The Origin of Species after 150 Years

One Hundred and Fifty Years without Darwin are Enough

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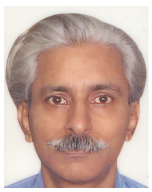

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A happy accident enabled the young Charles Darwin to go on a voyage of exploration around the world. Among the outcomes of that voyage was a book, *The Origin of Species*, which was published in 1859. In it Darwin developed a perspective of the living world that, as we have come to realise, encapsulates its essence. By viewing plants and animals as dynamical entities that were subject to external forces, he was able to show convincingly that they had evolved, on the whole by a process known as natural selection. In doing so he made the point that the living world was explainable on the basis of natural laws and, at the same time, that biology can lay claim to an autonomous status among the natural sciences. Paradoxically, he accomplished all this without knowing how heredity worked or variations occurred. This article attempts to look at *The Origin of Species* from the vantage point of the present. An account of the events that led to the writing of the book will be followed by a quick run through its contents. The essay ends with a mention of some issues that continue to engage evolutionary biologists today.

* Text of the L K Ananthakrishnan Memorial Lecture, Pune, 13 February 2009.

Background

The sub-title of this article is borrowed from two distinguished students of evolution, Hermann Muller and George Gaylord Simpson. Muller and Simpson seem to have independently chosen "One hundred years without Darwin are enough" as an appropriate way to express their dismay at the misunderstandings about Darwinism

Keywords
Evolution, natural selection, Darwinism, heredity, variation.

that prevailed at the time when the centenary of the publication of *The Origin of Species* was being celebrated. Confusion about natural selection, Darwin's revolutionary contribution to biology, persists to this day, as much among biologists as others. It may not be inappropriate for us to recall the message of Muller and Simpson by saying "One hundred and fifty years without Darwin are enough".

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On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life is the full, unwieldy title of the book written by Charles Darwin and published in London by John Murray on 24 November 1859. It sold out immediately, was quickly reprinted, and went through six editions in Darwin's lifetime. The editions contain extensive changes and revisions. Some changes were made to correct obvious misprints and errors, some were meaningful additions (the phrase 'survival of the fittest' appears in the fifth edition and 'evolution' in the sixth), and others involved a softening of stand on Darwin's part ('by the creator' is added after 'breathed' in the last paragraph of the second edition). It is generally believed that the first edition is truest to the real Darwin, and it is the one that is the theme of this article. Darwin's contributions to biology go far beyond writing *The Origin of Species*; he was to develop many of the ideas that he presented there in greater detail later. Nevertheless, because it contains both a comprehensive view of the evolutionary process and describes a plausible means by which evolution could occur (namely, by natural selection), the book retains an iconic status.

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The Origin of Species is sometimes spoken of in the same breath as Newton's *Principia*. As far as the importance of the two books in the intellectual history of the natural sciences goes the comparison is apt. However, it is misleading in two respects. One, even at the time it was written the *Principia* was heavy going (that it was written in Latin and used geometric methods were added difficulties). Generations of physicists can attest to its denseness; as recently as 1995 S Chandrasekhar came out with a guide entitled *Newton's Principia for the Common Reader* ('for the uncommon physicist' may have been closer to the mark). There is something of the magician in Newton and reading him makes it clear that deep truths are being conveyed. In contrast what Darwin says is transparent to the extent that one's first reaction is to wonder what the fuss is all about (though the apocryphal Victorian lady who said "Let us hope that what Mr. Darwin says is not true; but, if it is true, let us hope that it will not become generally known" caught on to its significance). *The Origin* became a hit with the literate public. Such is the quality of Darwin's prose that the book can be read to this day for sheer pleasure – almost bedtime reading material. J T Bonner, one of the leading evolutionists of our day, has drawn attention to the very ease of understanding of Darwin's writing as a reason why it makes some people doubt that natural selection can be correct (apparently the mathematician Harish-Chandra once told Bonner how he found it difficult to believe that anything that simple could account for the messiness of the living world). Many will have echoed T H Huxley's famous remark after first reading *The Origin*: How stupid of me not to have thought of that. There is another difference between the *Principia* and *The Origin of Species*. One hardly ever expects to find a reference to Newton's work in the literature of contemporary physics; Darwin continues to be cited all the time. Newtonian thinking had first to be assimilated by intermediaries and then transmitted by them. Only later on was it absorbed and adapted to serve different ends and citations to derivative writings began to accumulate. In contrast, people continue to read Darwin for themselves, continue to find new sources of inspiration in his writings, to discover new insights and develop them further. With some exaggeration, one could say

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that Newton wrote *Sutra*s that require *Bhashya*s to be understood; Darwin speaks directly to everyone.

The Beagle Voyage and Thereafter

A number of events contributed to shaping Darwin's career to the decisive moment when the book came to be written. The story is instructive; it illustrates that in human affairs, it is not easy to pinpoint causes. Born on 12 February 1809, Darwin grew up as the indulged son of a rich physician. Hunting for sport was the one thing about which he was passionate. Besides wanting to have a good time, he did not appear to be motivated to do anything. Despite that, Darwin developed and retained throughout his life a keen interest in the outdoors, in observing plants and animals, and especially when young in collecting beetles – part of a fad that had spread through Victorian England. His father Robert had tried to make him follow in his footsteps by sending him to study medicine in Edinburgh, but that was not a success. He found the lectures boring and was horrified by surgery, which at that time was carried out without anaesthesia. The father decided that a clergyman's life was the only option left for his son. A degree from Cambridge or Oxford was a prerequisite for ordination in the Anglican Church. The choice fell on Cambridge: Robert Darwin and his father Erasmus, both irreligious, both successful doctors (in Erasmus's case with wide-ranging tastes in areas that included natural history and evolution), had studied there.

