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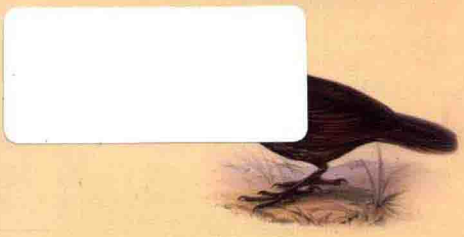
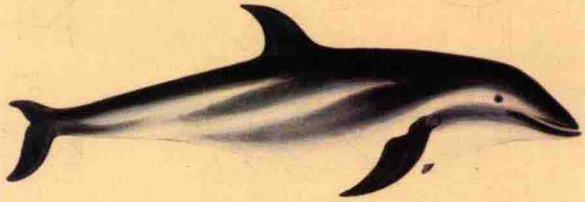


CHARLES DARWIN

THE ORIGIN *of* SPECIES

WITH AN INTRODUCTION BY SIR JULIAN HUXLEY



Charles Darwin

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION
OF THE PRESERVATION OF FAVOURED
RACES IN THE STRUGGLE FOR LIFE

SIGNET CLASSICS

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THE THEORY THAT SHOOK THE WORLD

Few other books have created such a lasting storm of controversy as *The Origin of Species*. Darwin's theory that species derive from other species by a gradual evolutionary process and that the average level of each species is heightened by the "survival of the fittest" stirred up popular debate to a fever pitch. Its acceptance revolutionized the course of science.

As Sir Julian Huxley, the noted biologist, points out in his illuminating introduction, the importance of Darwin's contribution to modern scientific knowledge is almost impossible to evaluate: "a truly great book, one which can still be read with profit by professional biologists."

"Darwin was one of history's towering geniuses and ranks with the greatest heroes of man's intellectual progress."
—George Gaylord Simpson in *The Meaning of Evolution*

INTRODUCTION

IT IS APPROPRIATE that this new edition of *The Origin of Species* should appear during the centenary year of Darwin and Wallace's joint paper at the Linnaean Society (July 1, 1858), for it was the bombshell of Alfred Russel Wallace's independent discovery of the principle of natural selection which stimulated Darwin to publish his book. He had been convinced of the mutability of species—what we should now call their evolution—by his experiences on H.M.S. *Beagle* and had been collecting facts bearing on the subject since 1837. But his cautious, and almost diffident, temperament held him back from publishing his conclusions (whose acceptance, he fully realized, would mean a revolution in scientific and general thought) until he could support them with adequate facts. Indeed, it was not until 1842 that he "allowed himself the satisfaction" of writing out a brief thirty-five-page abstract of his theory. Two years later he enlarged this into an "Essay" (though an essay of 230 pages), which is really a first draft of the *Origin*. However, he showed this only to Lyell and Hooker (and corresponded about his conclusions with Asa Gray). For fifteen further years he went on elaborating his ideas and collecting facts in support of them, with a view to publishing a truly convincing work—a "very big" book, "as perfect as ever I can make it"; and if it had not been for Wallace's moment of inspiration in Ternate, when the idea of natural selection flashed into his fever-stimulated brain, Darwin might well have continued doing so for another fifteen years, and the resultant book might have been unreadably monumental.

As it is, the *Origin* was written in the short space of little over a year, and was the product of a white heat of urgency working on the fruits of twenty-two years' industry and reflection. It is interesting to note that even as Darwin presented the manuscript to his publisher, his characteristic wariness did not leave him. He wrote to John Murray: "Accept your offer. But I feel bound for your sake and my own

to say in clearest terms that if after looking over part of the MS you do not think it likely to have a remunerative sale I completely and explicitly free you from your offer."* Such was his comment accompanying the emergence of a truly great book, one which after a century of scientific progress, can still be read with profit by professional biologists.

