(Re)Reading *The Origin*

Charles Darwin's 1859 book On the Origin of Species *is much referenced, especially in this double anniversary year. But, does anyone still read it? And, if so, what is the book itself like as a text? We have asked biologists from a range of fields — evolutionary biologists, but also geneticists, ecologists, paleontologists and molecular biologists — to re-read (or read)* The Origin *for* Current Biology*. Below are the responses, contributed by: Andrew Berry, Matthew Cobb, Simon Conway Morris, Jerry Coyne, Hopi Hoekstra, Peter Lawrence, Robert May, Christiane Nüsslein-Volhard, Mark Ptashne, Matt Ridley and Marlene Zuk.*

Jerry Coyne

Many of my colleagues say that we should quietly shelve the term 'Darwinism'. We don't, they argue, call classical physics 'Newtonism', nor relativity 'Einsteinism'. So why saddle our field with an eponymous personality cult, especially when we've learned so much since *The Origin of Species* appeared in 1859? Why not call it 'modern evolutionary biology', or the insidious-sounding 'neo-Darwinism'? The best answer to this revisionism is to re-read *The Origin* itself. In no other field has the work of a single individual created a research program that has endured for a century and a half. (It is inconceivable, for example, that a modern paper on electromagnetism would begin with the words "Ever since Faraday...") Besides Darwin's 'Big Five' ideas: evolution, natural selection, common ancestry, lineage splitting (speciation), and gradualism, *The Origin* broaches ideas only now coming to fruition — ideas often tossed out in one brief sentence.

We read, for instance, about how evolution can be constrained by pleiotropy, "the many unknown laws of correlation of growth". We encounter the idea that some traits might not be subject to any form of selection, and that these neutral traits could remain as polymorphic "fluctuating elements". There is the suggestion that punctuated patterns in the fossil record could be caused by rapid evolution in small peripheral populations that rapidly supplant their ancestors. The 'Kluge-Kerfoot hypothesis', published in 1973, proposes that the traits most variable *within* populations are those most likely to differ markedly *between* populations. This idea, now the foundation for sequence-based tests of natural selection on genes, appears in chapter five of *The Origin*. Darwin even suggests that family selection might explain the evolution of sterile insect castes.

No popular work of science — and we must remember that this book was written mainly for the public, not Darwin's colleagues — ever had such a dramatic impact on both scientific opinion and human consciousness. Buttressed by innumerable facts gleaned personally or through tireless correspondence, Darwin works his magic with a subtle but irresistible style of argument. He asks rhetorical questions, disputes with himself, raises and answers every objection to his own theories, and in the end so convinced his readers that they not only bought his ideas, but in the process jettisoned three thousand years of religious explanation for life and its apparent design.

And, from the outset, Darwin got it mostly right. Evolution occurred, all species have common ancestors, and the main (but not the only) engine of evolutionary change is natural selection. These ideas have endured unchanged, becoming scientific truths. Over the past century and a half, much of our time has been spent sweeping up after the Darwinian elephant, analyzing the droppings from *The Origin*. True, Darwin wasn't *always* correct: he got genetics wrong, and his views on species and speciation are pretty wonky. And of course evolutionary theory has advanced: systematics, continental drift, and population genetics are all areas untouched by his looming shadow.

Still, these advances amount to refinements of Darwinism rather than its Kuhnian overthrow. Evolutionary biology hasn't suffered the equivalent of quantum mechanics. But some biologists, chafing in their Darwinian straitjacket, periodically announce new world views that, they claim, will overturn our view of evolution, or at least force its drastic revision. During my career, I have heard this said about punctuated equilibrium, molecular drive, the idea of symbiosis as an evolutionary force, evo-devo, and the notion that evolution is driven by the self-organization of molecules. Some of these ideas are worthwhile, others simply silly; but none does more than add a room or two to the Darwinian manse. Often declared dead, Darwinism still refuses to lie down. So by all means let's retain the term. It is less of a jawbreaker than 'modern evolutionary biology', and has not, as was feared, misled people into thinking that our field has remained static since 1859. What better honorific than 'Darwinism' to fête the greatest biologist in history?

Jerry A. Coyne is an evolutionary geneticist in the Department of Ecology and Evolution at the University of Chicago. He works on the origin of species, using Drosophila *as a model organism, and is the author of the forthcoming book* Why Evolution is True*.*

Robert May

On being invited to re-read Darwin's *Origin of Species* and comment on it, my first question was which edition. As Darwin sought to mollify critics, successive editions lengthened, until the sixth and final edition is twice the length of the first. Some of these changes are adumbration of examples to strengthen an argument, others are circumlocutions to avoid problems (for example, given that the nuclear forces which fuel the sun were unknown to the physics of Darwin's day, Kelvin and others observed that the geological time available for evolutionary processes was at most a few million years; this is why, in successive editions, numerical estimates of the sweep of evolutionary time disappeared into a verbal fudge).

So I re-read the first edition. A century and a half has passed, but the language remains fresh, and the ideas compelling. As John Bonner and I wrote in introducing a reprinting of *The Descent of Man* in 1981, "It is the genius of Darwin that his ideas, clothed as they are in unhurried Victorian prose, are almost as modern now as they were when they were first published." And never before or since has a book so changed our view of the world, and of our place in it.

This being acknowledged, I doubt that *The Origin* is commonly read today as an inspiration for research. But it is heavily cited: a recent analysis of books in ecology and evolution puts it a close second to Fisher's *Genetical Theory of Natural*

Selection, and well ahead of most contemporary monographs (Elworthy (2007). Bull. Brit. Ecol. Soc. *38*, 55-57). I suspect, however, that this may owe more to the Darwin industry among historians and philosophers of science than to basic researchers. Ultimately, however, *The Origin* provides a telling illustration of the inadequacy of measuring true impact by counting citations.