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The task of getting a degree was not a demanding one but even so Darwin came close to failing. The situation was saved by the help of special tuitions from the Professor of Botany in Cambridge, John Henslow, who had become his friend and mentor. Henslow seems to have been the first person to have spotted in this young man a scientific mind that was out of the ordinary. Darwin managed to clear his BA finals but had to remain

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in Cambridge for a further six months to fulfil the University's residency requirement. Finding himself free of all other academic commitments, he made use of the break to do some reading for his own pleasure. A *Discourse* on natural philosophy by the mathematician and astronomer John Herschel made him feel eager to do something for science. Alexander von Humboldt's description of his South American travels captivated him to the extent that he decided to organise a small expedition to study the botany and geology of Tenerife, one of the Canary Islands off the African coast. The plan failed, but thanks once again to Henslow's assistance, Darwin had embarked on a course of preparatory training with the eminent Professor of Geology, Adam Sedgwick. Geology had bored him in Edinburgh; but Sedgwick's instruction awakened such an interest in the subject that he soon became something of an expert. Very soon thereafter, in 1831, Henslow, having considered and turned down the offer himself, recommended the 22 year-old Darwin's name for the post of unpaid companion-naturalist to Captain FitzRoy, who was to lead a naval expedition to chart the coast of South America. Darwin was overjoyed and wanted to accept at once. The exasperated father refused permission at the threshold of the step that was to change the world of science. Robert Darwin only saw yet another postponement of the day when his son would begin to make something of himself. The timely intervention of Darwin's maternal uncle Josiah Wedgwood made him change his mind (see *Box* 1 for an account written much later by Darwin's daughter Henrietta).

The five years that he spent on the *Beagle* (December 1831 to October 1836) were to prove the defining element in Darwin's career. The voyage took him around the world: southwards from England to Bahia in Brazil, around Patagonia, up the Chilean coast, westwards across the Pacific (with an epochal halt on the Galápagos

Box 1. 'The way in which my Father got to go with the Beagle'; Henrietta Litchfield, Oct 1873

(http://darwin-online.org.uk/content/frameset?itemID=CULDAR262.23.4&viewtype=text&pageseq=1).

The players in the story are Charles Darwin's father, his maternal uncle Josiah Wedgwood, John Henslow the botanist who was Darwin's friend and mentor at Cambridge, the Reverend George Peacock, a Cambridge mathematician, and Captain Fitzroy, a deeply religious naval commander who was looking for 'a good Christian and cultivated naturalist' to accompany him on a round-the-world voyage on the ship *HMS Beagle*, whose mission was 'completing the survey of Patagonia and Tierra del Fuego; to survey the shores of Chile, Peru, and some islands in the Pacific; and to carry a chain of chronometrical measurements round the world'.

In the words of his daughter Henrietta, "Capt Fitzroy sent through Capt. Beaufort to 'Old Peacocke' of Cambridge to ask if he knew of any energetic young man fit to observe the Nat. Hist of the countries at which they wd touch & to collect specimens - only reserving for himself the task of observing the savages with whom they might come in contact. For this purpose he generously offered to share his cabin if anyone could be found to come. Through Peacocke Prof Henslow stated that though my Father knew very little he would be fit for the purpose & would be active & zealous. My Father was delighted with the scheme: but he found that the Doctor thought it utterly wild & foolish & that to go would be the ruin of his career. He ended by raging, 'Well if you could find *one* sensible man who thinks it a wise scheme you may go.' Seeing how strong was his Father's disapproval my Father gave it up with many pangs. This took place just before the 30th Aug on wh. day my F. went over as was his universal custom to Maer a place about 20 miles off belonging to his uncle Mr Wedgwood ... When he arrived at Maer he was lamenting his fate & happened to repeat his father's last words to Mr Wedgwood. His delight was great on finding that Mr W. was of quite a different opinion ... The difficulty of his fathers objections was thus got over, & it was arranged to accept Fitzroy's offer. .. My father, however, heard afterwards from Fitzroy that he very nearly gave up taking him for an original reason. It appears that he had a great belief in physiognomy & on seeing my F. made up his mind that no man with such a nose could have energy ... I believe, however, that his brow saved him."

islands), to New Zealand, Sidney, Tasmania, around the Cape of Good Hope, a return to Bahia and then home. Sailing did not agree with him, but whenever the ship touched land and he could get down, he paid keen attention to plant and animal life, fossils included, made geological observations, collected assiduously and kept shipping specimens back to England. There was an especially long halt in Patagonia. The collections helped make his reputation as a naturalist when he was still

Figure 1. A marine iguana from the Galápagos islands, where Darwin found the famous finches that (as was demonstrated much later) showed evidence of speciation at work. They are unusual among lizards in living off the sea. Darwin called them "imps of darkness". (Credit: Wikimedia)

travelling. He maintained a diary during the voyage. It was published later as a *Journal of Researches* and became a best-seller (as did an abbreviated popular version entitled *Voyage of the Beagle*); even the great Humboldt wrote to say how much he had enjoyed reading it. The descriptions retain a vividness and charm to this day. After his return, and in the face of constant ill-health, for the rest of his life Darwin worked at a pace that can only be called staggering. 'Work' meant going over the observations recorded during his trip, talking to the experts about the specimens he had collected – both fossils and extant species –, framing questions constantly, corresponding with everyone who could conceivably help him with answers and, above all, pondering the implications of the accumulated information. All his speculations went into meticulously kept notebooks.

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Doubts about the fixity of species surfaced as early as 1836. This was when Darwin wondered whether the tortoises and mockingbirds of the Galápagos, some of them apparently restricted to certain islands, might be fundamentally different creatures. He wrote in his notes: "the zoology of Archipelagoes will be well worth examining; for such facts would undermine the stability of Species". The ornithologist John Gould said a year later that at least in respect of the mockingbirds, the suspicion that they were different species was correct. At the same time, he heard from the zoologist Richard Owen that a South American fossil sloth and fossil llama were creatures unlike anything known to science. Darwin slowly began to contemplate the possibility that what lay behind the geographical spread of animals on earth ('distribution in space') and their appearances and disappearances ('distribution in time') was a pattern of change in the course of which species came, went and became transformed .

