Charles Darwin

On the Origin of Species



A Facsimile of the First Edition

with an Introduction by Ernst Mayr Author of *Growth of Biological Thought*

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BY CHARLES DARWIN

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INTRODUCTION

The publication of the Origin of Species ushered in a new era in our thinking about the nature of man. The intelectual revolution it caused and the impact it had on man's concept of himself and the world were greater than those caused by the works of Copernicus. Newton, and the great physicists of more recent times. The effect was immediate. the first edition being sold out on the day of publication (24 November 1859): a second printing was issued a month later (28 December). In its first year the work sold 3,800 copies. and in Darwin's lifetime the British printings alone sold more than 27,000 copies. In addition there were several American printings, as well as innumerable translations. Quite rightly, the Origin has been referred to as "the book that shook the world." but only in our lifetime has it become clear how true this statement is. Only now can we appreciate in how many different ways the Origin departed from established concepts and how many new directions it opened up. Every modern discussion of man's future, the population explosion, the struggle for existence. the purpose of man and the universe, and man's place in nature rests on Darwin.

It is now more than 100 years since Darwin's classic was published and the science of evolution has come of age. Yet, even within the last 25 years this science has continued to make steady progress. There is now an international journal, Evolution, entirely devoted to the subject. More essays on evolution are now published in a single year than were published in a decade during the last

century. One would surely expect the *Origin* to be totally obsolete. It is startling to find that this is not the case. Though Darwin was wrong in his discussions of inheritance and the origin of variation, confused about varieties and species, and unable to elucidate the problem of the multiplication of species, he was successful in discovering the basic mechanism of evolutionary change. The evolutionist is closer today to the Darwin of 1859 than at any other period in the last 100 years. This is why the *Origin* is so timely a classic.

Charles Robert Darwin was born on 12 February 1809. the son of Robert Waring Darwin, a country physician. As a young man in school and university, he was far more interested in natural history than in medicine or divinity. the professions his family thought most suitable for him. All uncertainties about his future were dispelled, however. when in 1831 he joined the company of the survey vessel H.M.S. "Beagle" as a naturalist. The five-year period he spent on the "Beagle" (2 December 1831 to 29 October 1836) was the decisive event of his life. The longest portion of this period was devoted to a survey of the coasts of South America and the off-lying islands. Darwin (1839) described his many adventures and observations in a still very readable volume.1 Tropical forests in Brazil, Pleistocene and Tertiary fossils in the Pampas of Argentina, the Indians of Tierra del Fuego, the geology of the Andes, and most of all the animal life of the Galapagos Islands left an indelible imprint on his thinking. Darwin's two greatest virtues, keenness of observation and the ability to ask searching questions, enabled him to accumulate a wealth of material on this voyage. To the analysis and interpretation of his findings he devoted most of his time after the return of the "Beagle," first at London and, after 1842, in

¹ See the Bibliography for a list of Darwin's works and other relevant literature.

the small village of Down, Kent, 16 miles south of London, where he lived for the next 40 years. It was at Down that he wrote the *Origin*, as well as most of his other major publications. Owing to ill health, now believed to have been due to a tropical disease (probably Chagas's disease) acquired in Argentina during the voyage of the "Beagle," Darwin did no extensive traveling and refused to occupy public office. His death, after an extraordinarily productive life, came on 19 April 1882.

The immediate success of the Origin indicates that the world was ready for the theory of evolution. The fact that ten editions of a popular evolutionary tract. Chambers's Vestiges of the Natural History of Creation, had appeared prior to 1859, as well as the publications of Erasmus Darwin, Lamarck. Wells, Lawrence, Prichard, Matthew. Naudin, and others, indicate how widespread the idea of evolution was by the middle of the century. Curiously, at that time the concept appealed particularly to laymen. Those who were best informed about biology, and especially about classification and morphology, upheld most strongly the dogma of creation and the constancy of species. Indeed, in 1858 this dogma was virtually unanimously endorsed by anatomists, zoologists, and botanists, including some of Darwin's closest friends, whom he was later able to convert to his views. It is Darwin, and Darwin alone, who deserves the credit for having changed this situation overnight.