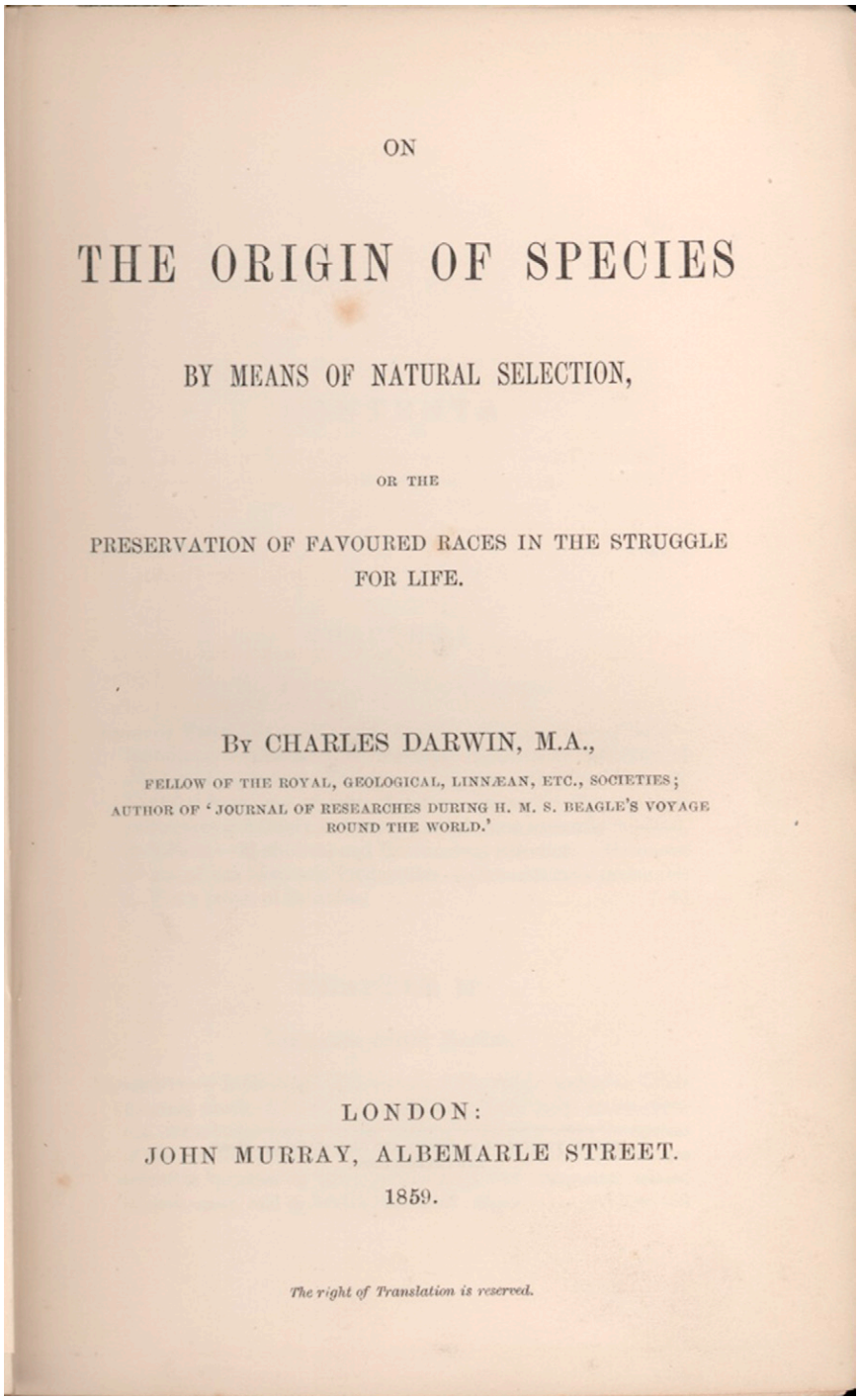
Interestingly, Wallace's books — including that which gave us the classification of biogeographical realms which we still use — do not feature in Elworthy's catalogue. Even in their own day, there was something of cricket's distinction (which persisted for a further century) between Gentlemen and Players in their relationship. It should, however, be acknowledged that Victorians often referred to the Darwin–Wallace idea of evolution by natural selection. All of which emphasises the disparity between the high-profile Darwin bicentennial celebrations and associated academic industry, and the relative neglect of Wallace. In the interests of equal time, I am now off to re-read Wallace.

Robert, Lord May of Oxford, OM AC FRS, is a physicist-turned-ecologist and Professor in the Zoology Department at Oxford University. He was Chief Scientific Adviser to the UK Government (1995–2000) and President of the Royal Society (2000–2005).

Matt Ridley

I deliberately picked up a late edition of *The Origin of Species*, the sixth edition, published in 1872, interested to see how Charles Darwin, an obsessive reviser of his own prose, had coped with all the comments the book had received in the 13 years since it had first come out. For instance, in this edition, Darwin enthusiastically adopts Herbert Spencer's coinage 'survival of the fittest'. The book certainly reads in places like a conversation with his critics, as in this sardonic passage: "My judgment may not be trustworthy, but after reading with care Mr Mivart's book, and comparing each section with what I have said on the same head, I never before felt so strongly convinced of the general truth of the conclusions here arrived at."

Biology is the science of exceptions to rules, and what is so striking about *The Origin of Species* is that Darwin builds his argument for a single great rule by finding hundreds of curious anecdotes, experiments, oddities and surprises in the cornucopia of nature, each one seemingly exceptional yet all pulling towards a general conclusion. The power of the book comes not from its relentless logic so much as its enormous reservoir of examples large and small. There is no topic on which he cannot find a race of pigeon or a species of barnacle, or story from a naturalist somewhere in the world, to illustrate his point. Lots of them would not pass muster today, being, to put it mildly, not from the peer-reviewed literature: "I may add, that according to Mr. Pierce, there are two varieties of the



ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

By CHARLES DARWIN, M.A.,

FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES;
AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE ROUND THE WORLD.'

