The Evolution of Evolutionary Theory

Massimo Pigliucci recounts the history of the theories of evolution, and asks whether evolutionary biology has ever shifted paradigms.

Evolution is arguably one of the most profound and controversial ideas ever to hit a human mind. *On the Origin of Species* flew off the bookshelves when it was published 150 years ago, and it remains one of the most crucial books in the history of science. However, despite the fact that the Darwinian view of the world was swiftly embraced by scientists, as much as half of the population in the United States still today doesn't buy it, because it seems to undermine their view of who we are, where we came from, and what we are here for.

But the theory of evolution currently accepted by scientists is no more straightforwardly 'Darwinian' than modern physics is 'Newtonian' – and indeed the entire field of evolutionary biology is still undergoing a revision and expansion of its views on the history and connectedness of life. Unbeknownst to the majority of the public, evolutionary theory has already passed through three major modifications since Darwin, and is in the midst of a fourth stage of its evolution. Yet I will argue that none of these changes fits the concept of a 'paradigm shift' proposed by philosopher of science Thomas Kuhn. In fact, evolutionary biology's only major shift of perspectives took place right at the beginning, at the hand of Charles Darwin himself.

Evolution Versions 1.0 and 1.1

The idea of evolution – that is, of biological change over time – did not originate with Darwin. It had been around in one form or another since the pre-Socratic philosophers, and several Victorian authors, including Darwin's grandfather Erasmus, had clearly toyed with the idea. Yet evolution became a scientific theory only after Darwin articulated in the *Origin* what he referred to as 'one long argument'. (It took him several years to write, and he was rushed into publishing by the fact that Alfred Russel Wallace, a much younger naturalist, had independently reached the same conclusions and was getting ready to publish them.)

Darwin's fundamental insight was grounded on thousands of observations and two principles: common descent and natural selection. Based on his detailed studies of the character and distribution of species across the world, Darwin built a robust inference to the conclusion that all living organisms share common ancestors and are therefore related to each other by a process of 'descent with modification'. But what was doing the modifying?

The brilliant answer was: natural selection. You see, the most difficult thing to explain in biology was the obvious 'fit' between organisms and their environments: wings are clearly for flying, eyes for seeing, spiderwebs for catching insects, and so on. This 'engineering' aspect of biological structures, this 'for-ness' as it's sometimes been called, is what leads so many people still today, and just about everyone in Darwin's time, to invoke intelligent design – if it's a watch, there must have been a watchmaker; if it's a wing, there must have been a wing-maker.

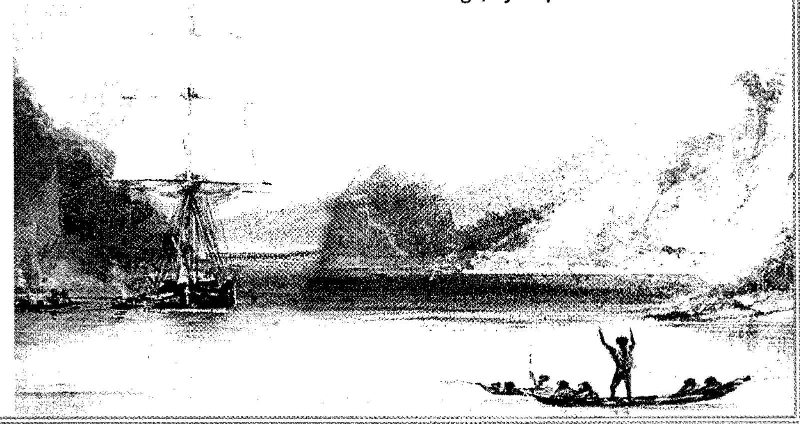
But Darwin managed to propose – and gather impressive evidence for – a new mechanism which would wrestle biology from the claws of natural theology and bring it into the realm of science. Ironically, the idea of natural selection derived from a direct parallel with human-driven *artificial* selection (ie selective animal or plant breeding) – obviously a type of intelligent design itself. Darwin reckoned that *if there is heritable variation among living organisms for traits that affect their fitness for their environment (ie their ability to survive and reproduce), then the ones with the most fit traits will be more likely to pass them on to progeny.* This will result in a continuous process of descent with modification, where the modifications are not random (as often misstated by creationists), but are in the direction of an improved ability of the organisms to function in their environment. Notice that the theory can be stated in an 'if... then...' form – a deductive conclusion which will be true if the premises are true. As it happens, biologists have confirmed over and over that Darwin's premises are indeed true.

