The Necessity of Darwin.

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February 12th, 2009 was Charles Darwin's 200th birthday, and **November 2009 represents the 150th anniversary** of the publication of his transformative book, The Origin of Species (Darwin 1859). It seems a good time to look back and assess Darwin's legacy within the perspective of current knowledge of genetics, cytogenetics, and molecular biology in general. Although a comprehensive understanding of evolution would no doubt have emerged eventually, it is difficult to imagine how anyone could have matched Darwin's prodigious and sustained efforts, as well as his talent for explaining things in simple terms.

The details of Darwin's early life are by now well known, thanks to several excellent biographies, for example David Quammen's superb book *The Reluctant Mr. Darwin* (Quammen 2006). We know, for instance, that Mr. Darwin's academic career had a somewhat inauspicious start, and he dropped out from his medical studies in Edinburgh and just barely graduated from Cambridge with qualifications that were supposed to help him on his road to becoming a clergyman in the Church of England. Nevertheless, there is no doubt that, from early on, he was an enthusiastic biologist of the 18th Century type, an outstanding collector of biological specimens, a shoot-and-stuff man, full of curiosity and energy. It certainly helped (as many of us have learned through our own personal experiences) to have had a distinguished mentor. For Darwin it **was** John Henslow, whom he met in Cambridge. We also know the details of how he was just barely able to seize the opportunity to go on the Beagle, against his father's advice, and we have followed how he gradually matured into a skilled fieldworker, thinker, and scientific investigator *par excellence*.

As is often the case with successful men, success depends on who you know as well as what you know, although this truism does not necessarily shield you from risks. The 30-year old Darwin married his cousin who brought with her a dowry of 5000 GBP (Desmond & Moore 1991,Gribbin 2003). The interest from this money, added to her 400 GBP annual allowance from her grandfather and Darwin's own considerable wealth, provided them with an annual income of around 9000 GBP (in today's terms, well over half a million GBP and not far short of one million USD; http://uwacadweb.uwyo.edu/numimage/Currency.htm). This income gave Darwin the financial independence that facilitated his research and his ability to convey the results of that research to men of influence, as well as to enjoy the superb solitude and working environment of his home at Down House in Kent. All of which makes his magnanimity towards the comparatively unconnected and decidedly impecunious Alfred Wallace, co-discoverer of Natural Selection, that much more admirable and even amazing, a real tribute to Darwin's essential humility and honesty.

As respectable as Darwin and his family undoubtedly were, it is easy to see how the idea of evolution via natural selection would have been seen as a shocking theory in late 19th Century England, essentially a creationist society dominated by a powerful church. Darwin was obviously mindful of this, even though he had lost his own religious faith, partly due to the development of his ideas, and partly as a reaction to the death of his beloved daughter Annie, who died writhing and screaming from a mysterious intestinal disease (Desmond & Moore 1991). Natural explanations (heredity, disease, chance) may not diminish tragedy and grief, but what divine plan would be worth torturing to death an innocent child?

The idea of evolution via natural selection was probably not as startling to Darwin as it was to many of his contemporaries, including Thomas Huxley, given that Darwin's grandfather Dr. Erasmus Darwin explicitly proposed a theory of evolution in one of this poetic works, and of course Charles must have known about that (Quammen 2006). Nevertheless, Darwin was apparently so concerned about the reactions to his theory that he set aside 400 GBP (today's equivalent, $48,000 USD) to cover its publication *after his death* (we can only speculate whether he expected to die before he published, in which case one could understand his "procrastination" in submitting the work for publication). Also, as he wrote to Charles Lyell, he was ready to turn all credit over to Wallace, even though it would, as he said, "smash" his life's work (Darwin 1992). But ultimately Darwin, not Wallace, became evolution's iconic figure and it is worth pondering why.

Darwin's legacy is a massive database - climbing plants, earthworms, barnacles, domestic animals, all of the Beagle material and lots more besides - painstakingly analysed over 30 years with the help of acknowledged experts such as John Henslow, Charles Lyell, Joseph Hooker, John Gould and Richard Owen, as well as the American botanist, Asa Gray; a slow, irresistible drip by drip release of the essence of the theory and its supporting evidence to the scientific community and the public. In the process Darwin even managed to redefine the scientific method itself, embracing speculation and imagination (even "hunches") as critical components of hypothesis testing and data analysis. His ideas and methods have truly revolutionised scientific research, particularly in biology and biomedicine, and so it is little wonder that Darwin is considered by many to be the most influential scientist of all time.

But we have to wonder, what would have been the fate of Darwin's "Dangerous Idea" (Dennett 1995) had it been released during a different time and in a different context?

