Why is it important to read

On the Origin of Species in 2009?

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In the previous lecture, I showed how the theory of evolution has an increasingly important role in present-day biology. Not only is evolutionary biology an important subdiscipline of biology, but evolutionary questioning is progressively being introduced into the different parts of functional biology. What was the origin of these complex molecular devices? Can we reconstitute the processes by which they were progressively elaborated during evolution?

My aim now will be different. It is to return to the main author of the theory of evolution, Charles Darwin. I will try to convince you that in 2009 it is still important to read *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (hereafter OS; Darwin 1859), more important than reading all the commentaries that have been written on Darwin. It is important, despite the fact that the theory of evolution is no longer what it was for Darwin. Reading OS remains crucial because it is a lesson in honest and excellent science.

I will successively remind you of some of the major facts concerning Darwin, but also how the theory of evolution has dramatically changed since his time. Then, I will turn my attention to OS, and give you a reader's guide. I will argue that Darwin, and Darwin's work, remain highly important for us today.

I Some important characteristics of Darwin's work, and the transformations of the evolutionary theory

As you all know, the work of Darwin is spread through various books. After he returned from his trip around the world on the HMS Beagle, Darwin progressively elaborated his theory of evolution by means of natural selection. His project was to publish a huge treatise, comprising all the data that he had collected in favour of his theory. This changed dramatically when he received in 1858 a manuscript from Alfred Russel Wallace proposing a theory very similar to his own. He decided to publish rapidly one book, OS, a kind of summary of the treatise he had been planning. The remaining material was presented in three other books: *The Variations of Animals and Plants under Domestication*, which contained his model of heredity known as the theory of pangenesis (1868), *The Descent of Man and Selection in Relation to Sex* (1871), and *The Expression of the Emotions in Man and Animals* (1872). These four books represent the core of Darwin's theory. But Darwin also wrote many monographs on highly different subjects: on the reproduction of orchids, on the role of worms in the formation of soils, on insectivorous plants, on barnacles, etc. Darwin was a true naturalist, interested by the facts of Nature. This is clearly apparent when one reads the notebooks that he published after his long journey on the Beagle.

Despite this diversity of interests, microorganisms, bacteria, are totally absent from OS. The book was published too early, at a time when microbiology was progressively emerging through the work of Louis Pasteur and Robert Koch. This is a pity when one knows the strong experimental support that microorganisms bring today to the theory of evolution.

Darwin also lacked any explanation for two important facts constituting the basis of his theory. He had no mechanistic explanation for the spontaneous variations that he observed in organisms, what he called "the plasticity of organisms". This lack of explanation forced him to ascribe to the direct action of the external environment a role not attributed to it by modern-day evolutionists. In a similar way, he had no explanation for the capacity of these variations to be transmitted to the offspring of affected organisms. He proposed his theory of pangenesis in his second book. This attempt generated the production of other models, and progresses towards a satisfactory theory of heredity, an objective reached with the rediscovery of Mendel's Laws in 1900. But his own model was clearly wrong, giving as it did a large role to the heredity of acquired characteristics, and contradicting the then young cellular theory.

These weaknesses and omissions in the work of Darwin were corrected by his successors, and I will briefly recall some of the major advances that have progressively shaped the modern theory of evolution.

In the 1880s, the German naturalist August Weismann provided strong theoretical and experimental arguments against the existence of the heredity of acquired characteristics. In the 1920s, there was a progressive emergence of population genetics, i.e., quantitative models of inheritance of the allelic forms of genes. They gave a precise, quantitative description of fitness. These models demonstrated that variations, leading to a small increase in fitness, are nevertheless capable of invading the population under study in a limited number of generations. The encounter between genetics and the Darwinian theory of evolution, initiated by the rise of population genetics, was completed in the 1930s with the wide movement of unification called the Evolutionary Synthesis. Three contributions to this synthesis are emblematic: Theodosius Dobzhansky demonstrated that the observations made by geneticists on *Drosophila* in their laboratories explained the variations observed in nature in wild populations. Ernst Mayr provided strong arguments in favour of the formation of new species by geographic isolation – the so-called allopatric model. George Simpson showed that palaeontologists' observations on fossils were not incompatible with the models elaborated by population geneticists. Evolutionary Synthesis remains the framework in which evolutionary biologists work today.