You may have noticed that one such premise is *inheritance*: advantageous traits have to be heritable, or natural selection will not be able to exert any long-lasting change in the population. Darwin was aware that he needed a theory of heredity, separate from the ideas of common descent and natural selection. Heredity is a fact, as we all know from the similarity between parents and offspring in all species, but what explains that fact?

Darwin flirted with a couple of possibilities, neither of which were particularly good. For some time he considered the solution

In 1831 the hydrographic survey ship HMS *Beagle* set sail on a five year expedition around the world. Aboard as ship's botanist was a young student called Charles Darwin. The observations he recorded, and the many hundreds of specimens he collected, eventually led him to formulate his theory of evolution by natural selection. He spent more than twenty years collating his observations and working on his theory, before finally publishing his epoch-making book *On The Origin of Species* in 1859, 150 years ago this year.

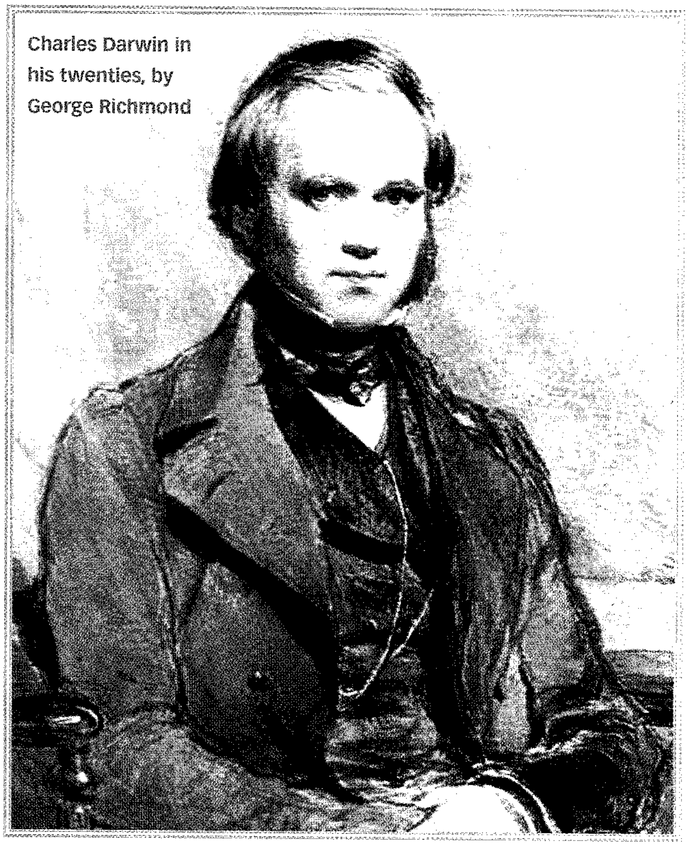
The HMS *Beagle* arriving at Tierra del Fuego, by ship's artist Conrad Martin



articulated at the beginning of the nineteenth century by Jean-Baptiste de Lamarck in France, that living beings can modify their appearance and behavior in response to environmental challenges, and that these modifications are then somehow inherited by the next generation. This is the so-called 'inheritance of acquired characteristics'. But already in Darwin's day there was compelling empirical evidence that Lamarckism didn't work. Darwin then proposed his own theory of heredity, based on an idea called 'blending inheritance' – also a non-starter when confronted with the facts, as the biologist himself readily conceded.