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1859.

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Original *Origin*: Frontispiece of the first edition 1859. Reproduced with permission from John van Wyhe ed., The Complete Work of Charles Darwin Online (http://darwin-online.org.uk).

wolf inhabiting the Catskill Mountains, in the United States, one with a light greyhound-like form, which pursues deer, and other more bulky with shorter legs, which more frequently attacks the shepherd's flock."

When Darwin goes wrong, it is nearly always because he relies on the wrong ideas of others — on received wisdom that turned out to be incorrect. There are three striking examples: first, heredity; with splendid, waffling obscurity, Darwin attributes variability to "changed conditions of life", to "correlated growth" and to the "use or disuse of parts". He even concedes the grossest of Lamarckian fallacies: "The evidence that accidental mutilations can be inherited is at present not decisive; but the remarkable cases observed by Brown-Sequard in guinea-pigs, of the inherited effects of operations, should make us cautious in denying this tendency."

Second, the age of the earth; Darwin accepts the calculation of Sir William Thompson (later Lord Kelvin) that the earth is about 200 million years old, but confesses uneasily that "it can hardly be considered as sufficient for the development of the varied forms of life." Thompson was out by a factor of seven, because he had omitted the effect of radioactivity which is slowing the cooling of the earth.

Third, continental drift; Darwin struggles to explain why different continents have different faunas on them, and why the geological record is so intermittent in most places. He thinks that land bobs up and down in the same place: "the great oceans are still mainly areas of subsidence, the great archipelagoes are still areas of oscillations of level, and the continents areas of elevation."

The Origin of Species is a fossilized scientific argument. That is to say, it is a moment of intellectual awakening frozen in its own time. It was superbly adapted to its Victorian environment, struggled successfully for existence, proved fit enough to survive and gave rise to still fitter living descendants, which survived many attempts to drown them in new-fangled fallacy, having shed along the way their worst features.

Matt Ridley is the author of, among other books, The Red Queen, Genome *and the biography of Francis Crick. He lives near Newcastle upon Tyne, UK.*

Peter Lawrence

"*The greatest scientific advance of the last 1000 years was providing the evidence to prove that human beings are independent agents whose lives on earth are neither conferred nor controlled by celestial forces…… nothing was more important than providing the means to release men and women from the hegemony of the supernatural*." (Mellman, I. and Warren, G. (2000). The road taken: past and future foundations of membrane traffic. Cell *100*, 99–112.)

In this vital mission to discredit the supernatural, nothing has proved more important than *The Origin of Species*. Here is just one nice argument from hundreds: "He who admits the doctrine of the creation of each separate species, will have to admit that a sufficient number of the best adapted plants and animals were not created for oceanic islands; for man has unintentionally stocked them far more fully and perfectly than did nature."

"The power of the book comes not from its relentless logic so much as its enormous reservoir of examples large and small."

(*Matt Ridley*)

I had only dipped into this wonderful book in my student days. But what a revelation for a somewhat jaded scientist to read it now! It is not only the brilliance, farsighted and original nature of the ideas, there is the sheer diversity of knowledge, the pervading presence of thought, of simple direct experiments, of debate, of argument, the consideration of other views and the style. In writing and reading scientific articles nowadays, we become imprisoned, constrained in what is considered appropriate and our vocabulary is reduced. Also our sentences are stifled by fashion and by journals that kill invention and independence with their strict word limits and their 'house style'. Just one example: punctuation. Darwin used everything, even the long dash and the exclamation mark. In my scientific writing I have been frequently told that these are not allowed — OK for great literature, but banned from scientific usage. I don't know why, but dulling down our scientific writing is not in our best interest. By contrast, in Darwin's time, Victorian fashion encouraged a flowery style as well as intellectual freedom; he took full advantage of both. He could write explorative and educative prose. He could spend many pages explaining narrow but important distinctions between different viewpoints and, time and again, one can see the outcome of careful reading and deep reflection. Our data-dominated publications, pared down to fit them into limited space, would be much more comprehensible if there were more argument, more explanation and more justification; indeed, if we reflected more, I think we could make big reductions in our published pages by making sure they carry and convey at least one message of note.

Although Darwin's book is primarily about arguments and evidence, he does not forget the power of a simple experiment. Just one example: he argues that the worldwide dispersal of some freshwater plants is due to migrating birds carrying mud on their feet; so he takes three tablespoons of mud from a local pond and, over 6 months, found he could grow 537 plants from it. Darwin has whole chapters discussing the points of view of others, dismissing contrary opinions with persuasive arguments. He took time to communicate extensively with other specialists. By contrast, in modern scientific discourse, we see the deadening hand of a new etiquette fuelled by careerist calculations. We now have little open debate, different views are avoided rather than confronted, controversial papers are not quoted and their publication is resisted. But, of course, Darwin not only had something important to say, he also did not have to keep in with opinion-formers in order to get grants!

Peter A. Lawrence has studied the genetics of animal design using insects for 45 years. He is currently working in the Zoology Department of the University of Cambridge and the MRC Laboratory of Molecular Biology, Cambridge, UK.

Matthew Cobb

Even the most ardent evolutionist regularly shakes his or her head in wonder at an amazing adaptation and asks: how on earth did that evolve?

Darwin was no different, as shown by what may seem to be one of the stodgier chapters of The Origin of Species — chapter eight on 'instinct'. This chapter deals with the evolution of behaviour and focuses on the astonishing behaviour of social insects, in particular, honeybees and their intricate honeycombs. As Darwin writes: "He must be a dull man who can examine the exquisite structure of a comb, so beautifully adapted to its end, without enthusiastic admiration."

