Comment

Many happy returns

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No one knew it at the time, of course, but 12 February 1809 was a red-letter day for the human race. On that day, thousands of miles apart, were born two of the greatest men in history.

Their lives were, in most respects, quite different. The American was born poor and endured many failures; the Englishman was the son of a wealthy doctor and never had to work for a living. The Englishman lived out his biblical threescore years and ten; the American was murdered before he reached 60. The American was a man of faith and remained so in spite of a family tragedy; the Englishman lost his faith because of a similar family tragedy. The Englishman hated politics; the American reveled in it.

But they had more in common than is sometimes recognized. Both men valued reason over ideology. Both men were not afraid to take unpopular stands when they thought they were right. Both men were widely reviled, and still are by some people. Both men were gentle of manner but courageous and tough. Both men changed the world. And both men are famous as much for what they wrote as for what they did: their words had the power to transform the way people thought. The American was Abraham Lincoln, 16th president of the United States. The Englishman was Charles Darwin, co-discoverer, along with Alfred Russel Wallace, of the principle of evolution by means of natural selection.

This being a scientific journal, my subject is Darwin (although it is worth noting that Lincoln was the founder of the US National Academy of Sciences). Most scientists probably know something of his story: destined for the ministry, he abandoned his studies to serve as companion to Captain Robert FitzRoy of the ship *Beagle* on its voyage around the world from December 1831 to October 1836.

On 24 November 1859, Darwin at last published his great book on evolution. The entire press run of 1,250 copies sold out on the first day at a price of 15 shillings each; if you can find one on the rare book market today, it will cost you about US$100,000. It has what may be the longest, dullest title in the history of great books: *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. For the rest of his life, through five more editions (some of which were considerable revisions), Darwin clung like a barnacle to this title, although he did drop the word 'On' for the sixth edition.

Here are some little-known facts about what Darwin said, and what he didn't say, and when:

> The one thing about which *On the Origin of Species* has almost nothing to say is the origin of species. The term 'species' is never really defined, and the idea of a species barrier based on reproductive isolation is never developed. Darwin cannot really be blamed for this, as he knew nothing about the concepts of genes, the genome and the laws of genetic inheritance. At exactly the time he was laboring over the manuscript, his contemporary, the Moravian monk Gregor Mendel, was busily breeding peas and discovering the transmission of characteristics in a predictable way by factors (genes) that generally remain intact (though they may mutate) and do not blend (though they may mask one another's effects). But Mendel published his findings in an obscure journal, *Proceedings of the Natural History Society of Brünn*, in 1866, and Darwin never incorporated them. (Pretty much nobody read about them then either; Mendel's work had to be rediscovered, 34 years later, by Hugo de Vries and Carl Correns.) Darwin died in 1882 without knowing the mechanism underlying his theory.
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> The word 'evolution' appears, I believe, fewer than ten times in even the sixth, and final, edition of *On the Origin of Species*, but the last word in even the first edition is 'evolved'.

In the entirety of *On The Origin of Species* there is only a single sentence on the subject of human evolution ("Light will be thrown on the origin of man and his history"). Darwin didn't explicitly address that topic, the one that causes apoplexy in so many religious fundamentalists, until 12 years later, in *The Descent of Man, and Selection in Relation to Sex*. But he didn't have to. The implication of his theory was immediately apparent to every educated person, because several previous, quite popular books by other authors had already advocated applying the idea of evolution to human beings. Given the anatomical similarity of apes, they were the obvious ancestor of choice. But all those authors proposed a direct line of descent from apes to man; none of them realized that the two are separate offshoots, derived from a common primate ancestor. Darwin didn't realize that, either.

The phrase 'survival of the fittest' doesn't occur in the first four editions of *On the Origin of Species*. In the fifth edition, published on 10 February 1869, Darwin used it for the first time, as a more graphic way of describing the concept of natural selection. The phrase wasn't original to him; he borrowed it from the philosopher Herbert Spencer.

Although Darwin was a good draftsman, like most Victorian naturalists, *On the Origin of Species* could have benefited from a judicious use of Photoshop™. There is only a single figure: an amateurish hand-drawn evolutionary tree (reproduced for this column, see figure 1) that conveys almost no detailed information.

You can probably win some money around the bar at many scientific meetings by betting on how many scientific voyages Darwin undertook in his life. The answer is one. After the *Beagle* voyage he never left England again; indeed, after he moved out of London in 1842, he seldom left his country town. Poor health is one reason (he suffered from a debilitating chronic illness that may have been Chagas disease, contracted in South America), but basically, after his marriage and the birth of the first of what would eventually be ten children, Darwin became a homebody - not particularly adventurous, except intellectually. The man whose travels produced the foundation of our understanding of the development of living things rarely traveled.

Though polite and soft-spoken, Darwin was not modest about his theory. On more than one occasion, he said that he expected all future biological observations would be consistent with natural selection, and would serve to confirm it. As scientific hubris, this remark ranks close behind that of Einstein, who, when asked how he would have felt had the famous experiment to measure the effect of gravity on light waves not produced the result predicted by his Theory of Relativity, replied, "In that case, I would have been sorry for God. The theory is correct."