The notion of biological change itself was not new. After all, if one species could be created, why not an entire succession? Erasmus Darwin, not to speak of the more famous Jean-Baptiste Lamarck, had been evolutionists. But the idea that one species could give rise to another, that too as part of the workings of nature, was radical – and the thought that human beings might be part of the same process all the more so. Early in 1838 Darwin visited the London zoo to view one of their prize exhibits, the orang-utan Jenny. He noticed that when the keeper refused her an apple, Jenny threw a tantrum just like a human child. After coming back he wrote in his notebook: "Let man visit the ouran-outang in domestication . . . see its intelligence. Man in his arrogance thinks himself a great work . . . More humble and I believe true to consider him created from animals". (The resemblance was not lost on Queen Victoria either. Upon seeing a later orang-utan, another Jenny, she described it as "frightful, and painfully and disagreeably human".) A different notebook entry from the same year has become famous: "Origin of man now proved. – Metaphysic must flourish. – He who understands baboon would do more towards metaphysics than Locke". Some one hundred years previously the English philosopher John Locke had posited that humans are born with an empty mind, a clean slate, whose development after birth depended on sensory impressions and reflection. Darwin was hinting that the mind of a new-born baby might already be a sophisticated entity, equipped by evolution to anticipate features of the external world.

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into the process of natural selection, came later in the same year when Darwin read the Reverend Thomas Malthus' *An Essay on the Principle of Population*. Malthus had reasoned that unless there was some form of reproductive control, in the long run food supply could never keep up with human population growth. In its absence, there would be intense competition for food; disease and starvation would act as natural checks on the population. Darwin reasoned by analogy that living creatures of the same kind (the members of a species) could be subject to a similar principle. Because many more were born than could be supported by the environment, individuals had to compete for resources. If the ability to succeed could be transmitted from parents to offspring, the ones that were more successful would gradually supplant the less successful ones.

Given that Darwin started to think about natural selection by 1839, why did it take him twenty years to come out with *The Origin of Species*? After all, he had found the time to write seven other books in the meanwhile. As it happens, by 1844 he had prepared a 230-page handwritten 'sketch of my species theory'. He described it in a private note addressed to his wife as 'a considerable step in science', and requested her, 'in case of my sudden death', to get it published and 'take trouble in promoting it'. So there is no question whatsoever that Darwin knew he was on to a big thing; and he was not one to shy away from public admiration and acclaim. We may never know all the reasons behind the delay, but some guesses can be made. The first guess involves Darwin's marriage in January 1839, five days after he was elected Fellow of the Royal Society. His wife Emma was deeply religious, and he may have agonised over the pain he would cause her by advancing a theory which so starkly opposed the Biblical version of creation. A second guess has to do with Darwin's feeling that he had not acquired the stature that was needed if he wanted to be taken seriously on as fundamental an issue as evolution. For all his fame as an explorer and student of natural history, his technical credentials as a botanist or zoologist were weak. His friend the botanist Joseph Hooker had disparaged someone else's writing on the grounds that the author had not contributed to the understanding of a single species. That prodded Darwin to do something that would give him professional clout. He started working on barnacles, marine crustaceans whose classification was (so the zoologists told him) a mess. Darwin plunged into the affair with typical obsessiveness. One thing led to another, and the result was years of toil that resulted in three massive books before 1859.

The Book

Finally *The Origin of Species* was put together in haste and released with much diffidence, almost apologetically, at a time not of Darwin's choosing. It was accompanied by the disclaimer that it was an abstract of a more comprehensive work that was in the making (and never got written). The story is well known. A much younger naturalist, Alfred Russel Wallace, whose role models were Humboldt and Darwin himself, had hit upon the idea of natural selection while recovering from a bout of malaria on the volcanic island of Ternate in eastern Indonesia (see *Resonance* March 2008). What makes this independent discovery almost incredible is that for Wallace too the essential insight came from the very same book by Malthus. In his enthusiasm he could think of no better person with whom to share his joy than Darwin. He wrote up his thoughts in a short essay entitled *On the Tendency of Varieties to Depart Indefinitely from the Original Type* and mailed it off to Darwin for his opinion. Realising that he had been scooped in a matter where the priority ought to have been his long ago, the stunned Darwin appealed to his friends Lyell and Hooker (the leading British geologist and botanist respectively)

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for advice. Their initiative, and the large-heartedness of Wallace, ensured that a compromise was reached that was agreeable to all.

The theory of evolution by natural selection was announced to the world jointly by Darwin (in the form of excerpts from the 1844 sketch, along with a letter by him to the Harvard botanist Asa Gray) and Wallace (in the form of the Ternate essay) at a special meeting of the Linnean Society held on 1 July 1858. In the absence of either author, the actual presentation was made by Lyell and Hooker. It was close to being a flop. The President of the Linnean was to state later that the activities of the Society during the year had lacked 'any of those striking discoveries which at once revolutionise, so to speak, the department of science on which they bear'. Goaded into rapid action thereafter, Darwin got to work. *On the Origin of Species by Means of Natural Selection* eventually appeared one year later.

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The chief things to remember about the book are that the huge mass of evidence in it settled once and for all the fact that evolution had taken place; on top of that it offered a novel and immediately plausible explanation for *how* it had taken place. Darwin took care to affirm that he believed natural selection to be the most important, but not the sole cause of evolution. In modern jargon, he was a pluralist – unlike Wallace, who remained a pan-selectionist. He was open to the possibility that a trait might evolve because its expression was correlated with another trait (on which selection acted). Also, he did not exclude the working of entirely chance factors affecting a trait. Now known as drift, this is what happens when changes in a trait are neither advantageous nor disadvantageous. Lastly, more than once he veered towards Lamarck's way of thinking about heredity. The ghost of Lamarck haunts *The Origin of Species*. Darwin is convinced that Lamarck's ideas cannot be right, especially the claim that evolutionary change can be brought about by an inner striving for self-improvement; he says so time and again. Occasionally he seems hesitant about accepting the possibility that acquired traits can be transmitted to offspring. At other times he is more forthright. For example, "I am surprised that no one has advanced this demonstrative case of neuter insects, against the well-known doctrine of Lamarck" (the point being that it is logically impossible for the trait of non-reproduction to be passed on; as the saying goes, celibacy is not heritable). Darwin's name was so strongly associated with natural selection that it became 'his theory'. Wallace's self-effacing nature contributed to this; he went so far as to write a book titled 'Darwinism'. In spite of the misleading implication, the word continues to be used as a synonym of natural selection.