Our admiration for his perspicacity grows when we consider how few of the facts on which the modern biologist bases his acceptance of evolution were then known. The number of known fossils was small, and no connecting links between major groups of animals had yet been discovered, such as *Archaeopteryx* between reptiles and birds, *Ichthyostega* between "fishes" and amphibians,

¹ S. Adler, "Darwin's illness," Nature 184 (1959), 1102-1103.

and the mammallike reptiles. What little was known about inheritance was misinterpreted. The then accepted zoological system of Cuvier recognized no more and no fewer than four "totally distinct" types of animals. Many branches of biology that have since contributed much evidence in favor of evolution, such as cytology and endocrinology, did not yet exist, and others, such as embryology, were still rudimentary. Yet Darwin not only convinced himself that the diversity of animal and plant life is due to descent from common ancestors, but argued his case so well that he eventually convinced the great majority of his biological colleagues. The variation of domestic animals and cultivated plants (Chapter I).1 variation in nature (Chapter II), the facts of paleontology (Chapter X), of geographical distribution (Chapters XI and XII), and of classification, morphology, and embryology (Chapter XIII) supplied most of his material. And he marshaled his evidence with supreme skill. The overwhelming impression one receives on reading these chapters is Darwin's complete mastery of the subject. He is equally at home in zoology, botany, and paleontology. He quotes studies in systematics, morphology. biogeography, animal and plant breeding, and behavior. He is a shrewd observer and vet, whenever possible, he tests his conclusions by experiment.

The Origin was the product of more than 20 years of dedicated labor. Darwin had become convinced of the occurrence of evolution some time between 1835 (his visit to the Galapagos) and July 1837, when he opened his first notebook on the "transmutation of species." By 1844, his views had reached considerable maturity, as shown by his manuscript "Essay," which occupies 160 pages organized into 10 chapters in a recently printed version (Darwin 1958).

¹ References throughout are to the first edition of the Origin.

DARWIN'S CONTRIBUTION

The Origin of Species was far from a mere accumulation of facts proving evolution. Let me discuss some aspects of it that account for its importance and its immediate success.

For Darwin, evolution was more than change of appearance due to the unfolding of preformed inherent tendencies. His concept of evolution required a real genetic change from generation to generation, a complete break with the so-called evolutionary concepts of Lamarck and virtually all other forerunners. Darwin started from a new basis by completely eliminating the last remnants of Platonism, by refusing to admit the *eidos* (Idea; type, essence) in any guise whatsoever.

As a young naturalist and explorer, Darwin had made a series of observations that he was unable to explain on the basis of the prevailing ideologies. Convinced that he had to start on an entirely new track, he realized that he must avoid at all costs the danger of being deflected from this true course by prevailing dogmas. Hence his fierce independence and the secrecy with which he concealed his basic ideas even from his closest friends. Neither naturalists nor philosophers were able to shake his determination.

No one resented Darwin's independence of thought more than the philosophers. How could anyone dare to change our concept of the universe and man's position in it without arguing for or against Plato, for or against Descartes, for or against Kant? Darwin had violated all the rules of the game by placing his argument entirely outside the traditional framework of classical philosophical concepts and terminologies. Perhaps this is the greatest difference between him and all of his predecessors, be they antievolutionists such as Linnaeus, Cuvier, and Louis

Agassiz, or evolutionists such as Lamarck. No other work advertised to the world the emancipation of science from philosophy as blatantly as did Darwin's *Origin*. For this he has not been forgiven to this day by some traditional schools of philosophy. To them, Darwin is still incomprehensible, "unphilosophical," and a bête noire.