Darwin was not the first person to think about the evolution of behaviour — his grandfather, Erasmus Darwin, as well as the Frenchmen Jean-Baptiste Lamarck and Pierre-Jean Cabanis, had all tackled the subject at the end of the 18th century. But Charles Darwin's approach was doubly different to those of his predecessors. He interpreted behaviour as a product of evolution by natural selection, thereby obliging himself to explain behavioural adaptations in terms of other, less developed characters. And, as shown by virtually every page of *The Origin*, he was incredibly rigorous, seeking to address all possible objections to his theory, grinding down criticisms one by one.

The material in chapter eight was particularly important to Darwin, and not only because it was hard to imagine how, say, bees might have evolved the ability to make hexagonal cells. He recognised that the existence of widespread sterility in social insects — dealt with in some detail in this chapter — presented him with "one special difficulty, which at first appeared to me insuperable, and actually fatal to the whole theory [of natural selection]". His resolution of this fundamental problem not only showed his genius, it also prefigured some of the most important developments in evolutionary theory over a century later.

Darwin starts his chapter on instinct by linking behavioural and morphological adaptations: "No complex instinct can possibly be produced through natural selection, except by the slow and gradual accumulation of numerous slight, yet profitable, variations", he writes, emphasising that these variations are "produced by the same unknown causes which produce slight deviations of bodily structure".

In the pages that follow, he emphasises the existence of variation for various 'instincts', and puts forward an explanation of how they might have evolved. In the case of pointing in hunting dogs, he points out it is merely "the exaggerated pause of an animal preparing to spring on its prey", while the evolution of cell-making in honeybees can be understood in terms of a series of the existence of discrete behavioural elements. Some of these putative stages can be seen in various bee species — the wax cells produced by bees vary from the cylinders produced by bumble bees to the elaborate hexagons made by honeybees.

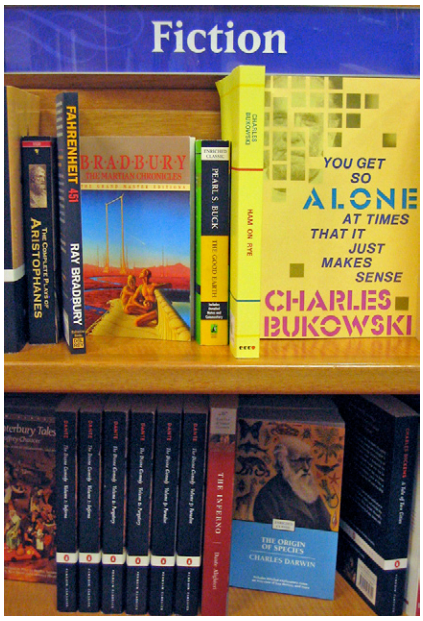
Darwin also describes a series of experiments he carried out which showed that the thickness of the cell wall was a decisive factor in indicating to the honeybees when to stop work. By adding coloured wax, he showed that several bees will act together on making cells, with one individual moving from one cell to another before it is finished, indicating that bees, like other animal architects described in the chapter, do not have an internal 'image' of what they are building. Darwin then argued that natural selection would have given an advantage to those bees that could make the most economic use of the precious wax, thereby encouraging the appearance of hexagonal cells.

But the most important part of this chapter centres on what Darwin called the "special difficulty" of sterility in social insects: "With the working ant we have an insect differing greatly from its parents, yet absolutely sterile; so that it could never have transmitted successively acquired modifications of structure or instinct to its progeny. It may well be asked how is it possible to reconcile this case with the theory of natural selection?"

Darwin's explanation of the selection of sterile individuals is that "selection may be applied to the family, as well as to the individual, and may thus gain the desired end." In other words, if individuals that are related to the sterile ants reproduce, and somehow share the character in question, then natural selection can lead to the evolution of sterility.

Although Darwin was referring to 'family selection', and used examples from cattle breeding and horticulture to back up his insight, there is a direct link between this explanation and what was probably the greatest development in evolutionary thinking in the last 50 years — Bill Hamilton's work on kin selection, 'inclusive fitness' and the evolution of altruism.

However, the most important contribution of this part of Darwin's book is its unstated implication that the human mind is on a continuum with those of animals. Just as his study of morphological evolution showed us that we are nothing special — just a particularly smart and talkative bipedal ape — his work on 'instinct' implies that human mental life can be understood as the product of evolution and, above all, that consciousness is a physical phenomenon. Darwin not only gave us the means to interpret the whole of the natural world, he also provided us with the tools needed to investigate one of the greatest scientific and philosophical conundrums: where our thoughts come from.



Fact: At New York's LaGuardia airport. Photograph kindly provided by Alex Gann.

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Christiane Nüsslein-Volhard

"*When we no longer look at an organic being as a savage looks at a ship...*" — the first thing that struck me when re-reading *The Origin*: Darwin's book is wonderful literature — exciting, interesting, very well written, in an almost colloquial style. Darwin goes to great lengths not to be too tedious and seems to be constantly worried about losing the reader. To anyone interested in biology, the book can never appear dull: there are so many facts and observations about natural history, the diversity of animals and plants — after all, this is the topic of the book — but also about agriculture, domestic crops or the breeding of pigeons, and spreading out into behaviour, geology, fossils, embryology. All of these observations are placed in the context of the "one large argument" of descent with modification. There is hardly any field that is left out — except for, perhaps, chemistry and physiology.