Why is *The Origin of Species* such a great book? First of all, because it convincingly demonstrates the fact of evolution: it provides a vast and well-chosen body of evidence showing that existing animals and plants cannot have been separately created in their present forms, but must have evolved from earlier forms by slow transformation. And secondly, because the theory of natural selection, which the *Origin* so fully and so lucidly expounds, provides a mechanism by which such transformation could and would automatically be produced. Natural selection rendered evolution scientifically intelligible: it was this more than anything else which convinced professional biologists like Sir Joseph Hooker, T. H. Huxley and Ernst Haeckel.

In neither case did Darwin shrink from drawing the most general conclusions. To begin with, he realized that evolution must be a universal phenomenon. If different species of groundfinches or armadillos could be produced by evolution from a common ancestor, then, given enough time, the same must hold for different families, orders, and classes and for the diversity of life as a whole: all living organisms must be related through their common descent from some simple original stock. Further, since all organisms vary, and all reproduce themselves in greater numbers than can survive, there must always be competition between variants; in other words, the principle of natural selection, too, is universally applicable.

For these reasons, Wallace himself rightly styled Darwin "the Newton of Natural History," or, as we should now say, of Biology. Each introduced the ideas of unity, order, and universally applicable principle into an enormous realm of experience.

In 1859, the area of biological ignorance was very large.

* Quoted by kind permission of Sir John Murray.

Nothing was known of the mechanisms of fertilization, heredity and variation, nor of embryonic differentiation; the scientific study of animal behaviour, biogeography and ecology had scarcely begun; no good paleontological series, like those of horse or elephant evolution, had been discovered, nor any fossils bearing on the ancestry of man; and the time-scale admitted by geologists and physicists was grossly inadequate. Yet in spite of this, Darwin in the *Origin* gave a remarkably good general picture of the evolutionary process, and followed out the implications of natural selection in a quite astonishing way.

Thus he deduced that natural selection must inevitably bring about the "improvement" of organisms, improvement which, as he characteristically added, was always in relation to the conditions of life. This, though he did not himself claim it, was in fact another universal biological law, covering detailed adaptations to particular circumstances (like the resemblance of leaf insects to leaves), specializations for a particular mode of life (like that of the horses for rapid running and grazing), advances in efficiency of major functions (like flight, or vision, or co-ordination of behaviour), or improvements in general organizational plan (like that of arthropods as against segmented worms, or of placentals as against primitive mammals).

He also deduced the inevitability of divergence or diversification—the fact that any successful type would inevitably diverge into two or more diverse types, each adapted to a somewhat different habitat or niche or way of life. This, too, could have been formulated as a universal biological law, for it operates, as Darwin showed, on every scale, from the formation of geographical races within a single species, through cases like that of the single groundfinch ancestor on the Galapagos splitting into a number of distinct genera and species, to the radiation of a large subclass like that of placental mammals into numerous orders, each with its own way of life, up to the divergence of plants from animals. Indeed, as he also pointed out, diversification is itself a biological advantage, since it enables a given area to support a greater bulk of living matter, and in general makes it possible for life to exploit the resources of the environment more fully. Though later-evolving groups are more highly

organized, he rightly argued that we should not expect all groups and types of organisms to evolve in the direction of higher organization. Thus single-celled forms, through the very fact of their small size and rapid reproduction, fill a certain natural niche more successfully than larger multicellular creatures can do.

He further showed that natural selection, by its nature, could never cause or promote the evolution of a character which was primarily of advantage to another species. This is a negative generalization as important in its way as the impossibility of perpetual motion is in physical science.

He anticipated modern evolutionary genetics by deducing that large species (with an abundance of individual members) and large genera containing many species will be more variable than small ones, and more likely to produce new species in the course of evolution.

Of course, his views have often had to be modified in detail. This is especially true when he is discussing heredity and variation, since in his day the mechanisms of genetics and mutation were completely unknown.