This does not mean, however, that evolutionary biology has not been enriched by many new contributions since the 1930s. After the Second World War, the interpretation of evolutionary facts in terms of strategies, strategies of organisms and, later, strategies of genes, appeared and has progressively assumed increasing importance, not only in explaining evolutionary facts, but also a heuristic tool, permitting biologists to imagine evolutionary scenarios. The development of molecular biology also had a huge impact on evolutionary theory. Molecular data provided decisive arguments in favour of a common origin for all organisms on Earth. Comparison of protein and gene sequences became the dominant tool to elaborate phylogenetic trees. Molecular data were used to correct previous phylogenetic trees – such as the relations between humans and our cousins, gorillas and chimpanzees. Molecular biology also explained the origin of the variations that underpin evolution, and showed their diversity: from the point mutation of a nucleotide, leading to the replacement of one amino acid by another in a polypeptide chain, to more drastic events such as insertions and deletions, gene duplication, and even duplication and translocation of part of or a whole chromosome.

Molecular data also showed that most of these variations are neutral, and escape the filter of natural election, as first proposed by the Japanese evolutionary biologist Motoo Kimura (Kimura 1983). More recently, the discovery of developmental genes – such as the homeotic genes – led to the formation of a new discipline, Evo-Devo: the evolution of organisms is related to the variations in structure or regulation of the family of genes involved in the control of development. Evo-Devo is one of these lines of research where the separation between functional and evolutionary biology is progressively erased. Other discoveries, such as microorganisms' capacity to control their rate of mutation in conditions of stress, have also contributed to the elaboration of this complex ensemble of theories, models and mechanisms that constitutes the modern theory of evolution. Epigenetic variations are also progressively being allocated a role in this complex ensemble.

The present state of evolutionary theory differs considerably from the theory elaborated by Darwin, and first published 150 years ago, even if the concept of natural selection still has an important place in present-day explanations. I will provide two examples to illustrate these huge differences. Darwin accepted the existence of an inheritance of acquired characteristics, whereas the modern theory of evolution totally rejects. Darwin did not experimentally test his theory, whereas experimental evolution, "evolution in a bottle", is playing an increasingly important part in the work of evolutionists.

The historical contribution of Darwin was decisive. But, for the reasons mentioned before, it is probably a mistake to call this complex ensemble of models and theories on evolution "Darwinism". First, because it is an anomaly in the landscape of scientific disciplines. The contributions of Newton and Einstein to physics were as important as those of Darwin to biology. Yet Newton and Einstein have not given their names to the theories and models that emerged from their work. To identify a theory and a man (or a woman) is the rule for ideologies – like Marxism – not for scientific theories. More seriously, to identify the modern theory of evolution with the name and work of Darwin leads to totally biased debates and questions. Was Darwin right or wrong? Is the theory of Darwin still valid today? These questions have no sense. Darwin was both right and wrong, and only a part of his theory is valid today. It is a common rule in science: scientific knowledge permanently evolves, and the contributions of scientists, even the most important ones, are bricks in the ever-evolving edifice of science.

In contrast, the right question is rarely asked: is this complex ensemble of theories, models and practices, which is called "the theory of evolution", likely to be found to be wrong in the more or less distant future? The answer is obviously "no". First, there is no other ensemble of theories and models likely to replace the present theory of evolution. The work of evolutionists does not consist in trying to falsify the theory of evolution, but rather in determining which scenarios are able to explain this and that evolutionary variation, the relative role of adaptation (selection), the constraints and neutral variations in one or other evolutionary transformation. Maybe new evolutionary mechanisms – including, for instance, epigenetic modifications – will be described, and their place in set of explanations available to evolutionary biologists discussed. More and more "molecular flesh" will be added to the skeletons of proposed scenarios. But the present theory of evolution provides a good framework in which to try to explain the evolutionary facts. This does not mean that evolutionary facts are already fully explained. Far from it. Much remains to be explained. Explanations are still preliminary, too abstract. A selection has to be made between different scenarios, and the molecular mechanisms underlying these scenarios have to be described. Nonetheless, researchers clearly have a theoretical framework well adapted to explaining the evolution of organisms.

II My personal feelings when reading On the Origin of Species

The above considerations do not diminish Darwin's major contribution or the interest in reading OS in 2009. Not to find in it eternal truths, but to see how scientific knowledge is progressively acquired. Considering the huge number of publications devoted to Darwin, his personal contribution and his time, it would be more time-consuming, and less fruitful, to read this abundant literature than to open OS. The reader must not expect an easy read: OS is hard-going, sometimes boring with its apparent repetitions, and its lack of an obvious organization. For instance, instead of immediately presenting his theory, Darwin starts his book with an apparent long digression on the variations observed in animals under domestication. This first impression is incorrect. OS is a highly organized book, but not simply so as to present the theory of evolution by natural selection, but rather to answer objections that might be, or had already been, raised. One must not forget that the first versions of the theory were elaborated twenty years before the publication of OS, that Darwin had already discussed it with some of the most famous scientists of his time, and that he himself was highly conscious of the difficulties his theory had to face.