One of the biggest misconceptions about Darwin is that *On the Origin of Species* had a hostile reception when it was published. It did attract some severe criticism from a few conservative clergy, but in general the book was well received. Most British clergymen of that era were quite progressive, and were prepared to accept the ideas in Darwin's book as a description of how the Creator worked. It was in America that the pot really began boiling. America was always more conservative in religious terms than Europe, so fundamentalist objections to evolutionary theory were much more widespread there. But what really stirred things up was the popularity among American intellectuals of Social Darwinism, Herbert Spencer's attempt to show that societies are organisms and, like living creatures, evolve. Social Darwinism was eventually used to justify notions of racial superiority and forced sterilization of the retarded - things Darwin would have abhorred. (For a detailed account of all this, I heartily recommend Barry Werth's wonderful new book *Banquet at Delmonicos: Great Minds, the Gilded Age, and the Triumph of Evolution in America*, Random House, 2009.)

So if *On the Origin of Species* isn't about the origin of species, what is it about? It's not about the idea of evolution (which the Victorians usually called 'transmutation'); Darwin took that as a given. It's about the mechanism of evolution. The problem with all the previous books and articles and philosophical discourses on evolution - and in a preface to a later edition of his book Darwin traces the concept all the way back to Aristotle - is that no one could explain how it happened (which led many naturalists to reject the idea and claim that species were immutable). Why were some traits, but not others, retained in a species over time? Why did different traits become fixed in certain populations and not others? What drove this relentless differentiation, which evolutionary theory said must have started with a small number of ancestral species, perhaps as few as one? Thanks to his observations on the voyage of the *Beagle*, years of thinking about how animal husbandry led to the diversity of livestock and domestic animal breeds, and an inspired insight concerning the implications of Malthus's ideas on overpopulation leading to competition for resources, Darwin was able to provide the answer to what was called by some the philosophical question of the day.

His answer, of course, was the concept of natural selection. For reasons he couldn't explain (not knowing about genes and how they mutate), populations contained a distribution of traits that appeared to arise by chance (although Lamarckian ideas were not ruled out). If a particular trait - say, longer length of the beak on a finch - conferred a particular survival advantage - say, increased ability to