There was a period, from about 1895 to about 1925, when Darwinism came in for a great deal of criticism, sometimes violent, from many of the leading biologists of the time. They questioned the very notion that characters such as cryptic or warning coloration are advantageous or adaptive, and indeed were inclined to dismiss the whole idea of adaptation contemptuously as mere teleological speculation. The Lamarckians and the Vitalists rejected the idea of natural selection as too materialistic and as giving insufficient weight to will and effort and other psychological forces. The early Mendelians, fascinated by the discovery of genetic units (gene-differences) with large effects (such as hornlessness in cattle, or albinism in many vertebrates), wanted to make mutation responsible for positive evolutionary change, and assigned to natural selection only the essentially negative function of getting rid of harmful variants. Many of them rejected the idea of slow biological improvement and gradual evolution in favour of stepwise mutational changes of large extent. The position was finally complicated by the fact that the biometricians, preoccupied with the gradual variation so often found in nature, wanted

to deny the importance of Mendelism, and confused the heritable variations of character produced by changes in the genes with the nonheritable ones produced by changes in the environment.

Eventually, however, these various contradictions were reconciled. Lamarckian and vitalistic explanations were ruled out when it was shown that acquired characters, whether impressed by the environment or resulting from use or individual effort, were never inherited. The advance of genetics showed that large mutations were rarer and of far less biological importance than those of small extent, and that, apparently, continuous evolutionary change could be, and often was, brought about by the accumulation of numerous small discontinuous mutations under the guidance of natural selection. And finally R. A. Fisher in 1930 made it clear that the fact of heredity being particulate—dependent on distinct self-reproducing units or genes, each of which could mutate into new self-reproducing forms—and the further fact that most mutants are recessive, at once got rid of the major difficulties that beset Darwin, who accepted the current view of blending heredity—the view that characters and the entities that determined them were commingled into a single blend when crossed. This would imply that any new character would be progressively diluted by crossing in each generation, and would make its establishment in the stock difficult. But a particulate genetic mechanism in which most mutants are recessive makes it possible for new mutants to be stored indefinitely in the constitution, and for new combinations of new and old genes to be formed, ready to be utilized by selection when conditions are favourable. Natural selection was seen, not as involving the sharp alternatives of life or death, but as the result of the differential survival of variants; and it was established that even slight advantages, of one-half of one per cent or less, could have important evolutionary effects.

With this, Darwinism took on a new lease of life. Neo-Darwinism, as we may call the modern theory of gradual transformation operated by natural selection acting on a Mendelian genetic outfit of self-reproducing and self-varying genes, is fully accepted by the great majority of students of evolution. Darwin would have rejoiced to see how,

even in the light of our enormously increased knowledge, it (and it alone) can account for the varied and often puzzling facts of evolution—the different types and degrees of adaptation; the (geologically speaking) rapid transformation of some types side by side with the unchanged persistence of others; the coexistence of lower and higher forms; the succession of constantly more improved types; extinction; the facts of geographical distribution; the evolution of insect societies based on elaborate instincts. Today, a century after the publication of the *Origin,* Darwin's great discovery, the universal principle of natural selection, is firmly and finally established as the sole agency of major evolutionary change.

In the *Origin,* Darwin had already adumbrated many ideas which he or others afterward followed out in more detail. Thus he mentions the existence of plants with two or three types of flower, like primroses, and explains it as a means of avoiding self-fertilization and inbreeding, a subject which he amplified in two books published in 1876 and 1877. He explained how psychological characters like instincts and emotions could and would be evolved by natural means, though it was not until 1872 that, with his remarkable book *The Expression of the Emotions in Man and Animals,* he initiated the comparative study of animal behaviour, or ethology as it is now called. By his constant emphasis on the complicated web of interrelations between different organisms in a given habitat or region he laid the foundations for the new and flourishing branch of science now known as ecology.

In the *Origin* he briefly outlines his theory of sexual selection, which he later (in 1871) developed at great length in his big book *The Descent of Man.* He regarded sexual selection as a subsidiary mechanism of evolution, needed to account for the development of male secondary sexual characters, notably weapons like stags' antlers or exaggerated plumes and conspicuous displays like those of many male birds. Though this theory has been bitterly attacked (often by those without adequate knowledge of the facts), and has had to be modified in various particulars, it provides another example of Darwin's originality and insight. He correctly deduced that such characters, though irrel-

evant in the general struggle for existence or in competition with other species, would be of advantage in what he called the struggle for reproduction, which must exist between differently endowed males. Selection here is therefore sexual, or as the modern formulation more correctly puts it, intrasexual—between members of the same sex. It is indeed the best example of intraspecific selection, the result of competition between members of the same species; and the resultant characters (for instance the fantastically exaggerated wings of the Argus pheasant) may even be a disadvantage in the struggle for existence.