Right from the first paragraph of the Introduction, the directness and understated style of *The Origin* hits the eye (see *Box* 2). Of the remaining 14 chapters, the first two deal with variation under domestication and variation in nature, and the third with the 'struggle for existence' (the insight from Malthus). Then, in almost deductive fashion, the fourth chapter spells out the principle of natural selection. The rest of the book is taken up with justifying the assumptions made earlier, tackling potentially troublesome issues and providing supporting evidence. A final chapter, entitled *Recapitulation and Conclusion*, summarises the thesis – which, in

Box 2. The First Paragraph of *T*he Origin of Species

WHEN on board H.M.S. Beagle, as naturalist, I was much struck with certain facts in the distribution of the inhabitants of South America, and in the geological relations of the present to the past inhabitants of that continent. These facts seemed to me to throw some light on the origin of species – that mystery of mysteries, as it has been called by one of our greatest philosophers*. On my return home, it occurred to me, in 1837, that something might perhaps be made out on this question by patiently accumulating and reflecting on all sorts of facts which could possibly have any bearing on it.

*John Herschel; Darwin learnt this from Captain FitzRoy.

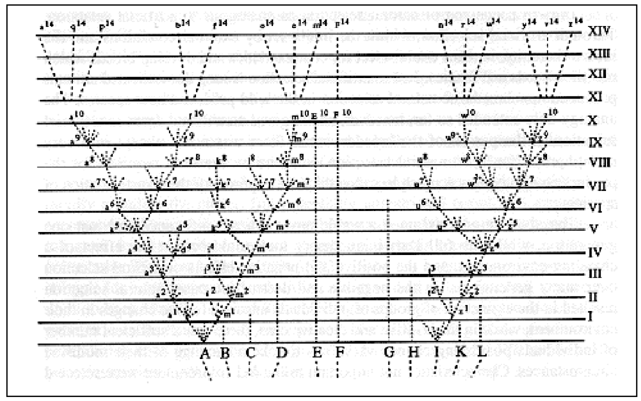

Figure 2. The only figure in *The Origin*, a tree diagram used by Darwin to illustrate speciation. It is to be viewed from the bottom up, with each horizontal line representing 1000 generations. "A", "B", etc., are different species at the start. Some lineages that begin from A (for example) go extinct. Others diverge so much as a result of natural selection that eventually they are classified as distinct species.

short, is that all life forms have been shaped by descent with modification from earlier, fewer and simpler forms, largely by a process known as natural selection.

Darwin's own description of the book was 'one long argument'. The argument was underpinned by a lesson that he had taken to heart from Lyell's *Principles of Geology*: unbelievably slow processes that act over long epochs can lead to dramatic changes. The truth of Lyell's lesson in turn depended on an assumption (also made use of in cosmology) known as Uniformitarianism. It states that the natural processes that are observable at work today are the same as those that were at work in the past, and its application to geology has been traced back all the way to the Persian (or, with equal validity, Arab) philosopher Ibn Sina. The approach was to land Darwin in trouble with the famous physicist William Thomson (Lord Kelvin). Darwin had used the rate at which sediments were deposited to estimate that some formations could be many hundred million years old. Thomson refuted it by saying that this was impossible: if the earth was that old, its rocks would have cooled down much more than they had. Thomson was wrong, of course, because he had no idea of the existence of radioactivity and its contribution to maintaining the temperature of the earth.

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Along the way Darwin tackled a number of issues that have since grown into major areas of research on their own. One was sexual selection: why are the males and females of the same species often so different in respect of traits that appear to have nothing to do with reproduction? A second was social behaviour: how could altruistic traits, which by definition benefit someone else, not the altruist, evolve? A third was complexity: how could a structure such as the human eye evolve via independent modifications of minor effect if, for its proper functioning, a large number of components had to complement each other precisely? Yet another was instinct: could mental traits also be the result of evolution and if so how? On all these matters Darwin anticipated many ideas that we tend to think of as modern.

Consider the issue of how a trait which benefits someone other than the individual in whom it is perceived, and in fact is detrimental to the individual in whom it is perceived, could nevertheless spread by natural selection. He frames it thus: "This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end ... Thus, a well-flavoured vegetable is cooked, and the individual is destroyed; but the horticulturist sows seeds of the same stock, and confidently expects to get nearly the same variety ... ". Later chapters highlight the importance of morphology and embryology for his theory. Darwin asserted that relatedness by common descent (homology), not similarity of function (analogy), was the right way to group living forms (an essential prequisite for making sense of the living world). By doing so, he provided the first rational basis for classification. He made the perceptive observation (made much earlier by William Jones in the context of tracing linguistic affinities) that the significant traits for inferring relatedness by descent are precisely those that seem to be of little use to their bearers. The book ends with a poetically worded summary (see *Box* 3).

Box 3. The Final Paragraph

It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us. There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

Natural Selection

In formulating the theory of natural selection Darwin was guided strongly by what he had learnt about the moulding of plant and animal traits to desired ends by means of selective breeding. The very first chapter of *The Origin* refers to the extensive use of artificial selection made by the Emperor Akbar for indulging his passion for fancy pigeons (*Ishqbaazi*). Plant and animal breeders had put their knowledge of heredity to enormous practical benefit ever since the dawn of agriculture if not earlier. Often they succeeded in reinforcing changes in traits that interested them, step by small step and over many generations. As Darwin put it, "The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him". It was obvious that artificial selection worked; Darwin and Wallace made it plausible that natural selection worked in a similar way.