Darwin did not know about microorganisms, and therefore his book deals little with pathogen resistance or health, a topic which nowadays is recognized as most important for the evolution of organisms. In retrospect, Darwin's biggest limitation — as many have pointed out — was that he did not understand genetics; this worried him a great deal, and he tried hard to delineate "laws of variation", but he could not explain the origin of variation. He emphasizes, however, that sexual reproduction increases variation and fitness, and acknowledges the "strong principle of inheritance". Reading these chapters, it sometimes feels as if Darwin got close to Mendel's laws, but all was buried in a big mess of often contradictory reports about all sorts of crosses among wild and domesticated species. Perhaps, in the case of inheritance, the abundance of observations and cases that make *The Origin* so entertaining to read, clouded Darwin's view and made it impossible for him to see the clear rules that Mendel recognized through his elegant experimental system.

The Origin is also a testimony of Darwin's obsession — a brilliant idea, conceived rather early and his fear he might be hanged for it, as well as an urge to be understood, to find support. A book like this could probably not be written by a present-day scientist: for one, much of the diversity of nature has disappeared in the meantime, and Darwin had a much more direct approach and closer contact to nature than is possible nowadays. Of course, he was singularly fortunate, because the long voyage on the Beagle allowed him as a naïve observer — unprejudiced and with a mind wide open — to collect and learn about a richness of facts that is exceptional. However, it would be entirely wrong to say that his theory depended solely on the opportunities given to him by the voyage.

"I had only dipped into this wonderful book in my student days. But what a revelation for a somewhat jaded scientist to read it now!"

(*Peter Lawrence*)

In the final chapter of *The Origin*, which impresses me most, the argumentation is based largely on well-known work of other naturalists, as well as his own thorough investigations of barnacles. The chapter deals with classification: "From the first dawn of life, all organic beings are found to resemble each other in descending degrees, so that they can be classed in groups under groups." People have ordered plants and animals long before, most notably according to Linnaeus' *systema naturae* (1735), a 'natural' system, which takes affinities or relationships between organisms into account as opposed to an 'artificial' classification based on, say, size, colour, habitats or type of food. It had been realised that different traits are of different value for classification, and that similarities could also arise in parallel: the different value of homologous (similar by common type) as opposed to analogous (similar by common function) structures was clearly appreciated. Darwin emphasises that his theory of descent with modification has the power to explain the natural system, and he mentions the intuition of the biologists before him: "Community of descent is the hidden bond naturalists were unconsciously seeking" in their classifications.

The fact that in embryos the more general features that characterise a type develop earlier than the specialised ones had also been observed before, in particular by Karl Ernst von Baer. Embryonic as well as larval traits had been most important in defining larger groups in the natural system. Darwin explains this pattern by the use and disuse of organs: as there is no selection acting on embryonic forms that are not yet functional, embryos or larvae will reveal the 'prototype' of a given group, while the adults are often highly specialised and adapted to their lifestyle. The barnacles Darwin studied, for example, can be recognised as crustaceans only by virtue of their larval form. Likewise, he explains the existence of rudimentary organs that would have no reason to exist were it a creator's world. Although this evidence for his theory is often overlooked, and developmental biology until recently played little if any role in post-Darwinian evolutionary theories, the mere fact that a natural classification is possible at all is most compelling, and one wonders why others before Darwin have not interpreted common traits by assuming common ancestors. It is striking that the famous single illustration of the book is used to explain this argument, underlining the importance Darwin himself attributed to it. In this illustration, Darwin fills in the missing intermediates by designing a hypothetical pedigree to explain the natural system: if all the species that had ever existed would come to life again, the missing intermediates — together with all those that died out in side branches — would also appear, allowing an undisputable natural classification, based on common descent with modification.

When settled at Downe, having the advantage of living on the family purse, without the need for grant writing, job finding and scientific administration, Darwin could follow up his thoughts and obsessions with utmost freedom, interrupted only by his family and illness. We owe his great book also to a loving wife, his kids, pigeons and plants, and a walk around the sandwalk everyday. I don't envy him for the illness or for his fame, but for his independence and for the peace of the place which provided the setting for the development of the great theory of evolution.

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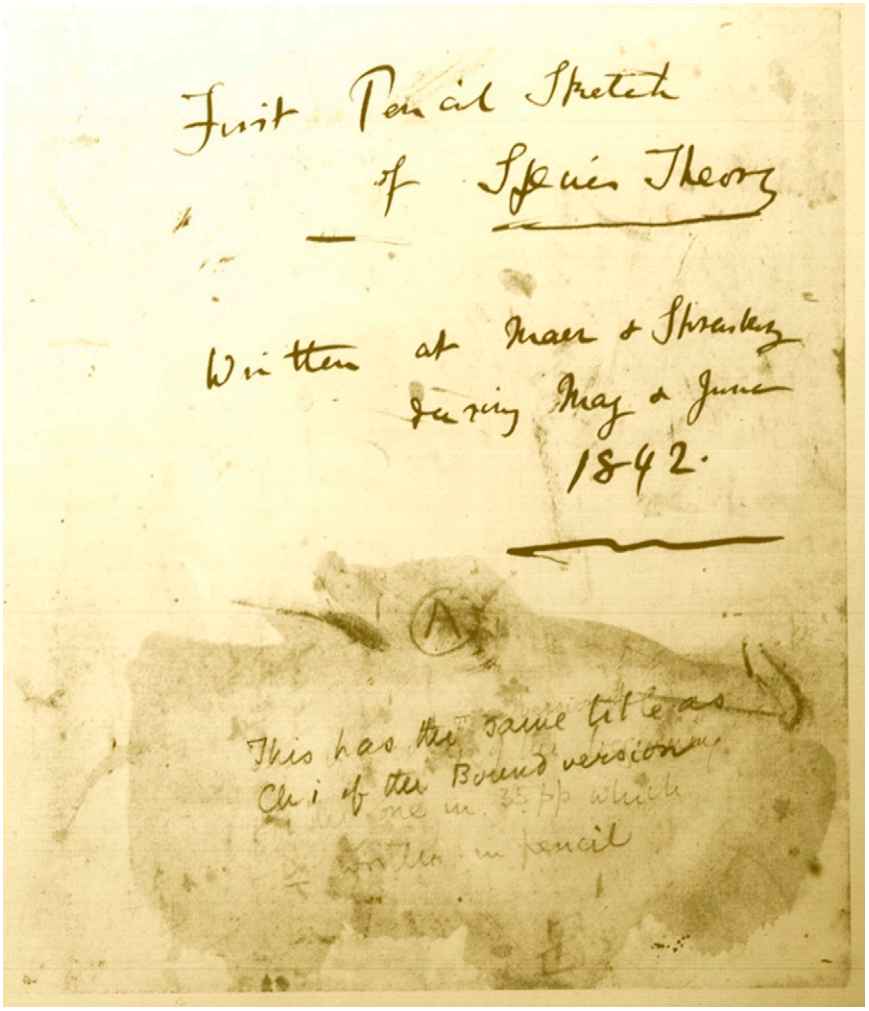
Mark Ptashne