Further, though most courtship-display characters are directed to raise the female's readiness to perform the act of mating rather than towards her choice of one male rather than another as mate, it remains true that, as Darwin suggested, they exert their effect via the sense organs, mind and brain of another individual—in this case the female. They are among the most obvious examples of such *allaesthetic* characters, as we now style them. Thus Darwin had hit on the important principle that selection could be of different types, acting in different and sometimes contradictory ways, and through different operational channels.

Though Darwin was cautious not to put forward unsupported conclusions, once he had established the validity of his ideas to his own satisfaction he did not hesitate to draw the fullest implications from them—though even here, his modesty was always in evidence. Thus at the end of the *Origin* he writes that when his and Wallace's views "or analogous views on the origin of species are generally admitted, we can dimly foresee that there will be a considerable revolution in natural history"!

He then proceeds to much firmer prophecies, all of which have come true. "A grand and almost untrodden field of inquiry will be opened, on the causes and laws of variation, on correlation, on the effects of use and disuse." "Our classifications will come to be, as far as they can be so made, genealogies; and will then truly give what may be called the plan of creation." "Psychology will be based on a new foundation," and finally that immortal understatement, "Light will be thrown on the origin of man and his history."

Today we can go much further: owing to Darwin, our

entire picture of man and of his place and role in nature has been transformed. At first, the emphasis was on origins. Darwin did not call his great book *The Evolution of Life,* but *The Origin of Species*; and when he later came to discuss human evolution his title was not *The Ascent* but *The Descent of Man.* This approach characterized most of the work done during the remainder of the nineteenth century in the vast field which Darwin had opened up. Biologists largely concerned themselves with establishing relationships and constructing forests of family trees. As regards man, it became ever clearer that he had originated from an ancestor sufficiently ape-like to be placed in the same group with the existing great apes. Man could no longer be regarded as the Lord of Creation, a being apart from the rest of nature. He was merely the representative of one among many Families of the order Primates in the class Mammalia.

However, as time went on the approach changed. The fact of evolution had been established and was no longer in need of further proof. Later, the underlying mechanisms of genetics and variation were discovered and the principle of natural selection was established as the method of evolution. It now remained to study the course of evolution as a process.

This approach yielded several important new points of view. In the first place, not only did discovery still further enlarge the time-scale of evolution, so that it now has to be measured not in millions but in thousands of millions of years, but emphasis began to be laid on its future as well as on its past. It became clear that man had as vast spans of time before him as those he had enjoyed for his entire evolution from his first submicroscopic ancestor. Secondly, evolution came to be increasingly looked at as a process of realization of new possibilities, and so involving an element of progress. And thirdly, evolutionary succession, in which an earlier successful or dominant type is wholly or largely replaced by a new and biologically improved type, began to be studied. Darwin had noted and correctly interpreted a few cases of succession. It now became clear that succession was a widespread and indeed general fact of evolution, and constituted the method by which major

evolutionary advance was achieved. The reason that the reptiles were largely replaced by the mammals as dominant land vertebrates was because the mammals were in a perfectly legitimate sense of the word *higher* organisms than the reptiles. It further emerged that man constitutes the latest dominant group, and is today, thanks to his new method of evolving by the cumulative transmission of experience, the only type capable of realizing important new possibilities and of achieving further major advances in the future. Thus, in the light of the science of evolutionary biology which Darwin founded, man is seen not just as a part of nature, but as a very peculiar and indeed unique part. In his person the evolutionary process has become conscious of itself, and he alone is capable of leading it on to realizations of possibility. A century after Darwin's modest statement that light will be thrown on the origin of man, we can truly say that, as a result of Darwin's work in general and of *The Origin of Species* in particular, light has been thrown on his destiny.