The principle of natural selection consists of three assumptions and an implication. The assumptions are these: members of a species vary in respect of certain traits; the traits can be passed down from parents to offspring; and some variations can make their possessors more successful in living and reproducing than others. In short, individuals are assumed to exhibit variation, heritability and differential fitness (it is implicit that they are capable of reproducing). If the assumptions are true, a logical implication follows: the composition of a population changes over the course of generations, that is, the population evolves, with the relatively more successful types becoming more common. The philosopher Herbert Spencer coined the phrase "survival of the fittest" to describe natural selection. Darwin was sufficiently taken up with the description to use it in the later editions of *The Origin.* Few things have caused more confusion. The phrase conflates the outcome of natural selection with its causes and risks making the entire theory sound like a tautology, which it is not. The assumptions listed earlier amount to testable, and therefore falsifiable, assertions concerning living creatures. It is only if the assumptions are true that the implication is valid.

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Evolution by natural selection involves a continual testing of traits with regard to how well they equip a plant or animal to perform relative to others of its kind and under specified conditions. Therefore it brings into play considerations of engineering design, of efficiency, of what one might call 'economic' criteria – with the number of surviving offspring as the currency in which evolutionary success is measured. Cornish-Bowden has referred to this aspect of natural selection as the pursuit of perfection. An older and more common word, adaptation, describes the end result. Evolution by natural selection is an adaptive process. Seen the other way round, adaptation is the signature of natural selection. To the extent that living creatures exhibit adaptations, one may infer that natural selection has been operating. At any rate, no one has come up with a better causal explanation for adaptations. To suggest that they can come about by 'intelligent design', as some have done of late, is absurd in the extreme. Crucially, natural selection works from one generation to the next: it deals with the short term. When one looks back over a great many

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generations, successive adaptations are seen to have accumulated and given rise to a major transformation, to what looks like a product of design. But the design is unintended, without purpose. There is no way in which evolution can plan for the future; it has no long-term goal. Evolution cannot exhibit foresight. It can be compared to a game of chance that rewards successes – if they happen. This is why it is said that evolution is opportunistic. Opportunism implies that it is not easy to trace the actual path taken by an evolutionary transformation.

Adaptation is to a set of circumstances – the 'environment' – that comprises the physical environment and the biotic environment. 'Biotic' includes other members of the same species as well as other species. Prey, predators, parasites and infectious agents fall into the latter category. Since the other species are also subject to selective pressures, it is obvious that the evolution of a species cannot be viewed in isolation. The adaptive outcome that it attains must take into account all other adaptations simultaneously. An adaptive response to the environment by one species changes the biotic environment of another species. Or, as frequently happens, the physical environment may change. What all this means is that evolution is a continuous process; it does not come to an end. As the palaeontologist Van Valen points out, this implies that as a species evolves, it does not improve itself in any absolute sense. If it does not go extinct (which has been the fate of the vast majority of all species – yet another piece of evidence against betterment), the best it can do is to keep up with all the other species. He sums up the situation in the words of the Red Queen: "It takes all the running you can do, to keep in the same place" (Lewis Carroll, in *Through the Looking Glass*).

Evolution is opportunistic, comparable to a game of chance that rewards successes.

Variation and Heredity

Considering that variation and heredity are two of the essential pre-requisites for natural selection, it seems remarkable that Darwin got as far as he did while being (along with everyone else at the time) ignorant about the workings of both. Today we know that for all practical purposes variations occur 'at random'. That is, the likelihood of occurrence of a variation is independent of its outcome. Darwin took variation as a fact, as something that was there. As to postulating mechanisms, he hazarded the guess that 'Effects of Use and Disuse', 'Acclimatisation' and 'Correlation of Growth' might be involved. Apart from the last factor, this again meant a tilt in the direction of Lamarckian ideas. Being unable to come up with good alternatives, he could not shake off Lamarck entirely. But he summed up the prevailing state of knowledge fairly by confessing that "Our ignorance of the laws of variation is profound".

Evolution is a continuous process; it does not come to an end.

Regarding the mechanism of heredity too, Darwin was entirely in the dark. Years later he came up with a blending theory of inheritance called Pangenesis; it was seen to be unsatisfactory right from the start (see *Box* 4), He did not know that the first steps in solving the riddle of heredity were being taken by his contemporary Johann Mendel. There is every reason to believe that Darwin should have learnt of Mendel's discovery, which was published in 1866, in time for the later editions of *The Origin*; but he did not. Ironically, Darwin's own experiments on crossing different varieties of the snapdragon (*Antirrhinum*) gave clear evidence of the 'Mendelian' 3:1 ratio, and therefore of the atomistic nature of hereditary factors. Unfortunately he did not understand the implications of what he had found. Unlike Mendel, Darwin lacked a hypothesis, a viewpoint, which would make him recognise and then analyse the significance of a 3:1 ratio. The process by which the laws of Mendelian heredity found their rightful place in

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Box 4. Pangenesis

Darwin's theory of heredity was published in *The Variation of Animals and Plants Under Domestication* (1868). He developed it in order to explain how traits that had been modified by selection could be passed on to offspring. The idea was based on 'gemmules', which were supposed to be carriers of hereditary traits distributed all over the body, each gemmule being specific to the part to which it belonged and modifiable by the use made of that part during an individual's pre-reproductive life. They were brought together in preparation for transmission to the next generation. Critically, in the next generation the gemmules of the parents were assumed to mix, to blend as colours might. In his own words: "It is universally admitted that the cells or units of the body increase by self-devision, or proliferation, retaining the same nature, and that they ultimately become converted into the various tissues and substances of the body. But besides this means of increase I assume that the units throw off minute granules which are dispersed throughout the whole system; that these, when supplied with proper nutriment, multiply by self-division, and are ultimately developed into units like those from which they were originally derived. These granules may be called gemmules. They are collected from all parts of the system to constitute the sexual elements, and their development in the next generation forms the new being; but they are likewise capable of transmission in a dormant state to future generations and may then be developed." Gemmules would have been a way for transmitting traits that were acquired during life, and their existence would have pleased Lamarck. Fleeming Jenkin, professor of Engineering in Edinburgh, shot down the proposal's utility by pointing out that the variation in each generation would be halved by blending – in which case, over time, what would remain for natural selection act on? Darwin's cousin Francis Galton thought he had disproved pangenesis when he transfused blood between different breeds of rabbits and found that the recipients bred true to their original types.

evolutionary biology was far from smooth (see below). Despite his lack of firmness on the matter, the suggestions that (a) variation and heredity might work independently and (b) the pace of evolution was driven by selection, not variation, are important contributions of Darwin to evolutionary theory – perhaps next only to natural selection itself. It is the lack of coupling between variation and heredity which explains how seemingly purposeful entities can evolve in the absence of design. Further, it endows the principle of natural selection with almost limitless power when it comes to constructing complexity. Mathematicians and physicists have borrowed the strategy to search for quick and acceptable solutions to seemingly intractable problems. No wonder the philosopher Daniel Dennett calls natural selection "Darwin's Dangerous Idea".