Origin of *The Origin*: The first pencil sketch (1842). Reproduced with permission from John van Wyhe ed., The Complete Work of Charles Darwin Online (http://darwin-online.org.uk/).

In the last chapter of the first edition of *The Origin of Species* Darwin famously says "...this whole volume is one long argument...", and urges the reader to weigh all the pros and cons. Sly fellow, as though all scientific positions, 'proofs', are not arguments that aim to convince the reader. What is so unusual about *The Origin*, and what makes it so thrilling, is the *abstraction* involved here. We are urged to accept the idea that species arose by natural selection in the face of an incoherent picture of how variation arises and is transmitted, and the then-unimpeachable testimony of the physicists that the earth cannot be as old as required. Darwin rarely left his house, motivated, I would guess, by his dread of facing attacks he knew were irrelevant or wrong, but which he couldn't answer.

I say 'encountering' *The Origin*, rather than 're-encountering', because my previous attempts to read the book failed. Who has the patience to dig through the convoluted sentences, extracting the buried nuggets? Other writings of Darwin are delightful, and maybe this dangerous book was written so as, once again, to deflect confrontation. In any event my Kindle came to the rescue — there I found a 'condensed' version of *The Origin* in which each sentence has been pared down by the elimination of unnecessary words. And in this version the book comes to life. Had I stuck to the original I might have gotten the 'big picture', but I would have skimmed the details, the astounding array of observations brought to bear. Here's one with an implied prediction: "the absence of distinctive breeds of cat [...] may be attributed to selection not having been brought into play." I suspect that Rocky, my Abyssinian, would reject the idea that humans have since moulded his type rather than the other way around.

Darwin jolts us into confronting an inspiring fact: the world is not transparent. Every interesting scientific construct is a product of the imagination. I was recently assured that the lambda switch — the molecular mechanism controlling lysogeny *versus* lysis of the lambda bacteriophage — was there for the taking, i.e. an easily understood set of interactions that required more looking than thinking. Thank heaven (*sic*) that is not true, for how dull our tasks would have been (and continue to be). The good Bishop, stumbling across the lambda switch in its current guise, would surely remark on the impossibility of evolving this intricate, seemingly irreducibly complex machine. We would have him over a barrel: we can explain how a set of simple binding reactions, each additional binding reaction making the machine work a bit more efficiently, went into making the switch the marvellous thing it appears to be.

Darwin of course knew nothing about lambda — in fact, *The Origin*, in its first edition, considers only 'recent' evolution, that which resulted in the diversification of plants and animals. In hindsight *The Origin* illustrates a principle of scientific analysis: if you want to uncover universal mechanisms, concentrate on the simplest examples; because, paradoxical as it might seem at first, Darwin was analyzing the 'simplest' examples of evolution. Unlike what happened during the evolution of bacteria, essentially no new enzymatic activities appear in the elaboration of plants and animals. In fact, we are made up of a number of genes embarrassingly close to those found in a fly, and the fly genes encode proteins very similar to those found in us.

The trick natural selection exploited, so as to use common enzymes to produce disparate organs and organisms, was to vary the *regulation* of these common enzymes. Many of these enzymes

have a wide array of possible substrates, and what changes during evolution are the *specificities* imposed by binding reactions. The Blind Plumber will work on any pipe in your house — you have to lead, or 'recruit', him to the one or more pipes that should be worked on. Similarly, the enzyme RNA polymerase will transcribe into RNA essentially any gene to which it is recruited. This trick applies to every aspect of the regulated production of proteins and other macromolecules — including transcription of genes, splicing, transport and translation of mRNA, proteolysis of proteins, transduction of extracellular signals, and so on. Over recent evolutionary timescales it is the recruiters and their sites on targets — genes, proteins, RNA — that changed, not the enzymes themselves. And that, it would seem, is an easy task for natural selection. It is not surprising that we understand less well how the earlier stages evolved.

A regulatory world that uses binding reactions to impose specificity inevitably looks messy, you might say unnecessarily 'complex'. To get these rather crude reactions to work properly requires add-on after add-on, usually in the form of more binding reactions that inhibit one or the other step, that result in destruction of a protein when it exceeds a certain concentration, that inhibit another crucial binding reaction, and so on. These ever-tinkered-with systems work, but at a price: just as the regulatory world can be assembled stepwise, so is it rather easily disassembled, with each subtraction making the situation worse. Glance through a modern cancer textbook and you will see a kind of 'evolution in reverse' — the accumulation of mutations that take the cell back to a more 'primitive' state, one devoid of the usual controls. Almost without exception, every mutation involves, directly or indirectly, a binding reaction, or the creation or destruction of a binding site by an enzyme.

The good news — Darwin would have loved it — is that it is easy to see in principle how changes in just a few surface residues of a protein can, by affecting binding reactions, contribute to recent evolutionary change. The bad news is that one cannot predict where these changes will be found and, once found, these changes may be hard to interpret. Surely that is a big part of the problem in analyzing the multi-factorial contributions to human variation and disease. Darwin never said it would be easy. Indeed his vision predicts it can't be.