It is rather ironic that the answer to the question of heredity was being worked out during Darwin's time, by the Augustinian priest Gregor Mendel. Mendel's investigations were largely ignored until the turn of the 20th century, mostly because he published them in an obscure journal and so they were little known to the most influential biologists of the time. Moreover, as we shall see in a moment, Mendel's work, when rediscovered, even appeared to deal a fatal blow to Darwinism.

Before the end of the 19th century we already see the first shift away from Darwinism, to what is known as neo-Darwinism: Evolutionary Theory 1.1, so to speak. Neo-Darwinism was the idea articulated by Alfred Russel Wallace (the co-discoverer of natural selection) and German biologist August Weissman, that Lamarckism was definitely out, and that whatever the answer to the question of heredity was going to be, it had to take into account that living organisms completely separate the reproductive cells (the germ line) which convey inheritance from their body cells (the somatic line). Although Weissman's germ-soma separation turned out to be far from universal (plants don't do it), neo-Darwinism set the stage for the next two chapters in the history of evolutionary theory.


Charles Darwin in his twenties, by George Richmond

Evolution Versions 2.0 and 2.1

The original version of evolutionary theory was in crisis at the turn of the 20th century – a period historians of science have termed the 'eclipse' of Darwinism. Few people doubted the idea of common descent, but natural selection was not yet accepted as a sufficient, or even important, mechanism for evolutionary change; and then there was the nagging issue of the missing theory of heredity. In fact, things got worse immediately after the rediscovery of Mendel's work, because the discrete nature of mutations and of their inheritance under Mendel's laws seemed to be at odds with the Darwinian assumption that evolution proceeds by gradual change involving quantitative (ie, not discrete) agents.

A brilliant group of theoretical biologists reconciled neo-Darwinism and Mendelism in a series of papers that were published between 1918 and 1930. Ronald Fisher, J.B.S. Haldane, and Sewall Wright showed that not only was there no contradiction between Darwin's views and Mendel's work, but that Mendelism, generalized through statistical analysis to the case of quantitatively-changing traits, was the long-sought theory of heredity which had eluded Darwin. Evolution 2.0 was born!

During the following two decades, into the late 1940s and early 50s, another group of biologists, including Theodosius Dobzhansky, Julian Huxley (the grandson of Darwin's Bulldog, Thomas Huxley), Ernst Mayr, George Gaylord Simpson and George Ledyard Stebbins, further extended our view of evolution in several directions. Their collective work showed how mutation and natural selection can account for long-term changes in the fossil record; how speciation, the origin of new species, naturally takes place in populations (despite the title of his book, Darwin didn't really address the question of the origin of species); and how selection can be demonstrated (ie observed) to take place in contemporary natural populations of plants and animals. The so-called 'Modern Synthesis' (Evolutionary Theory 2.1) was born, and is still the standard model in biology. It is founded on Darwin's original principles, with the addition of a mathematical-statistical theory, a theory of heredity, and a much more extensive empirical base than Darwin and his contemporaries had been able to assemble.

Evolution 3.1? The Extended Synthesis

Just as the Standard Model in physics is undergoing challenges and revisions (think of string theory, for one), so is the Modern Synthesis in evolutionary biology being challenged. An increasing number of scientists – including yours truly – have grown dissatisfied with the fact that the current version of the theory does not adequately address many important questions. These include the role of developmental processes in evolution, the origin of completely novel traits (such as the turtle's shell, for instance), the increasingly-plausible possibility of so-called 'soft' inheritance (ie, mechanisms of heredity that do not depend on DNA), and even whether and how the propensity to evolve – the so-called 'evolvability' of a lineage – can change during the course of evolution.