The essence of the idea is that variation takes place at one level and the consequence of the variation is tested at another level. August Weismann first emphasised its centrality to evolution when he highlighted the distinction between reproductive tissue (the germ line) and the rest of the body (the soma). The germ line is functionally sequestered and transmits hereditary traits whereas the soma, which is exposed to the environment, expresses those traits. However, the distinction between germ line and soma is obvious only in multicellular animals. It is murky in the case of plants and non-existent when it comes to unicellular life. What actually lies behind Weismann's distinction, and the reason why Lamarckian inheritance does not work, became clear only in the mid-20th century. It needed a recognition of the essential difference between genes and proteins. Genes contain symbolic information for making proteins and variant genes lead to variant proteins. But it cannot work in reverse. As far as we know a variant protein cannot alter the information content of the gene that encodes it.

It is not unknown for a robust theory or set of 'laws' to thrive in the absence of a known mechanism that can justify them.

Ignorance of how heredity or variation worked were certainly handicaps. Despite those handicaps, Darwin and Wallace managed to develop the hypothesis of natural selection and explore many of its ramifications. It is not unknown for a robust theory or set of 'laws' to thrive in the absence of a known mechanism that can justify them. Newton's theory of gravitational attraction is one example, and Mendelian genetics is another. Genetics flourished for half a century and, by building on Mendel's laws, geneticists built up an impressive formal structure of theoretical genetics before they knew what a gene was.

For the scientific community, a big lesson to draw from *The Origin* was that the living world could be explained on the basis of natural laws.

What did the *Origin of Species* Achieve?

On the lay public, the biggest impact of the book was the implication that human beings did not occupy a special place in the universe. The last chapter of *The Origin* tantalisingly held out the promise that "In the distant future ... light will be thrown on the origin of man and his history", but the book made it amply clear that humans were on a par with all other creatures in the living world. In terms of the familiar tree of life, evolution by natural selection implied that humans were at the end of one branch, dogs of another, tapeworms of a third, mangoes of a fourth, and so on. In an objective sense, none of them could be said to be more advanced than or superior to another. For the scientific community, a big lesson of *The Origin* was that the living world could be explained on the basis of natural laws. The persuasive claim that one species could give rise to another lent additional support to the lesson. Evolution in the sense of a transformation of forms and properties is inherent to chemistry (if not to physics, with cosmology being a prominent exception). By making it plausible that biological evolution could occur naturally, Darwin and Wallace showed that biological change was at least formally analogous to chemical change. Theirs was the first step in the still-ongoing integration of the natural sciences. They made it meaningful for us to think of biology as we do today, as the science of living matter. True, the problem of the origin of life was left unaddressed. But *The Origin of Species* made people think of it as an approachable problem, as something that could be tackled with the methods of conventional science. Some people claim that the age-old issue of how to distinguish between living and non-living has now been settled: any entity that can evolve by natural selection can be said to be alive.

Life was a property of any entity that could evolve by natural selection.

Interestingly, while pushing biology closer to physics and chemistry, natural selection also formalised the special status of biology within the natural sciences. It showed that even though living systems must operate entirely according to the rules of physics and chemistry, the traits that they exhibit are not *necessary* outcomes of the rules. The reason is that chance intervenes between the laws of physics and the products of biological evolution. Heritable changes occur in unpredictable ways, and the likelihood that a particular change occurs has nothing to do with whether it is advantageous or disadvantageous. This realisation is at root of our understanding of natural selection. Chance plays an essential role in evolution, both during mutation and recombination (the shuffling of genes). Natural selection showed how biology is different from physics in another respect. In physics, as often as not the object of study is the 'isolated system', for example the single hydrogen atom. The underlying assumption is that all hydrogen atoms are identical; and the essence of an atom can be studied in isolation. This approach does not work in biology because the proper understanding of an individual plant or animal requires taking into account its existence within the context of the rest of the population, that too a population whose members differ significantly.

Chance plays an essential role in evolution, both during mutation and recombination.

The third way in which natural selection showed how biology differs from physics and chemistry is that it focussed on the fundamental importance of the past for understanding the present. It made us realise that besides proximal explanations for the existence of a trait (i.e., the usual causal explanations based on physics and chemistry), biology permits us to assign 'ultimate' explanations. The distinction was known to Aristotle. He said that the existence of a house can be explained in two ways. One can say that the house is there because bricks, mortar and so on were put together. However, one can also say that the house is there because someone wanted to live in it. The second sort of explanation, which invokes the consequence of that which is sought to be explained, is central to any argument based on

Natural selection enables us to account for the presence of a trait in ourselves by saying that its possession enabled our ancestors to be more successful at survival and reproduction than others who did not possess it.

natural selection. For example, suppose we want to explain the existence of colour vision. We can say that we see colours *because* we possess the appropriate cone cells in the eye. On the other hand we can equally legitimately say that we see colours *because* those of our ancestors in whom the cone cell pigment variant first arose had an advantage over those who had only rod-based black-and-white vision. Natural selection enables us to account for the presence of a trait in ourselves by saying that its possession enabled our ancestors to be more successful at survival and reproduction than others who did not possess it, or possessed it in a different degree. Thus natural selection accounts for the aspect of purpose that is characteristic of all life forms. But it does so by invoking historical contingency, not design.