Another difficulty when reading OS is that it appears that Darwin has not yet made up his mind on some important issues regarding his theory, such as the inheritance of habits, and more generally the inheritance of acquired characteristics. At some places in the text, Darwin gives the former an important role, whereas at others, he gives natural selection the dominant if not exclusive role.

Another characteristic of the way Darwin proceeds which, when discovered, makes the reading of OS more evident is his extensive use of the specialized studies he has done on pigeons, barnacles, orchids, etc. They are treated as model systems in which different facets of the theory can be tested, at least in thought experiments. This recurrent use of the same examples explains the apparent repetitive character of the book.

When these obstacles have been overcome, the richness of the book grips the reader. The developments on Man and sexual selection, which were fully explored in the later books, are already clearly depicted in OS. Facts emerging from the study of human beings are used to support the theory, as are those from the study of other organisms. For the careful reader, it is absolutely obvious that Man fully belongs to Nature, and that his evolution has obeyed the same rules as those followed by other organisms. The importance of sexual selection, besides natural selection, is also clearly mentioned.

What is most striking is that OS prefigures many of the developments of the theory of evolution which occupied research throughout the 20^{th} century, and the attendant debates. By this I do not mean that Darwin was a precursor, that he anticipated the work of 20^{th} century biologists. Rather, by exploring the difficulties that his theory encountered, Darwin guessed some of the directions where it would be possible to overcome them. I will just give a few of many examples. Darwin insists on the important role of unselected variations in the evolution of organisms, a clear anticipation of the neutralist theory developed by the Japanese researcher Motoo Kimura in the 20th century. Darwin suggests also that the rate of variations can be modulated by the environment. Such a possibility was demonstrated at the end of the 20th century in microorganisms, and its significance actively discussed. Nonetheless, one has to admit that it was impossible for Darwin to see the true significance of this possibility, at a time when nothing was known about the mechanisms generating these variations, and when it was even conceived as possible that the environment directly moulded organisms. Darwin also perceived the possibility that a variation could be beneficial not to its owner, but also to the other members of the same species. But he was not able to develop the conceptual tools – kin selection, group selection – that would be necessary to justify such a possibility.

The book is also important because it exhibits the difficulties of Darwin's theory. The first originates in the fact that Darwin proposed a radically new principle of explanation, at odds with those used in other disciplines. Consider physics: scientists try to explain the phenomena they observe by the existence of laws, or of mechanisms. The theory of evolution by variation and natural selection is not a law, and even if it is frequently described as a mechanism, it has nothing in common with the mechanisms considered by physicists. Not only is the theory unusual, but its validity is limited to the domain of organisms, a scandal for many physicists! Since organisms are a part of the natural world, how is it possible that they obey specific laws? These unusual characteristics of Darwinian theory partially explain the opposition that it has encountered, and the reluctance with which it has been accepted.

This theory is also difficult *per se*. First, because it is a theory accounting for historical facts. Direct experiments to test the theory were not realized at the time of Darwin, and the theory could only provide scenarios. As we have seen, this is no longer the case today, when experimental evolution is assuming an increasing role in the work of biologists. Nevertheless, the weakness of any historical explanation persists.

A second difficulty of the Darwin's theory stems from the complexity of the events under study. The action of natural selection is the result of a complex interaction between all the organisms present in a given ecosystem – if we adopt a present-day expression – not, as is commonly said, the result of the direct interaction of an organism with its environment. The full description of this complex interaction is highly difficult for the naturalist, if not impossible. The same is true if one considers extinctions, the extreme possible consequence of the "struggle for life". Once again, it is impossible, according to Darwin, to understand why a given species has disappeared in the past. This emphasis on the complexity of the relations between organisms, and between organisms and their environment, is a characteristic of Darwin's thought. It has deep resonances with the present-day use of the theory of complexity to unravel the functioning of organisms and ecosystems. The bad side of this emphasis is that the explanatory and predictive power of Darwin's theory is reduced to the point where it vanishes altogether!

Another challenge to the theory concerns the explanation of discontinuities in the evolutionary process, the most obvious of which is the formation of new species. Darwin's theory is based on the existence of a continuous spectrum of variations. For Darwin, naturally occurring variations are of small amplitude. The transformation of organisms is a continuous process. Nevertheless, evolution of organisms is characterized by huge evolutionary leaps, discontinuities, one of which is the formation of new species. How can discontinuity originate from a continuous process? How can a new species emerge? This is a highly difficult and recurrent question. The problem of speciation occupied the minds of many evolutionary biologists during the 20th century, and is still doing so at the beginning of the 21st century.