Moreover, some evolutionary biologists think evolution is a much richer phenomenon than the Modern Synthesis allows, and includes the ability of natural selection to act not only on individual organisms, but at both lower (gene) and higher

(species) levels. Perhaps more speculatively, but also most interestingly, some of us are pursuing research that for the first time since Darwin looks seriously at the possibility that natural selection may not be the only natural mechanism generating complexity. Intriguing mathematical models borrowed from complexity theory suggest that intricate forms and behaviors may be generated 'for free' as an emergent property of certain types of non-linear systems, of which living organisms are but one example (other examples include meteorological phenomena such as hurricanes, and computer-based algorithms, such as the appropriately named game 'life').

It is too early to tell where these new directions in evolutionary research are leading the field. Some of them may turn out not to be profitable lines of inquiry, and will not survive. Others have already flourished into full fledged fields of study, as in the so-called 'evo-devo' (for 'evolution of development'); a well established sub-discipline in evolutionary biology which expressly addresses the question of how developmental mechanisms (such as cell-cell and tissue-tissue interactions) facilitate or hamper the evolutionary process.

Just as in the case of discussions in physics surrounding string theory, here too we have scientists who do not mind openly speculating on new possibilities, while others complain that not enough empirical evidence has been brought to bear on the question of the alleged extended evolutionary synthesis. Both sides are right, of course, in the sense that they together reflect the way science normally proceeds. We need the conservatives to keep us on our toes and firmly anchored to the data; but there is also a niche for the *nouvelle vague* who push for revolution and attempt to break new theoretical barriers. However, even assuming that we are witnessing a major change in the conceptual structure of evolutionary biology, does it amount to a Kuhnian *paradigm shift*? Has Darwinian biology ever undergone such a shift in its history?

Expansion Without Shift

According to Thomas Kuhn in *The Structure of Scientific Revolutions* (1962), 'paradigm shifts' are replacements of the core theories scientists use to describe the world. We can say more loosely that they are 'fundamental changes in perspective'. The classic examples of paradigm shifts tend to come from astronomy and physics. They include the replacement of Ptolemaic astronomy by the Copernican system, or the transition from Newtonian mechanics to Einstein's relativity. These pairs provide good examples of what Kuhn sometimes referred to as 'incommensurable' theories: there is no way to make sense of a Ptolemaic model of the solar system from a Copernican perspective. Actually, the first one is just plain wrong and has been abandoned. The situation is similar for the Newtonian *vs* Einsteinian view of space-time: a rigid unchanging medium in the Newtonian case, a pliable fabric in the Einsteinian.

But when it comes to the evolution of evolutionary theory we see much more continuity than incommensurability. True, parts of the original Darwinian doctrine were abandoned almost immediately (eg, Darwin's theories of heredity); but the core concepts which did fit reality were retained and built upon. Likewise, whatever shape or form an Extended Synthesis may take over the next several years, most of the crucial ideas that structured the Modern Synthesis of the 1930s and 40s will remain, from the central role of natural selection to the mathematical models of population genetics. In this sense, therefore, I do not think that evolutionary theory has ever undergone a true paradigm shift. With one exception.

In the *Origin of Species* Darwin devoted an entire chapter to discuss the potential difficulties his theory had to overcome in order to be accepted by the scientific community. He also devoted a significant amount of space to a discussion of William Paley's ideas on intelligent design. Paley was a natural theologian and a respected naturalist who made famous the 'watch' argument for design, and intelligent design was pretty much the only game in town when Darwin approached the writing of *Origin*.

Now, intelligent design as a philosophical idea had already been famously demolished by David Hume in his *Dialogues Concerning Natural Religion* (1779), but Hume could only provide a plausible criticism of intelligent design, not an alternative explanation for the complexity and diversity of life. That job was Darwin's chief contribution to humanity – and this alternative explanation truly was a paradigm shift, whose effects still reverberate in the modern creation-evolution 'controversy'. To abandon a supernaturalist view of life on earth in favor of explanations based on natural causes does create an incommensurability – one that finally moved biology from the realm of natural theology and mythology to that of serious science. Charles Darwin will justly be celebrated this year for this momentous achievement in the history of thought.

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