Natural Selection after Darwin

After an initial flush of enthusiasm the appeal of natural selection declined. At one time many had given up on it as a plausible mechanism for explaining evolution. Difficult as it is to believe, the rediscovery of Mendel's laws in 1900 was responsible for this. The impression gained ground that differences in the Mendelian carriers of heredity were associated with discrete, qualitative changes (for example, in Mendel's own experiments, the yellow versus green colours and round versus wrinkled shapes of peas). How then could they explain the slow, quasi-continuous process of evolutionary change that natural selection demanded? 'Darwinists', who were convinced of the truth of natural selection, came to the conclusion that Mendel's laws were incidental to its understanding. 'Mendelians' drew the opposite inference. They thought that natural selection was all very well for explaining gradual, quantitative transformations. But the real stuff of evolution had to be something else, namely mutations that changed traits in a major way. The birth of a genetical theory of natural selection had to await three developments. The first was a deeper understanding of genetics provided by the experimental work of T H Morgan and his school (ironically, for a long time Morgan himself remained sceptical about the usefulness of natural selection for explaining evolutionary change). The second was the development of a mathematical treatment of the spread of genes in populations initiated by J B S Haldane, R A Fisher, S Wright and S S Chetverikov. Finally, a combination of laboratory and field work in palaeontology, natural history and genetics made natural selection respectable once again and gave rise to the construction of what we now call the modern or neo-Darwinian synthesis. Before that happened, things had reached such a pass that Haldane used the epigraph "Darwinism is dead – Any sermon" to lampoon the situation in the very first chapter of his book *The Causes of Evolution*.

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The one major modification to the Darwinian picture of evolution came from discoveries made in molecular biology from the 1960s onwards. To everyone's surprise, it turned out that at the molecular level, most changes in the hereditary material (as inferred from DNA and protein sequences) were almost 'neutral' – neither advantageous nor disadvantageous. Of all the changes that occur in DNA, only a tiny fraction seems to be significant for evolution at the level of the organism. As a result, the tempo of molecular evolution appears to depend more on the rate of mutation than on natural selection. Molecular biology has kept throwing up other surprises with regard to the details of the processes through which genetic information gets decoded, and we do not yet know how to fit them into a coherent evolutionary picture. At a more basic level, we are still to assimilate the implication of the extraordinary distinction that exists within living creatures between quasi-symbolic informational entities (DNA, RNA) and their meaning (proteins), or indeed why evolution has made the distinction.

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We still lack a satisfactory genetical theory of speciation or of the origin of the major groups.

Evolutionary Theory 150 Years after *The Origin*

By no means did the acceptance of natural selection settle all issues. A number of them continue to be vigorously debated; only a few can be mentioned here. The debates are of a curious sort, because with the exception of those cases in which physical catastrophes have played a role hardly anyone questions whether natural selection can account for the origin or maintenance of a trait. Rather, the issue is whether there might be an alternative way of accounting for the trait, one that does not invoke selection explicitly. For example, it may be that the trait follows automatically from the principles of physics and chemistry. Thus the possibility of natural selection being responsible for a trait is not questioned; the plausibility of its having done so is. The splitting of lineages into different species and the appearance of major novelties (e.g., nucleated cells, multicellularity, and the vertebrate limb) are other examples. Are these better explained by something other than natural selection? One reason for asking is that we still lack a satisfactory genetical theory of speciation or of the origin of the major groups. Mathematical genetics can deal with genetic differences that are correlated with differences in quantitative traits, but is unable to bridge the gap between species. Another debated issue is the suddenness (as some claim) with which major novelties appeared. The standard selectionist response is that the seeming abruptness of many evolutionary changes is more apparent than real, an artefact deriving from the paucity of fossil records in general (a problem to which *The Origin* devotes much space: the risk of mistaking the absence of evidence for evidence of absence is always present). Recent work in palaeontology has underscored the importance of not rushing to final judgement: dramatic findings have revealed long-sought transitional forms, for example in the evolution of tetrapods. Also, geological time scales can be misleading. On a scale of

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100 million years, one million years look like an instant. But a million years can encompass an enormous number of generations and provide enough time for qualitative changes in traits to take place.

The general opinion remains that there is no way of understanding adaptation, the defining characteristic of living organisms, other than as a result of natural selection. On the other hand, some evolutionary biologists have been drawing attention to the ability of matter to organise itself spontaneously into ordered states. The outcomes can be striking when they resemble generic features of plant and animal form (e.g., branching, symmetry, serially repeated structures). By comparing the different parts of an organism to the 'centrifugal governor of the steam engine' that maintained stability by using feedback, Wallace anticipated the general philosophy. It is sometimes described as a 'systems', as opposed to reductionist, approach. This way of looking at plant and animal form harks back to the early 1900s and the advocacy of D'Arcy Wentworth Thompson, a staunch anti-evolutionist. Among other things, he argued strongly that vertebrate skeletal morphologies were best understood as equilibrium structures that were the result of mechanical forces, not as products of evolution. Then the mathematician Alan Turing showed in 1952 that diffusible chemicals that were able to catalyse their own synthesis could spontaneously give rise to a range of spatial patterns. However, there are problems with biological order that is independent of genetic information. There is no assurance that the same pattern will recur generation after generation: for example, the environment may fluctuate or critical substrates may be in short supply. A way to get around this difficulty has been proposed. If a self-organised pattern is stable it can recur generation after generation. Suppose it is also beneficial and persists over a sufficiently large number of generations. Then genetic changes could occur in the

Traits can and do vary in the absence of genetic variation.

interim and ensure that the processes that generate the pattern become independent of external stimuli and unaffected by external perturbations. In this picture the role of natural selection is more to fine-tune a trait than to cause its appearance.

Traits can and do vary in the absence of genetic variation. Non-genetic variation cannot lead to immediate evolutionary consequences, but as we have just seen it has the potential do so if it persists over many generations. That apart, it appears likely that under certain situations non-genetic variation is a useful strategy to adopt by a group that is made up of genetically similar, perhaps identical, individuals. The argument is that a group in which different members do different things is better off than a group in which everyone does the same thing.