It is impossible to believe simultaneously in two opposing theories explaining the same set of phenomena. In Darwin's day the prevailing explanation for organic diversity was the story of creation in Genesis. Darwin himself had subscribed to this when he shipped on the "Beagle." and he was converted to his new ideas only after he had made numerous observations that were to him quite incompatible with creation. He felt strongly that he must establish this point decisively before his readers would be willing to listen to the evolutionary interpretation. Again and again, he describes phenomena that do not fit the creation theory. Three sets of observations, in particular, impressed Darwin: that fossils from South America are related to the living fauna of that continent rather than to contemporaneous fossils from elsewhere: that the faunas of the different climatic zones of South America are related to each other, rather than to animals of the same climatic zone on different continents: and. most important, that the faunas of islands (Falkland. Galapagos) are related to those of the nearest mainland and that related species occur on different islands of the same archipelago, Chapter 13 (pp. 349-387) is devoted largely to such evidence. Other cases are mentioned on page 95 (fossil lineages), page 129 (the order of the natural system), page 139 (the similarity of cave animals on all continents), page 167 (homologous variation in related species and genera), page 352 (disjunct distributions), pages 355 and 396-399 (the relationship of island species to those of the nearest continents), page 390

(the vulnerability of island species), page 394 (the unbalanced biota of volcanic and other oceanic islands), and pages 473–474 (rudimentary characters), to single out the more important instances. All these observations were to Darwin incompatible with any creationist explanation, yet were entirely consistent with an evolutionary interpretation.

Creationism was not the only ideology unacceptable to Darwin; so also were various previously proposed evolutionary hypotheses. He argues, for instance, the improbability of evolutionary progress by major steps (pp. 4, 194), noting that such saltations would make it difficult for natural selection to act, since this would interfere with the mutual coadaptation of different kinds of organisms.

Darwin takes special pains in the first edition of the Origin to refute the probability of a direct effect of the environment on evolving organisms (for instance, pp. 3. 10, 134, 336). He quite rightly singles out the case of the adaptations in the neutral castes of social insects as inexplicable by any kind of Lamarckian theory: "For no amount of exercise, or habit, or volition, in the utterly sterile members of a community could possibly have affected the structure or instincts of the fertile members. which alone leave descendants. I am surprised that no one has advanced this demonstrative case of neuter insects, against the well-known doctrine of Lamarck" (p. 242). Darwin was equally emphatic in rejecting (Chapter 10 and page 351) any "law of necessary development," later designated as orthogenesis. Here, as in so many other cases. he is strongly supported by modern researches. Darwin. however, did make some concessions to the possible existence of evolutionary factors other than random variation and natural selection, as I shall discuss below.

The works of Darwin's forerunners had so little impact

because they were either vague speculations, uninformed and uncritical compilations, or entirely incidental remarks in works devoted to other subjects. The Origin was the first publication to present scientifically sound, wellorganized evidence for evolution, and to present it in abundance. Darwin had devoted more than 20 years to excerpting an enormous body of biological literature, to corresponding with an impressive array of specialists of all sorts, to observation, and to experimentation, Only a few other volumes now in print marshal the evidence in favor of evolution in so complete and convincing a manner; Darwin's thoroughness is one of the reasons that the Origin is still readable today. Most impressive is the expert handling of the data: the years Darwin devoted to the preparation of his four-volume monograph of the barnacles contributed importantly to his education as an evolutionist

That the Origin presented a deliberate challenge by science to religion is a misrepresentation; nothing was further from Darwin's mind than to extend such a challenge. Indeed, the wording throughout the Origin is extremely careful so as not to offend sensitive readers. If a challenge was contained, it was to Darwin's scientific peers. The ridicule heaped on Chambers's dilettante Vestiges of Creation and even on the more serious efforts of Lamarck and Geoffrov Saint-Hilaire caused Darwin to wait more than 20 years before publishing his theory. Indeed, publication might have been delayed even beyond 1859 had Darwin not been virtually forced into action by the independent discovery of natural selection as the main agent of evolutionary change by Alfred Russel Wallace (1858). That a number of outstanding naturalists had come out against evolution in the 30 years preceding the publication of the Origin compounded the difficulties.