According to John Horgan (Horgan 1996), most (if not all) of the major central ideas, or theories (or organising principles) of science have by now been discovered or formulated, and modern 21st Century science is mainly a process of filling in the details. Thus, as Horgan puts it, when it comes to evolution, modern biologists have to "endure" Darwin's legacy with the realisation that nothing quite so important or central as Darwin's theory of evolution by natural selection will ever be possible again. It's done, it's over, get a life. But we know that Darwin's original theory contained a serious flaw: Darwin had no idea how inheritance actually worked. He did not know about meiosis, or chromosomes for that matter, much less genes, DNA, or the basic principles of

Mendelian genetics such as random segregation and independent assortment. In fact, it is apparent from his own writing (Darwin 1896, 1899) that he had no idea at all how variation, the center stone of his theory, came about. How would Darwin have presented his theory if he knew what we now know about the molecular/cellular mechanics of inheritance in the age of genomics?

What is surprising is that Darwin, in his thinking years (1835-1870), paid absolutely no attention to the cell and developmental biology and genetics that was beginning to happen at the same time in Europe. Why were scientists in continental Europe not talking to their UK colleagues? Was Darwin perhaps too much of a naturalist and a thinker and, in his later years, just too tired and ill to keep himself up-to-date with all the exciting and rapid developments that were happening at the cellular level? Was this an early version of the kind of methodological chasm that hampered communication between mid 20th Century Wellington-booted ecologists and their white-coated molecular biology colleagues (a chasm that was ultimately bridged by computers and DNA)?

The cytological basis of genetic continuity had been worked out by the time of Darwin's death, and the physical basis of heredity (i.e. chromosomes) was fast becoming apparent, although it was not to be fully understood until the turn of the century. Reportedly, Darwin did know of Gregor Mendel's work in pea plants. We can only speculate whether he would have appreciated or even understood it if he had actually read Mendel’s paper on particulate inheritance. Doubtful, since no one else did at the time either. Perhaps most astonishingly, Darwin performed a simple cross with snapdragons in his garden at Down House and got Mendelian ratios in the progeny but he failed to see the significance, and interpreted them on the basis of Lamarckian principles! The true significance of Mendel's work would have to wait until the turn of century when his seminal paper was rediscovered by De Vries, Correns and Tschermak 40 years after its publication.

Mendel actually visited the Great London Exhibition in 1862: he was 40 years old and at the peak of his research. Darwin was 53 and had just published the first edition of "The Origin". If Mendel had but boarded a horse-drawn carriage and made the 20-mile trip to Down House, the two of them could have changed the world on their very first day together! Mendel would have loved Down House, with its gardens and greenhouses and all Darwin's experiments scattered about. If it had been one of Darwin's good days health-wise, they would have had a wonderful time together! But if Mendel had spent time with Darwin when they were both messing about with plant breeding, would they have come up with something exciting without ever knowing about chromosomes?

What would have happened if Darwin had read Mendel's paper and also understood it? To make it more interesting, let's turn things around and imagine that the chromosomal theory of inheritance, as well as Watson and Crick's discoveries of genome structure and function, predated Darwin's theory of evolution by natural selection. How would this have affected Darwin's work?

It is by now a well-known component of the history of genetics and evolutionary biology that, far from instigating a grand synthesis, the incorporation of Mendelian genetics into biology created a schism of sorts between Darwinian naturalists and Mendelian geneticists. The latter figured that Darwin had got it all wrong: The driving force of evolution was not natural selection but mutation, as their work with fruit flies and other model organisms seemed to imply. Thus, in the true sequence of events, Mendelian genetics at first seemed to herald the death of the Darwinian theory of evolution. One has to wonder: if things had gone the other way around, would Darwinian evolution via natural selection have been strong enough to challenge Mendelian genetics in the same way? We would like to think that regardless of the answer to this question, subsequent history would run a similar course, as bright minds realised the synthetic fusion of these two grand theories, and we would have eventually reached the modern Theory of Evolution, as we now know it. But would Darwin himself have had the stomach to push his theory forward in the face of a robust and contradictory paradigm?

Here is the scenario: an almost unbelievably complex genome, full of all sorts of "junk" DNA. A genome characterised by genetic (allelic) variation, mostly obeying the principles of particulate, Mendelian genetics at the level of individuals, and of Hardy-Weinberg at the level of populations. Top this off with what we know about the mechanics of inheritance - chromosomes, meiosis, DNA replication, etc. - that Darwin would presumably have found to be a dream come true. Or would he have found it a nightmare? In fact, would Darwin's ideas even have been necessary? Would his work have been redundant before he had even begun? What difference would it have made?

Darwin's basic idea is nothing if not surpassingly *simple*. Little wonder that Thomas Huxley reportedly slapped his hand against his forehead perplexed that he had not thought of it first. In his recent book about Darwin's works, David Sloan Wilson (Wilson 2007) devotes just two paragraphs to a description of Darwin's theory of natural selection, comparing it to a recipe with three ingredients: *variation* in traits among individuals, *consequences* of this variation in terms of survival and reproduction, and *heredity*. As Wilson points out, when these ingredients are combined, they lead to a seemingly inevitable outcome: an increase in fitness, or evolutionary adaptation. The inevitability of this outcome led Daniel Dennett (Dennett, 1995) to describe the process of evolution via natural selection as an algorithm, probably the closest thing we have in biology to a law.

