result from the victory of his methodology but from additional facts and the gradual refutation of opposing ideologies.

Many authors have called attention to the spectacular unifying capacity of Darwin's paradigm. As Dobzhansky stated it, "Nothing in biology makes sense except in the light of evolution"; I might modify this by saying "in the light of Darwinian evolution." I think it is quite misleading to suggest, as is done by Kitcher, that it was the goodness of his methodology that had this unifying effect.

There is a widespread belief among philosophers that a theory has virtually no chance of being accepted unless an appropriate mechanism is proposed simultaneously. This is indeed often true. Wegener's theory of continental drift was not accepted by the geophysicists until the mechanism for the movement of continents had been elucidated in the theory of plate tectonics. It is not *necessarily* true, however, as shown by the theory of common descent. Darwin's proposed mechanism, natural selection, was almost universally rejected, but since the fact of evolution and the theory of common descent were so completely convincing after Darwin had pointed them out, other evolutionists simply adopted—instead of natural selection—various other kinds of mechanisms, whether teleological, Lamarckian, or saltational. Indeed, for Darwin himself, as much as he believed in natural selection all his life, it was obviously not this mechanism that was of first importance for him but the evidence for evolution and common descent. Hence the completely unbalanced assignment of space to these two subjects in the *Origin*.

The version of Darwinism that developed during the evolutionary synthesis was characterized by its balanced emphasis both on natural selection and on stochastic processes; by its belief that neither evolution as a whole, nor natural selection in particular cases, is deterministic but rather that both are probabilistic processes; by its emphasis that the origin of diversity is as important a component of evolution as is adaptation; and by its realization that selection for reproductive success is as important a process in evolution as selection for survival qualities.

The Pluralism of Darwinism

It is now clear that no simple answer can be given to the question "What is Darwinism?" When someone asks this question, he is bound to receive a different answer depending on the time that has passed since 1859 and on the ideology of the person that was asked. Such pluralism is not congenial to many philosophers, and they have been trying to find some method by which they could attach the term Darwinism to a very definite meaning. The suggestion was made, for instance, that one should select an "exemplar" to fix the meaning of the term Darwinism, analogous to the action of a taxonomist who selects a type specimen in order to anchor a species to a definite name. Hull (1983; 1985) has indeed attempted to do so, but I have shown elsewhere (1983, 1989) what insurmountable difficulties oppose the application of the exemplar method.

The majority of the nine meanings of the term Darwinism discussed above are clearly either misleading or unrepresentative of Darwin's thought. Looking at the situation as a historian, I am impressed that two meanings have had the widest acceptance. After 1859, that is, during the first Darwinian revolution, Darwinism for almost everybody meant explaining the living world by natural processes. As we will see, during and after the evolutionary synthesis the term "Darwinism" unanimously meant adaptive evolutionary change under the influence of natural selection, and variational instead of transformational evolution. These are the only two truly meaningful concepts of Darwinism, the one ruling in the nineteenth century (and up to about 1930), the other ruling in the twentieth century (a consensus having been reached during the evolutionary synthesis). Any other use of the term Darwinism by a modern author is bound to be misleading.