It is generally believed that along with the development of culture, natural selection has slowed down or become insignificant in humans. Instead, cultural evolution, which unlike biological evolution is largely Lamarckian, is said to have taken over. While that is largely true, the interesting thing is that cultural evolution too may not be free of biology. With the possible exceptions of language, cooking and life cycle rites, there are many 'characteristically' human cultural traits – for instance tool use, agriculture, art, music and ritual – for which it is not too far-fetched to think of analogies in animals. A question engaging attention is, are they more than analogies? Is it meaningful to talk of animal culture? And if so, can one trace links with the corresponding human traits?

Natural selection moulds living organisms so that they function as efficiently as they can under the genetic and environmental conditions to which they are subject.

Natural selection moulds living organisms so that they function as efficiently as they can under the genetic and environmental conditions to which they are subject. Genetic variations occur randomly, and the ones that lead to adaptive changes spread through the population.

Adaptation is said to be to an environment; ecologists speak of an organism's 'niche'. Even though the environment includes other organisms, this is a passive view of the role of the evolving organism itself. But what if animals and perhaps plants take an active part in constructing their own environments, something that we know happens all the time? Weaver bird nests, termite mounds and beaver dams are spectacular examples. Cases such as these have fuelled the growth of what is called niche construction theory, a theory still in its infancy. Its goal is to incorporate the element of self-reinforcement (or feedback, or autocatalysis) implicit in such situations into standard evolutionary discourse.

Only time will tell whether the possibilities mentioned here will modify the Darwinian picture of evolution in an interesting way or merely add footnotes to it.

Darwin after *The Origin of Species*

In the long run, the success of a theory has to do with a number of factors. Its scope and explanatory power, whether it continues to fulfil a need, holds its own vis-à-vis alternative theories, and so on, all come into the picture. But if a theory is to catch on when it is first proposed, it must be novel and it must 'smell right'. An underlying mechanism for implementing the assumptions of a theory is something to be prized, a bonus. But it is not essential. Darwin's comprehensive analysis of evolution in *The Origin of Species*, in which natural selection was the most important but not sole engine of evolutionary change, smelt right. When subsequent advances in biology uncovered the details behind heritable variations, the feeling was reinforced.

The eight books that Darwin wrote after *The Origin* – there were sixteen in all – initiated research in diverse areas of biology. *The Descent of Man, and Selection in Relation to Sex* is, as the title suggests, two books in one. *The Expression of the Emotions in Man and Animals* established the evolutionary basis of epistemology and founded the (currently controversial) field of evolutionary psychology. Of the remaining seven, six were on plants and, as J B S Haldane put it, are concerned with those aspects of plant life which are most like animal and human life. Haldane went so far as to say that these, not the theory of evolution, constituted Darwin's most original contribution to biology. They deal with sensory perception, movement, predation and reproductive strategies. (The work on plant behaviour was carried forward brilliantly by J C Bose.) Darwin remained active till the end. His last paper was published thirteen days before he died on 19 April 1882. It contained a vindication of the claim that even a sedentary shellfish (cockle) could disperse over large distances by latching on to the leg of a water insect or frog. The work was based on a report that he had received from Francis Crick's grandfather.

Further Reading

The Darwin Online site (*www.darwin-online.org.uk*) is a gold mine; it claims that it has all of Darwin's published and unpublished writings. If no citation is given, it should be assumed that a quotation used in this article comes from there. There is also a less comprehensive *Alfred Russel Wallace Page* (*www.wku.edu/~smithch/index1.htm*); a review of Peter Raby's *Alfred Russel Wallace: A Life* (Princeton University Press, 2002) draws attention to the different route that led Wallace to natural selection (*www.ias.ac.in/resonance/March2008/p277-282.pdf*; *Resonance*, pp.277-282, March 2008). Two modern, scholarly and readable biographies of Darwin are by Adrian Desmond and James Moore (Darwin: A tormented evolutionist; Penguin, 1992) and E Janet Browne (Charles Darwin: Voyaging and Charles Darwin: Power of Place; Jonathan Cape, 1995 and 2002). A much smaller but insightful biography is Cyril Aydon's Charles Darwin (Robinson, 2002). The Galápagos finches are exemplars of speciation and adaptive radiation. Their story is told in *The Beak of the Finch: A Story of Evolution in Our Time* by Jonathan Weiner (Vintage, 1995). As a brilliant piece of detective work by the historian of science Frank Sulloway showed, the significance of the finches was established only in the middle of the 20th century. See *Darwin and His Finches: The Evolution of a Legend* (F J Sulloway, Journal of the History of Biology, vol. 15, no. 1 pp. 1-53, 1982). J Maynard Smith's *The Theory of Evolution* (Penguin Books, 1993) covers much of evolutionary biology, not just natural selection. The best description of

natural selection that I know is *The Blind Watchmaker* (Penguin, 1990) by Richard Dawkins. Two excellent books explore how it works in detail: A Cornish-Bowden's *Pursuit of Perfection* (Oxford University Press, 2004) does so in the case of biochemical pathways and J T Bonner's *Why Size Matters* (Princeton University Press, 2006) shows how a simple theme can lead to varied outcomes. G G Simpson treats the theme of evolutionary opportunism in *The Meaning of Evolution* (Yale University Press, 1949). See *The contribution of Ibn Sina (Avicenna) to the development of earth sciences* (Al-Rawi *et al*., Foundation for Science Technology and Education, 2002; *http://www.muslimheritage.com/uploads/ibnsina.pdf*) for an early example of uniformitarianism. *On Growth and Form* by D'Arcy Thompson (Cambridge University Press, 1992; abridged edition by John Tyler Bonner) is a classic exposition of the physicalist approach to biological form, and a recent book on the subject by Forgacs and Newman is reviewed in *http://www.iisc.ernet.in/currsci/dec102006/1568.pdf*. M Morange discusses Darwinian and other approaches to the origin of life in *Life Explained* (Yale University Press, 2008). S Sarkar's *Doubting Darwin?* (Wiley-Blackwell, 2007) contains a robust rebuttal of 'creationist designs on evolution'. J T Bonner's *The Evolution of Culture in Animals* (Princeton, 1986) considers how biology might have played a role in cultural evolution. The story of Darwin's last paper is given in *Discoverer of the Genetic Code* by Matt Ridley (HarperCollins, 2006).

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