Darwin realized that it was not enough to present evi-

dence in favor of evolution, but that he would have to anticipate all conceivable counterarguments and try to answer them one by one. His forerunners had failed so miserably to convince their readers because they minimized the difficulties. In his Autobiography. Darwin wrote: "I had during many years followed a golden rule, namely . . . whenever [I came acrossl a published fact, a new observation or thought... which was opposed to my general results to make a memorandum of it without fail and at once: for I had found by experience that such facts and thoughts were far more apt to escape from the memory than favorable ones. Owing to this habit very few objections were raised against my views which I had not at least noticed and attempted to answer." Accordingly, the sixth chapter of the Origin is entitled "Difficulties on Theory." However, the comment in the Autobiography is perhaps a little optimistic, because in the sixth edition Darwin added a new chapter of about 40 pages, entitled "Miscellaneous Objections to the Theory of Natural Selection," and (as we shall see below) found certain objections sufficiently grave to modify some of his earlier views. Nevertheless, he was right in claiming that he had given thought to most of the possible objections to an evolutionary interpretation, and we now know that nearly all of his answers were correct, particularly his insistence on the imperfection of the known geological record.

Darwin was the first evolutionist to advance a theory of evolution that did not seek refuge in "final causes" or vitalism. His mechanism, natural selection, would seem at first sight simplicity itself: if always the best, the fittest, survive, and if there is a difference in genetic endowment among individuals, the race will by necessity steadily improve. No wonder T. H. Huxley said on reading the *Origin*, "How extremely stupid not to have thought of that."

Even more important is the particular role that Darwin gave to natural selection. He realized from the very beginning that evolutionary change is a two-step process: the first step consists of the production of variation, and the second, of the sorting of this variability by natural selection. Many opponents of Darwinism failed to understand the complementary roles of variation and selection and protested that Darwin had postulated a brute. mechanical, soulless universe, depending on the whims of accident. Valid when raised against the evolutionary concepts of the early Mendelians (Bateson, De Vries, and other mutationists), who explained evolution as the result of mutation alone, the protest misses the mark when raised against Darwin. To be sure, Darwin was vague and confused about the origin of genetic variation, a point cleared up only in the 20th century (De Vries. T. H. Morgan, H. J. Muller, Avery, and Watson and Crick). But Darwin, with his customary keen ability to observe, concluded that the abundant variability always present in nature resulted not from major saltations but from the accumulation of small changes occurring at random with respect to environmental conditions. What Darwin was far more interested in, intensely so, was what nature did with this abundantly available genetic variability. And here is the essence of the whole concept of natural selection: survival, the ability to contribute to the genetic content of the next generation, is not at all a matter of accident, but a statistically predictable property of the genotype. The immense power and universal occurrence of natural selection have, in the meantime, been demonstrated by thousands of modern selection experiments and by controlled observations of individually marked natural populations. That natural selection is a direction-giving force, within the limitations of the evolutionary potential set for a given species by its genotype, has now been substantiated abundantly. It is now apparent how absurd is the glib claim that Darwinism expounds the production of perfection by accident, the rule of "higgledy-piggledy," as Samuel Butler called it.

The full title of the Origin indicates clearly how important Darwin considered natural selection to be. Chapter IV (pp. 80-130) is specifically devoted to this concept, as is Chapter III. entitled "Struggle for Existence." It has often been deplored that Darwin adopted from contemporary writers such misleading terms as "struggle for existence" and "struggle for life." because it gave currency to the idea that he shared Tennyson's concept of "nature red in tooth and claw." Actually, Darwin took great pains to point out that he meant something much broader: "I should premise that I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny" (p. 62). How highly he rated mutual dependence is evident also from his discussion of the neuter castes in social insects (pp. 237-238). It is a revelation to the modern reader how fully aware Darwin was that success in leaving progeny is a more important component of natural selection than is mere survival. His discussions also make it abundantly clear that he considered selection not a purely negative force that eliminates the unfit, but a positive, constructive force that accumulates the beneficial (see, for instance, pp. 61, 79, 81, 95, 127, 170, 233, 320, 433, and 467). He was also aware of the probabilistic character of natural selection: "Natural selection will not produce absolute perfection" (p. 202). In retrospect, it is evident that nearly all the denunciations of Darwin's ideas on natural selection were based on an incomplete knowledge of the Origin and on misunderstanding.