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"...my previous attempts to read the book failed. Who has the patience to dig through the convoluted sentences, extracting the buried nuggets?" (*Mark Ptashne*)

Simon Conway Morris

A small confession: No! No! Not that one! I confess, yes, this is the first time I have read *The Origin* cover to cover. And could it be that, as with another well-known sphere of human engagement, a little experience, dare I say maturity, helps? A book of genius? Of course! But what suddenly became clear is that this is a book haunted by the ghost of William Paley — the grandfather of creationist thinking and exponent of seemingly irrefutable arguments for organic design. *The Origin* is Darwin's riposte. Its metaphorical power depends on suspense and a scattering of clues, but significantly Paley himself is mentioned only once. And cleverly not in the context of his ideas on organic design but in an oblique dig at the question of natural evil. First and foremost, *The Origin* is an exorcism of the doctrine of special creation, and conducted by one of the most skilled exorcists science has ever seen. The brief crescendo in the last chapter is preceded by repeated and sudden flashes of disdain, a quick insertion of the knife before the narrative calmly continues in its ostensibly more objective purpose of piling up the evidence. Darwin knew his enemy intimately, but was far too astute to engage in a head-on clash.

Darwin was right, and he knew it. His expressions of doubt are largely rhetorical and how seamless — at least from a distance — is the edifice upon which he constructs his theory. Yet, it is equally intriguing how he conceals his intellect: the carefully marshalled facts are allowed to speak for themselves and the implications introduced with restraint and circumspection— a *sotto voce* naturalist. Darwin never doubted his abilities. *The Origin*, however, offers precious few clues as to the roots of his intellectual adventure. Cambridge, where his scientific mind actually crystallized, goes unmentioned. In the opening line of *The Origin,* Darwin hints at the *Beagle* being the catalyst, but what a contrast this book is to what we usually refer to as *The Voyage*. In this earlier work plenty of questions are posed, but very few answered. True the Malthusian formula is invoked, but the sense of enquiry is far more one of muddle. The seeds were sown, but germination was a slow process and in many ways *The Origin* is a late flower. Yet it reveals glimpses of an intense acuity of vision. Combine this with an enviable gift of lateral thinking and, if the dark brain of Darwin is not exposed, it is at least visible. Such is also clear because even though *The Origin* is a deep book, its surface sparkles with prescient insights. Of course, *a priori* readings from our vantage point can make too much of half-articulated thoughts, but in this mind of a genius we see a catalogue of potentialities. These include hypotheses that we now identify with r-selection, group selection, the red queen, incumbency, biogeographical barriers, character states, stratigraphic hiatuses and embryological recapitulation. So, too — in a way that still seems to puzzle half the biologists I know — Darwin succinctly explains how ancestors are themselves not the direct intermediates, and, as we know now, may bear precious little resemblance to their distant progeny. But even when his genius fails him there is still a whiff of future discoveries.

But there is something obsessive about Darwin. Just as he piled up the evidence, so his whole view of evolution was ultimately relentless, an unceasing, almost manic conviction that no piece of evidence was too trivial, too unimportant. Where time is effectively endless, the scrutiny of selection unsleeping and untiring, the most trivial advantage seized upon so *The Origin* becomes effectively the calculus of biology, where fathomless aeons of geological time witness evolution creeping along gradualistic paths. No wonder his eliding of variety with species and agonizing over the nature of hybrids and the question of sterility is so central to his argument of continuum and why, so rightly, he was deeply puzzled by what we now refer to as the Cambrian 'explosion'.

Yet for all of that, the *Origin* has some strange lacuna. Despite Darwin's enthusiasm for the perfection of form and the integration of the organism, the book contains remarkably little on functional biology. He knew some medicine, was a skilled dissector, and it is all the odder because — even if he lived in tranquil Down House — England hummed with the sound of machines and technological innovation. Is it a gentleman's aversion to a sordid reality? I don't think so. Again, the ghost of Paley and his siren voice of organic design must be expelled. Only later, with *The Origin* entrenched, did Darwin reveal his deep knowledge of contrivance, as in the form of climbing plants. And if *The Origin* is an exorcism against Paley, so obliquely Darwin arrives with a mouthful of nails to finally hammer shut the coffin of Lamarckism. Why else the strenuous and repeated insistence that the physical environment can effectively play no role in his theory? After all, if biological form should be so moulded then might not organisms simply be responding to the ebb and flow of inanimate forces?

Darwin knew he stood on a Darien peak with almost unlimited vistas, but was seemingly unaware that he was also staring into an abyss. Integral to his scheme were metaphors of struggle, the weak and dominant, victory and extinction, battle and yielding, invasion and retreat: "let the strongest live and the weakest die", but all to the greater good as in panglossian mode he also wrote "no fear is felt, that death is generally prompt, and that the vigorous, the healthy and the happy survive and multiply". Like many others after him, Darwin muffed the profound problem of natural evil. Despite his generosity of nature when he came to any sort of metaphysics, again like some of his most fervent supporters today, he was hopelessly out of his depth. But at least he knew some of his limits. It is no accident that even as he supposed, absolutely correctly, that famously "Light will be thrown on the origin of man and his history", he suspected that mind and the origin of life might forever fall outside his theory. And, as in so many other ways, Darwin might just be right.

Back to the roots: Darwin's sandwalk and 'thinking path' near Down House in Kent. Photograph from wikipedia.org.

Simon Conway Morris is Professor of Evolutionary Palaeobiology in the Earth Sciences Department at Cambridge, and is working on his next book, Darwin's Compass.