—Sir Julian Huxley

AN HISTORICAL SKETCH

OF THE PROGRESS OF OPINION ON THE ORIGIN OF SPECIES, PREVIOUSLY TO THE PUBLICATION OF THE FIRST EDITION OF THIS WORK

I WILL HERE give a brief sketch of the progress of opinion on the Origin of Species. Until recently the great majority of naturalists believed that species were immutable productions, and had been separately created. This view has been ably maintained by many authors. Some few naturalists, on the other hand, have believed that species undergo modification and that the existing forms of life are the descendants by true generation of pre-existing forms. Passing over allusions to the subject in the classical writers,* the first author who in modern times has treated it in a scientific spirit was Buffon. But as his opinions fluctuated greatly at different periods, and as he does not enter on the causes or means of the transformation of species, I need not here enter on details.

*Aristotle, in his 'Physicae Auscultationes' (lib. 2, cap. 8, s. 2), after remarking that rain does not fall in order to make the corn grow, any more than it falls to spoil the farmer's corn when threshed out of doors, applies the same argument to organisation; and adds (as translated by Mr. Clair Grece, who first pointed out the passage to me), "So what hinders the different parts [of the body] from having this merely accidental relation in nature? as the teeth, for example, grow by necessity, the front ones sharp, adapted for dividing, and the grinders flat, and serviceable for masticating the food; since they were not made for the sake of this, but it was the result of accident. And in like manner as to the other parts in which there appears to exist an adaptation to an end. Wheresoever, therefore, all things together (that is all the parts of one whole) happened like as if they were made for the sake of something, these were preserved, having been appropriately constituted by an internal spontaneity; and whatsoever things were not thus constituted, perished, and still perish." We here see the principle of natural selection shadowed forth, but how little Aristotle fully comprehended the principle, is shown by his remarks on the formation of the teeth.

Lamarck was the first man whose conclusions on the subject excited much attention. This justly celebrated naturalist first published his views in 1801; he much enlarged them in 1809 in his 'Philosophie Zoologique,' and subsequently, in 1815, in the Introduction to his 'Hist. Nat. des Animaux sans Vertèbres.' In these works he upholds the doctrine that all species, including man, are descended from other species. He first did the eminent service of arousing attention to the probability of all change in the organic, as well as in the inorganic world, being the result of law, and not of miraculous interposition. Lamarck seems to have been chiefly led to his conclusion on the gradual change of species, by the difficulty of distinguishing species and varieties, by the almost perfect gradation of forms in certain groups, and by the analogy of domestic productions. With respect to the means of modification, he attributed something to the direct action of the physical conditions of life, something to the crossing of already existing forms, and much to use and disuse, that is, to the effects of habit. To this latter agency he seems to attribute all the beautiful adaptations in nature;—such as the long neck of the giraffe for browsing on the branches of trees. But he likewise believed in a law of progressive development; and as all the forms of life thus tend to progress, in order to account for the existence at the present day of simple productions, he maintains that such forms are now spontaneously generated.*

Geoffroy Saint-Hilaire, as is stated in his 'Life,' written by his son, suspected, as early as 1795, that what we call

*I have taken the date of the first publication of Lamarck from Isid. Geoffroy Saint-Hilaire's ('Hist. Nat. Générale,' tom. ii. p. 405, 1859) excellent history of opinion on this subject. In this work a full account is given of Buffon's conclusions on the same subject. It is curious how largely my grandfather, Dr. Erasmus Darwin, anticipated the views and erroneous grounds of opinion of Lamarck in his 'Zoonomia' (vol. i. pp. 500–510), published in 1794. According to Isid. Geoffroy there is no doubt that Goethe was an extreme partisan of similar views, as shown in the Introduction to a work written in 1794 and 1795, but not published till long afterwards: he has pointedly remarked ('Goethe als Naturforscher,' von Dr. Karl Meding, s. 34) that the future question for naturalists will be how, for instance, cattle got their horns, and not for what they are used. It is rather a singular instance of the manner in which similar views arise at about the same time, that Goethe in Germany, Dr. Darwin in England, and Geoffroy Saint-Hilaire (as we shall immediately see) in France, came to the same conclusion on the origin of species, in the years 1794–5.