Ironically, evolution via natural selection is so fundamental, so central to all of biology, that it would surely have emerged eventually, Darwin or no Darwin, perhaps not as a distinct theory, but as something implicit to the vast, ever-growing field of biology. We probably would not even call the mechanism natural *selection*; a curious term if ever there was one. What in nature is doing the selecting? Instead, we no doubt would be talking of "non-random differential propagation" or some equally inelegant phrase. This would be similar to what has happened in other major fields of biology, for example the modern field of developmental biology: no Darwin, no Mendel, no Big Theory. Developmental Biology instead emerged smoothly from the fusion of molecular and cellular biology with classical embryology and, in the guise of "EvoDevo", evolutionary biology (Carroll 2005). Even in molecular genetics, the work of Watson and Crick is not referred to as the Watson & Crick Theory of DNA, but as a description and a mechanism. In other words, we probably would have worked out how evolution happens without Darwin or Wallace. Except that it would have been a *team effort* and it would have taken a lot longer.

Would we have been better off?

Big theories, especially when connected to big personalities (cf. Marxism), can sometimes lead to a kind of ideological canonisation that can cause a lot of trouble. Darwinism brought new meaning and significance to biology, to be sure. And it also brought controversy. Like other Big Theories, Darwinism makes a convenient target for critics who find the idea of evolution repugnant or threatening, especially as it applies to humans (Miller 2008). It is an astonishing fact that, despite Dobzhansky's decades old assertion that "nothing in biology makes sense except in the light of evolution", more than half of all of Americans today do not accept evolution as true (Miller 2008) and the vast majority of humans around the world, regardless of religion, do not accept evolution as the explanation for the origin of humans. We still have not been able successfully to reconcile popular faith in the supernatural with equally popular fascination with science. The hard work that science has done to show how everything can be explained from natural phenomena without recourse to the supernatural all too easily founders on the rock of faith in the supernatural. The ease with which these hard-won scientific discoveries can be brushed aside by beliefs for which there is no empirical, physical evidence is mind boggling, to say the least.

Perhaps part of the problem comes from the failure of scientists to teach others the difference between a theory (in the vernacular sense) and a *scientific* theory, as well as the difference between a scientific theory and a fact. There is no doubt that evolution, as a process of heritable changes in populations, is plainly and simply a fact: an observable phenomenon in field and laboratory. As an observable fact, it is simply not open to argument. Darwin knew this, and so did many of his scientific contemporaries. Darwin's (and Wallace's) main contribution was to identify the primary mechanism by which evolution occurs: natural selection. As pointed out before, natural selection is an algorithm with three components and an all-but assured outcome: adaptive evolution. Again, this is not open to argument. The Big Enchilada, the *Theory* part, has grown from the hypothesis that evolution via natural selection can account for the origin and diversification of all life on Earth (or as Darwin would have put it, "descent with modification"), a hypothesis that, ever since Darwin, has been repeatedly tested and confirmed by such a vast quantity of data that it is now considered to **be the central** principle of life.

Evolution via natural selection is happening around us all the time at levels that we have long since come to accept: tumour cells battling against onslaughts of the immune system, the survivors metastasising to new environments in the host; bacteria struggling against antibiotics, the resistant ones carrying on the infection until we hit them again with a new weapon; trypanosomes, with truly amazing "cleverness", surviving by repeatedly changing their disguise to baffle the immune system; mosquitoes and other insect pests quickly becoming resistant to pesticides. And consider HIV-AIDS; thanks to evolutionary biology, we now know that the virus was introduced into humans at least three times from chimpanzees and twice from monkeys, and we understand why we have failed to develop an effective vaccine - the viruses adapt through evolution by natural selection (Freeman & Herron 2007). Evolutionary theory has also illuminated such things as social behavior including altruism, morality, and even religiosity (Wilson 2007). The list is endless – an enormous body of data that after decades of objective and rigorous and sometimes very expensive research has quietly proved beyond any reasonable doubt that evolution by natural selection is a normal formative process in the history of life on earth. In fact, the modern theory of evolution is by now such a central component of biology that no biologist or biomedical researcher - indeed, no scientist in this day and age - can claim to be fully educated without a basic understanding of it.

Darwin provided the bedrock foundation of all that followed in the life sciences. Had there been no Darwin, the development of a comprehensive understanding of evolution, if not a formal scientific theory, would have been long and tortuous and detached from the realities of human day-to-day life. Darwin worked with material drawn from everyday life to which anyone could easily relate: no molecules, no mathematics, just animals, plants and fossils. His timeless legacy is what few scientists have ever managed to do: he wrote down and published his ideas in a manner that could be understood by everyone, reaching out not just to fellow scientists but to people in all walks of life, all nationalities, all creeds and cultures, and all ages. And who else ever wrote a scientific book that sold out before it had even been published, went to six editions, each with tens of thousands of copies, and is still printed, sold and read 150 years after its first appearance? His ideas, formulated in the 19th century, were so astonishingly far ahead of their time that they have been confirmed, time and time again, and continue to be confirmed by experiments that are right at the cutting edge of modern molecular biology.

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