There are two additional difficulties with Darwin's theory. The first concerns the notion of progress. Is the evolution of organisms synonymous with progress? Darwin was deeply influenced by the French physiologist Henri Milne Edwards, and considered that, in human societies as in organisms, evolution leads to a diversification of the functions of the different parts, a process of specialization, which can be considered as progress. But he was also convinced that evolution had no sense, no direction, that it depended on the complex interactions of organisms in a permanently changing environment. How was it possible to reconcile these two opposing views? Darwin did not, and ambiguity on the existence (or not) of progress in the organic world pervades the pages of OS. In some parts of the book, Darwin uses the words "superior" and "inferior" to designate different animals and plants without any restrictions, whereas in other parts of the book he states that it is impossible to provide any valid criterion to justify the assertion that one organism is superior or inferior to another.

This balance between two different opinions is a recurrent characteristic of OS (and of all the other works of Darwin). In some parts of the book, Darwin considers, for instance, that there are no differences between what one calls "varieties" and "species", and in others Darwin states that the difference is obvious, or looks for criteria to distinguish them. These hesitations must not be considered as weaknesses of OS. They are testimonies to the difficulties Darwin encountered in exploring the radically new questions raised by his theory. They are the signs of ongoing intellectual efforts to find satisfactory answers to highly difficult questions. OS is a report of a "work in progress". These hesitations also show the honesty of Darwin, who never sweeps the difficulties encountered by his theory under the carpet.

In addition, Darwin does not exclude that alternative theories and models might have an explanatory value. He favours the power of natural selection, but leaves the inheritance of acquired characteristics a role in the overall process of evolution. Likewise, he underlines the role of variations of small amplitude, but does not exclude the existence of variations of large amplitude, and of leaps in evolution. This is not a sign of cautiousness – as is frequently said – but simply reflects the fact that these alternative theories and models were the best placed at that time to explain some of the observations that had been made. For Darwin, it would have been dogmatic to favour one explanatory model to the exclusion of all others.

Reading OS is also important for two additional reasons. The first is that it demonstrates the plethora of observations and facts that Darwin recorded on both animals and plants. Such an encyclopaedic culture was already exceptional among naturalists of Darwin's time, and Darwin has been criticized for "dissipating" his efforts. We must remember this characteristic of Darwin's science. The work of Darwin is praised by all contemporary biologists. But do they realize that such work would be impossible in the present-day context, when specialization and fragmentation of disciplines are dominant within biology (and other sciences)?

Another, rarely mentioned, characteristic of the work of Darwin is the role that humans played in the discovery of the theory of natural selection. Most of the examples used by Darwin originate in human practices: the action of artificial selection, but also the changes which were the consequences of the colonization of new territories by Western Europeans, and the reciprocal acclimatization of plants and animals which resulted from this process. Darwin even used the experience he accumulated in his private garden. It is evident that OS, which concerns the evolution of organisms in Nature, would not have been possible without the observations made on the transformation of Nature by human actions. This shows that science is not the passive observation of Nature, but rather the result of the active transformation of it by human beings.

Conclusion

Reading OS in 2009 is important. Not because the book represents the state of the art on the mechanisms of evolution. Our knowledge has advanced immeasurably since Darwin's day! It is important, because it shows how scientific knowledge is progressively acquired, through hesitation and error. It shows what scientific activity must be: an open enterprise, with a spirit of honesty, an emphasis on particular explanatory schemes without rejection of others, if there are no reasons to exclude them.

It would be a mistake in this anniversary year to praise Darwin, and his work, without mentioning its limits, hesitations, and errors. Darwin made a decisive breakthrough in biological thinking. This breakthrough was so decisive that he was alone, ahead of his contemporaries, trying to fit his theory with the observations made by naturalists over centuries. The amplitude and the difficulty of this task are most evident in what concerns the place of human beings in Nature. Darwin devoted two of his major books to show how closely humans are related to other organisms, that they share with them many different behavioural, anatomical and physiological characteristics. The natural consequence was that Darwin was convinced that the mechanism of evolution by natural selection operated in the formation of human beings, and is still operating in and among human populations. Nevertheless, Darwin hesitated. With fewer racial prejudices than most of his contemporaries, scandalized by slavery, he emphasized the importance of altruistic behaviours among humans. How to reconcile these opposing views on the widespread action of natural selection and on the specific characteristics of human societies? Darwin did not, and he refused to eliminate the action of natural election from human societies. How would it have been possible to do that for the naturalist who included human history in the natural history of organisms? Darwin did not consider the disappearance of some primitive human populations "unnatural", or the control of human reproduction useless. To acknowledge this duality in Darwin's writings is simply to admit the difficulty of finding the right place for radically new theories. Darwin was not a saint, but a great scientist and an honest man.

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