Its startling simplicity was the most formidable obstacle that the selection theory had to overcome. Students of the phenomena of life found it undignified to explain progress. adaptation, and design in nature in so mechanistic a manner. "How can the beauty and harmony of the universe have evolved by accident?" they asked, in spite of Darwin's careful proof that survival depends not on accident but on genetic properties. For Darwin had pointed out patiently that only some individuals in every population reproduce (fewer than one in a million, in the case of the spat of ovsters and the offspring of large trees). that they all differ in their genetic properties, and that the probability (not certainty) of their reproductive success depends on these genetic properties. The next generation will be enriched by the characteristics of "favored" individuals, and thus the adjustment to the environment will be improved from generation to generation. In this way Darwin solved the problem of teleology. a problem that had occupied the best minds for the 2000 vears since Aristotle.

It is almost universally stated that Darwin was no philosopher, that he was totally unphilosophical. Even though he himself would probably have pleaded guilty, this accusation is actually quite misleading. To be sure, Darwin did not belong to any of the established schools of philosophy, nor did he ever publish an essay or volume explicitly devoted to an exposition of his philosophical ideas. Yet few writers in the last 200 years have had so profound an impact on our thinking. This holds for logic, metaphysics, and ethics. It has taken 100 years to appreciate fully that Darwin's conceptual framework is, indeed, a new philosophical system.

The novelty of thought that students of intellectual history discern more and more in Darwin's *Origin* is so elusive because it is so modern. Darwin's historical

approach, his modelmaking, his demolition of unsatisfactory models before proposing new ones, his elimination of prediction from causation, his "population thinking." the very special way in which he uses the "comparative method," all of this is now so thoroughly accepted that it is difficult to appreciate how modern and outright revolutionary much of it was in Darwin's day, and how overwhelming in the total combination in which Darwin presented it. It was quite overlooked, in the uproar over evolution, religion, and man's place in nature, that Darwin had introduced a new way of thinking. Darwin himself was apparently unaware of it. He never challenged but simply ignored the established concepts of the various schools of philosophy. As a consequence, philosophers found it exceedingly difficult to deal with this new thinker. but none of the new concepts caused them more trouble than population thinking:

"What is this population thinking and how does it differ from typological thinking, the then prevailing mode of thinking? Typological thinking, no doubt, had its roots in the earliest efforts of primitive man to classify the bewildering diversity of nature into categories. The eidos of Plato is the formal philosophical codification of this form of thinking. According to it, there are a limited number of fixed, unchangeable 'ideas' underlying the observed variability, with the eidos (idea) being the only thing that is fixed and real, while the observed variability has no more reality than the shadows of an object on a cave wall, as it is stated in Plato's allegory... Most of the great philosophers of the 17th, 18th, and 19th centuries were influenced by the idealistic philosophy of Plato, and this school dominated the thinking of the period...

"The assumptions of population thinking are diametrically opposed to those of the typologist. The populationist stresses the uniqueness of everything in the organic

world. What is true for the human species — that no two individuals are alike — is equally true for all other species of animals and plants . . . All organisms and organic phenomena are composed of unique features and can be described collectively only in statistical terms. Individuals, or any kind of organic entities, form populations of which we can determine the arithmetic mean and the statistics of variation. Averages are merely statistical abstractions, only the individuals of which the populations are composed have reality. The ultimate conclusions of the population thinker and of the typologist are precisely the opposite. For the typologist, the type (eidos) is real and the variation an illusion, while for the populationist, the type (average) is an abstraction and only the variation is real. No two ways of looking at nature could be more different." 1

Any attachment to metaphysical idealism, any commitment to an unchanging eidos, precludes belief in descent with modification. The concept of evolution rejects the eidos, replacing it with the variable population. Gradual evolution and natural selection, emphasized so strongly and consistently by Darwin, are inconceivable except through population thinking. And, having abandoned the eidos in the context of evolutionary theory, one finds it untenable also in every other way. The philosophical consequences of this aspect of Darwinism have not yet been fully exploited.

CRITICISM

The Origin of Species did not fare well at the hands of its critics. Perhaps more works were published in the first 50 years after 1859 that tried to discredit or disprove Darwin than those that supported him. In addition to

¹ E. Mayr, in *Evolution and Anthropology* (Washington: Anthropological Society of Washington, 1959), p. 2.