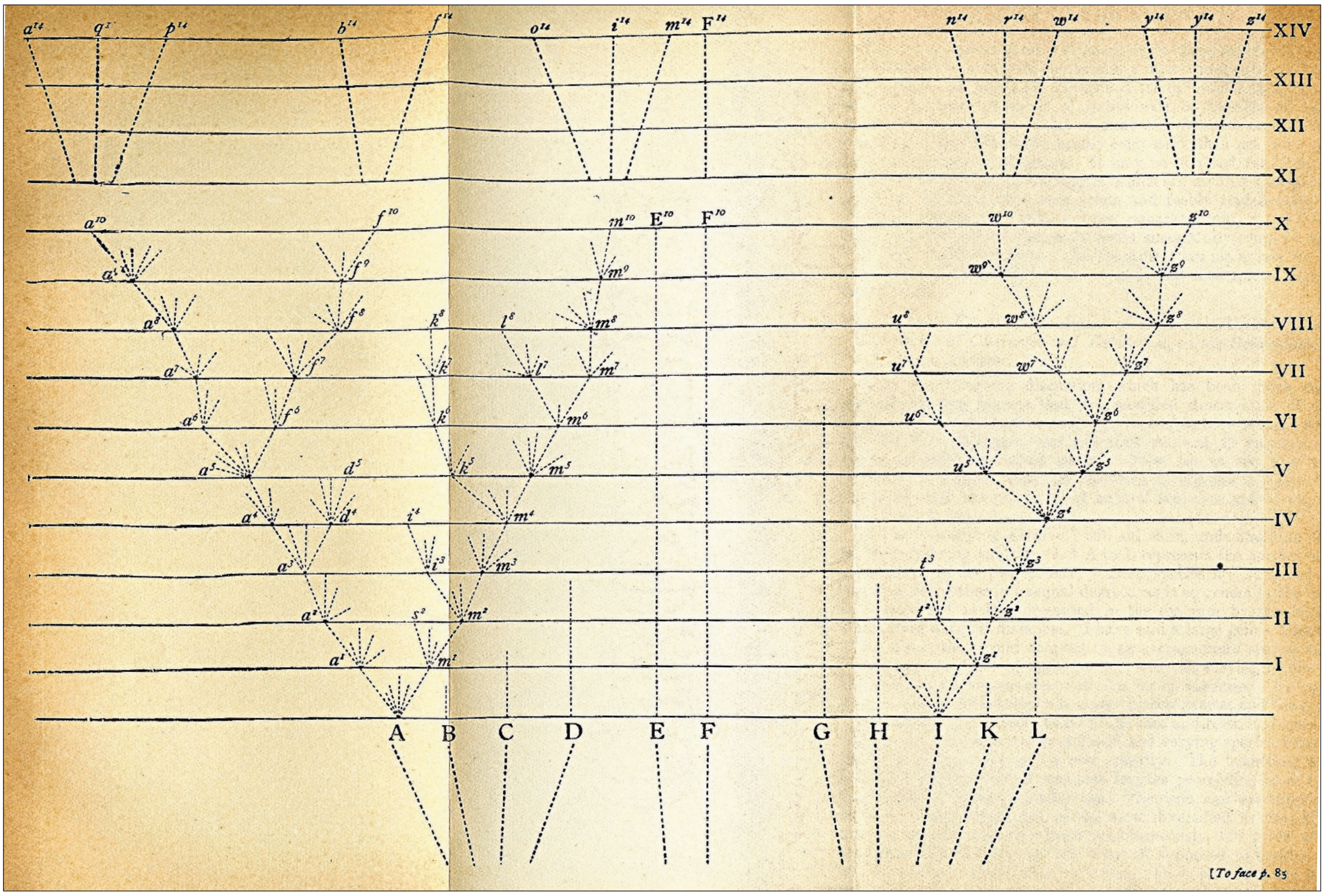

Figure 1
Darwin's graphical representation of the principle of descent with modification and how new varieties would be formed over long periods of time by natural selection. The intervals indicated by Roman numerals "may represent each a thousand or more generations" (*Origin of Species*, 6th edition, p85). The capital letters along the bottom indicate original species. "The little fan of diverging dotted lines of unequal lengths proceeding from (A), may represent its varying offspring. The variations are supposed to be extremely slight, but of the most diversified nature; they are not supposed all to appear simultaneously, but often after long intervals of time; nor are they all supposed to endure for equal periods. Only those variations which are in some way profitable will be preserved or naturally selected." So, after a thousand generations, "species (A) is supposed to have produced two fairly well-marked varieties, namely a^1 and m^1", and so on. Darwin explains that he has chosen the "extreme species (A) and the nearly extreme species (I) as those which have largely varied, and have given rise to new varieties and species".

acquire food - over members of the population that did not have it, that individual would be more likely to produce offspring and they, too, would have that trait, which would make them more likely to produce offspring, and so on until the trait became characteristic of the species. Darwin did not actually devote much space in his book to his famous finches, but they have been much studied since as examples of how morphological changes can aid survival.

Ironically, Darwin's finches have been employed by creationists as examples of the supposed failure of evolutionary theory: they claim that beak changes in Galapagos finches during a severe drought cannot explain the origin of species by natural selection because the changes were reversed after the drought ended, and no net evolution occurred. Of course, this is one of those misnamed 'exceptions' that really do prove the rule: the finch data perfectly illustrate that populations change their average physical features in response to changes in the environment, and document how the physical features of an organism can affect its success in reproduction and survival. Moreover, they show that such changes can take place more quickly than was previously thought - an important point in the timeline of evolution. That complete new species did not arise within the duration of the study is a feature of the short time-scale of the climate changes involved.

The theory of evolution by natural selection is the cornerstone of biology, and one of the towering achievements of the human intellect. Yet there isn't a statue of Darwin (or of Wallace, who ought to get at least some of the adulation as well) in any public space in the United States, as far as I know. Religious fundamentalists still fight to keep his ideas out of public school science classes, and when they can't do that, they attempt to teach a trumped-up 'scientific controversy' about alleged 'weaknesses' in the theory of evolution, though the theory is practically as solid as atomic theory. Even the National Academy of Sciences failed to honor him until this year: a statue of Einstein graces the arbor outside its headquarters on Constitution Avenue in Washington, DC, in full view of passers-by, but you have to go inside to find a life-size bust of the greatest biologist of all time.

Darwin is probably the most controversial scientific giant since Galileo - and we all remember what the forces of ignorance did to Galileo. More so than anyone else, Darwin's findings demand that we give up the idea of the literal truth of the Book of Genesis, and see it as metaphor - soaring, beautiful, lyrical metaphor, but metaphor nonetheless. Yet, despite the widespread use of metaphor elsewhere in the Bible ("Behold the lamb of God", "I will make thine enemies thy footstool", and so on), many people who would never take those other passages literally still insist that we do just that with the story of creation. Surely it is not too much to ask that, on this 200th anniversary of Darwin's birth, his fellow biologists stand up and proclaim, with the same courage he showed in the face of opposition, "Happy birthday, Charles. You were right."

Fifty years ago, on the sesquicentennial of 12 February 1809, the poet Carl Sandburg gave this eulogy in the United States Congress: "Not often in the story of mankind does a man arrive on Earth who is both steel and velvet, who is hard as rock and soft as drifting fog, who holds in his heart and mind the paradox of terrible storm and peace unspeakable and perfect." He was referring, of course, to Abraham Lincoln. But the words could equally well apply to Charles Darwin.

For more on Darwin, why he didn't discover Mendelian inheritance, and his influence on modern biological research, see the February issue of *Journal of Biology*:

Q&A: What did Charles Darwin prove:
Paul Harvey

Why didn't Darwin discover Mendel's laws?:
Jonathan Howard

Evolutionary genomics and the reach of selection: *Laurence Hurst*

Mayr, mathematics and the study of evolution:
James Crow

Darwin and Huxley revisited: the origin of allometry: *Charles Stevens*

Apes, lice and prehistory: *Robin Weiss*