species are various degenerations of the same type. It was not until 1828 that he published his conviction that the same forms have not been perpetuated since the origin of all things. Geoffroy seems to have relied chiefly on the conditions of life, or the *'monde ambiant'* as the cause of change. He was cautious in drawing conclusions, and did not believe that existing species are now undergoing modification; and, as his son adds, "C'est donc un problème à réserver entièrement à l'avenir, supposé même que l'avenir doive avoir prise sur lui."

In 1813, Dr. W. C. Wells read before the Royal Society 'An Account of a White female, part of whose skin resembles that of a Negro'; but his paper was not published until his famous 'Two Essays upon Dew and Single Vision' appeared in 1818. In this paper he distinctly recognises the principle of natural selection, and this is the first recognition which has been indicated; but he applies it only to the races of man, and to certain characters alone. After remarking that Negroes and mulattoes enjoy an immunity from certain tropical diseases, he observes, firstly, that all animals tend to vary in some degree, and, secondly, that agriculturists improve their domesticated animals by selection; and then, he adds, but what is done in this latter case "by art, seems to be done with equal efficacy, though more slowly, by nature, in the formation of varieties of mankind, fitted for the country which they inhabit. Of the accidental varieties of man, which would occur among the first few and scattered inhabitants of the middle regions of Africa, some one would be better fitted than the others to bear the diseases of the country. This race would consequently multiply, while the others would decrease; not only from their inability to sustain the attacks of disease, but from their incapacity of contending with their more vigorous neighbours. The colour of this vigorous race I take for granted, from what has been already said, would be dark. But the same disposition to form varieties still existing, a darker and a darker race would in the course of time occur: and as the darkest would be the best fitted for the climate, this would at length become the most prevalent, if not the only race, in the particular country in which it had originated." He then extends these same views to the white inhabi-

tants of colder climates. I am indebted to Mr. Rowley, of the United States, for having called my attention, through Mr. Brace, to the above passage in Dr. Wells's work.

The Hon. and Rev. W. Herbert, afterwards Dean of Manchester, in the fourth volume of the 'Horticultural Transactions,' 1882, and in his work on the 'Amaryllidaceæ' (1837, pp. 19, 339), declares that "horticultural experiments have established, beyond the possibility of refutation, that botanical species are only a higher and more permanent class of varieties." He extends the same view to animals. The Dean believes that single species of each genus were created in an originally highly plastic condition, and that these have produced, chiefly by intercrossing, but likewise by variation, all our existing species.

In 1826 Professor Grant, in the concluding paragraph in his well-known paper ('Edinburgh Philosophical Journal,' vol. xiv. p. 283) on the Spongilla, clearly declares his belief that species are descended from other species, and that they become improved in the course of modification. This same view was given in his 55th Lecture, published in the 'Lancet' in 1834.

In 1831 Mr. Patrick Matthew published his work on 'Naval Timber and Arboriculture,' in which he gives precisely the same view on the origin of species as that (presently to be alluded to) propounded by Mr. Wallace and myself in the 'Linnean Journal,' and as that enlarged in the present volume. Unfortunately the view was given by Mr. Matthew very briefly in scattered passages in an Appendix to a work on a different subject, so that it remained unnoticed until Mr. Matthew himself drew attention to it in the 'Gardener's Chronicle,' on April 7th, 1860. The differences of Mr. Matthew's view from mine are not of much importance: he seems to consider that the world was nearly depopulated at successive periods, and then re-stocked; and he gives as an alternative, that new forms may be generated "without the presence of any mould or germ of former aggregates." I am not sure that I understand some passages; but it seems that he attributes much influence to the direct action of the conditions of life. He clearly saw, however, the full force of the principle of natural selection.

The celebrated geologist and naturalist, Von Buch, in his