Marlene Zuk

Although the students in our graduate program in evolutionary biology take a core course in evolutionary theory for which *The Origin of Species* is required reading, one could certainly describe the book as a work that everyone cites, but few people have actually read. So is Darwin's masterpiece still valuable 150 years later? Or is our requirement just a form of intellectual hazing, making the newcomers suffer as a rite of passage? I am always struck by Darwin's ability to use details of natural history without being transfixed by them or viewing them as an end in themselves. Amidst the carefully compiled notes from Mr. Chauncey Wright or the Rev. W.B. Clarke, one never loses sight of why Darwin is mentioning an example. The antennae of the Hymenoptera, for example, "as Westwood has remarked, are most constant in structure; in another division they differ much, and the differences are of quite subordinate value in classification; yet no one will say that the antennae in these two divisions of the same order are of unequal physiological importance" (chapter 14). The actual nature of hymenopteran antennae is of little interest to me, but it is abundantly clear that we are reading about them in such detail because Darwin was wrestling with the question of how we choose characters for classification of organisms, which remains an important question to this day. Few modern biologists can both appreciate natural history and recognize that it is not an end in itself.

As a behavioral ecologist, I appreciate Darwin's grappling with behaviour as a trait, and his trying to understand, in chapter eight, whether behaviour is subject to natural selection in the same manner as morphology. Behavior presented Darwin with one of his greatest challenges, altruism, and it is clear that Darwin saw the study of behaviour as a legitimate avenue for evolutionary biology. In contrast, modern scientists spend far too much time splitting disciplinary hairs, distinguishing ecology from evolution from behaviour, and often disparaging whatever subfield with which they do not identify.

The title of the book is misleading, at least in its usual usage as simply *The Origin of Species* without the continuation *by Means of Natural Selection or The Preservation of Favoured Races in the Struggle for Life*. How species begin and how one group splits up into two is only a small part of the focus of the book, and even the subtitle doesn't do it justice. The book is about how, when, and why organisms can change through time, a breathtaking scope that is nonetheless thoroughly plumbed. *The Descent of Man* is similarly unfortunately titled and therefore also perhaps not read as much as it should be and, although its subtitle, *And Selection in Relation to Sex*, is more descriptive of the contents, it too is not particularly compelling. *The Descent of Man* is about sexual differences writ large, in humans as well as other organisms, another blockbuster. Who knows – if Darwin had better titles, maybe he would have been even more influential. Although it's hard to imagine how he could have sexed up his last work, *The Formation of Vegetable Mould through the Action of Worms with Observations on their Habits*.

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Andrew Berry and Hopi Hoekstra

Instead of actually re-reading and commenting on Darwin's *Origin* ourselves, like the other contributors of this series, we report here on what our students had to say about reading it for the first time. As part of our mid-level course on evolution at Harvard, we assign *The Origin* (alongside a selection of recent/classic papers and textbook readings) to be read chapter by chapter throughout the semester. This exercise is mildly controversial; colleagues have criticized us, saying that we should focus on current science rather than revisiting the past. Our response is twofold: uniquely among the sciences, evolutionary biology is dominated by the one authority, the one book. If Steve Gould hadn't entitled his first collection of essays *Ever Since Darwin*, we would still be starting our papers with these very words. Second, the continued relevance and freshness of *The Origin* is especially remarkable when you consider what Darwin didn't know.

"*The Origin* is an exorcism of the doctrine of special creation, and conducted by one of the most skilled exorcists"
(*Simon Conway Morris*)

Natural selection is an explicitly genetic theory, and yet Darwin had no viable theory of transmission genetics; biogeographic arguments play an important role for Darwin and yet he had no knowledge of continental drift; and speciation, arguably the linchpin of the evolutionary process, was *terra incognita* for Darwin. That Darwin's "one long argument" remains compelling and coherent today is testimony to his unwillingness — except on rare occasion, such as in the case of bears evolving into whales — to go beyond the data before him. For example, as an acute observer, he was familiar with the extent of phenotypic, and therefore genetic, variation in natural populations and was content to treat genetics as a black box; only later, when his hand was forced, did he produce a specious model of genetics, pangenesis. *The Origin* is thus a book-length testament to the scientific method.

We expected the students to respond in the same way as we did when we first read it – to groan at the occasionally lumbering Victorian prose, but to appreciate the insights that crop up so frequently and so unexpectedly. But, curiously, our students seldom have such a balanced response: they either love it or hate it. Our statistical analysis of these data hasn't gone beyond mere eyeballing, but there seems to be no major disciplinary effect: life-science majors are as likely to love (or hate) *The Origin* as physicists or historians or engineers. Here are a few quotations from a recent set of anonymous evaluations:

"Textbook unnecessary. Darwin's '*Origin of Species*' a great reason to take course. Journal articles useless."

"*The Origin* = Very Painful"

"I enjoyed reading Darwin's *Origin*. It seemed appropriate to read *the* primary source, even if not every idea has found still to be correct".

"The reading of Darwin was pathetically useless. It did nothing to add to the course and just made discussion groups worthless as well."

"*Origin* — Awesome! So cool to read!"

"It's OK when he's not talking about plants and pollen, like that time with the slave-making ants (that was pretty cool)."

"Origin is awful (sorry). Way too long and redundant."

"Reading the last chapter of *The Origin* over the last week was magical."

"Reading Darwin is a nice requirement, but I don't think it should be tested on the exam."

We would, of course, like to transform the "Origin = Very Painful" crowd into the "Origin — Awesome" one, but we suspect that this will remain a case of not being able to please all the people all of the time. Regardless, we are confident that, ten years on — as they go about their work in hospitals, at biotech companies, and perhaps occasionally at universities — even the students who were not enamoured with *The Origin* when they took our course will recall with pride that they read every word of the book and grappled with even its more obscure and unquoted passages. The details of what we taught them will be long gone, but *The Origin* and all of its lessons will remain.

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