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A non-Darwinian Darwin: An introduction

Un Darwin non darwinien : introduction

Had Wallace not sent his manuscript on natural selection to Darwin in 1858, the latter might have never published *The Origin of Species* in the form we know it. Nevertheless, he would have left an outstanding body of scientific work. By the age of 50, he was renowned for his works on the origin of coral reefs, on the anatomy of cirripeds and on fossil vertebrates from South America. He had already taken substantial notes on the stages of child development by observing the arousal of the faculties of his elder son, and he was carrying out a number of investigations on plants, especially *Primula*, orchids, cross-fertilization, and climbing plants. Finally, if he had not been motivated to publish the *Origin*, Darwin probably would have still published his later books on the expression of the emotions in man and animals, and on earthworms (Table 1).

Thus, Darwin probably would have been known as a prolific writer and as a mighty forerunner in a variety of fields. Regardless of the fate of the *Origin*, he would have been the first to put forward some of the ideas that are at the foundation of what we nowadays call quantitative ecology (in his earthworm work), population ecology (in studying the co-adaptation of plants and insects), ethology (through his book on the expression of emotions), and comparative anatomy (from cirripeds and flowering plants to large fossil mammals). He would have still been the father of dynamic geomorphology because of his work on the origin of coral reefs. And he would still be acknowledged as the admirable writer of one of the first scientific adventures. This is because the *Beagle* journeyed around the world just one generation after the pioneering explorations of Wallis, Carteret, Bougainville, Cook and La Pérouse, because few naturalist-voyagers had carried out as systematic a scientific enterprise as Darwin did, and because his voyage preceded the great era of scientific expeditions, which occurred during the end of the 19th century and the beginning of the 20th.

One of the last natural historians, Darwin devoted whole days to systematic investigations in his garden at Down. There, he kept away from the city to cure his poor health, which probably resulted from the expeditions of his youth, carried out at a time when tropical medicine was in its infancy. A garden is a prolific reserve of living beings displaying their ordinary habits, and thus it offers manifold sources of reflection to an experienced naturalist. Like Claude Monet, who took advantage of the outdoor studio afforded by his estate, Darwin put good use to the garden surrounding his family's mansion, made possible by the fortune of his wife and first cousin, Emma Wedgwood. Monet created masterpieces by sitting at an easel on the edge of the nymphea pond he established on his property. Doing so day after day enabled him to make sparkling interpretations of the reflections of light. Similarly, Darwin revolutionized ideas about interactions between species by making diligent observations of the organisms that populated the private field station afforded by his wife's estate. Although he did not have the modern notion of "population", Darwin may be seen as a pioneering experimenter in what we would call "population biology" today.

Of course, Darwin was also, and above all, an evolutionary biologist. Upon returning from the *Beagle* in 1837, he began filling up his "transmutation" notebooks that would lead to what would be the great achievement of his life. In 1840, the logical framework of his theory of natural selection was settled. Two years later, in 1842, he completed the first draft of his book, and he only needed to expand it for publishing his *Origin of Species*. In fact, when Darwin received the famous letter in which Alfred Russel Wallace asked whether his essay was worth being published, Darwin had already written a huge manuscript of 225,000 words (compare this with the 150,000 words of the *Origin*). Thus, when Wallace sent his manuscript in the spring of 1858, Darwin had already been working on his theory for more than 20 years.

Darwin might have waited longer, as he was facing a difficulty which would be solved by science only two

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generations later. The laws of hereditary variation were unknown in Darwin's time (see e.g. the former special issue of this journal on the rediscovery of Mendel Laws [1] and references therein, and [2]). They provided a firm basis for natural selection, as was to be demonstrated in 1930, when population geneticists published the first mathematical synthesis showing that the theory of natural selection was compatible with Mendelian inheritance [3]. The theory that Darwin proposed in his *Origin of Species* opened a huge field of research that made both inheritance and populations a priority for biological research.

It would be hazardous to try to tell what the story would have been had Wallace not sent his manuscript, since in fact, everything ended well. Darwin did receive Wallace's letter, and published it together with two previously unpublished excerpts of his own work, in a famous joint communication presented to the Linnean Society of London on July 1st, 1858. Over the next few months, he feverishly wrote a partial "abstract" of his "Big Species Book", which he finally entitled "On the Origin of Species" (instead of "Abstract of a Book on the Origin of Species", a title that was refused by the publisher, who could not accept that a book of 490 pages could be presented as an "abstract"). The material of the "Big Species Book" finally led to a trilogy much larger than the original manuscript of 1858: together, *The Origin of Species by Means of Natural Selection* (1859), *The Variation in Plants and Animals under Domestication* (1868), and the *Descent of Man and Selection in Relation to Sex* (1871) make up 2288 pages. These books are the corpus of Darwin's legacy about evolution. Major parts of these 2288 pages are read with as much attention by scientists today as they were hundred and fifty years ago.

What about the other books? Taken individually, they constitute a constellation of sparse studies. Nothing seems to bind them, except the curiosity of a great man. We can hardly tell in detail what their relation is to Darwin's evolutionary theory, and his meticulous notebooks shed no light on this. Each of these books was really new to science, and was soon translated into most European languages. Did they share only the curiosity of a powerful thinker? Were they auxiliary studies to his opus magnus on the origin of species? Did they contribute to the scaffolding of his theory of evolution by natural selection? Can we imagine that this great encyclopaedia of biology was the first "evolutionary synthesis"? Or was it perhaps the last example of a scientist's attempt to provide a comprehensive view of the natural world, in the mould of Alexander von Humboldt's *Kosmos*?

Whatever the relation between Darwin's core trilogy and his other books, the idea that life resulted from a unique historical process led by a powerful law met with immediate success, even though its reception took a diversity of forms in different fields. Thus, embryology, zoology, physiology, botany, horticulture, palaeontology, and psychology, which were so tightly connected in Darwin's thought, remained relatively independent from each other for a long time. They shared very few concepts, and allowed for minimal views about evolution. For a time, "evolutionism" was open to individual speculations, which did not generally survive an author or a local school. It was only in the second half of the 20th century, after the decisive impulse of the Modern Synthesis, that a unified field of research known as "evolutionary biology" linked together molecular biology, population studies, ecology, ethology, palaeontology, the genetics of development, agricultural research and evolutionary medicine. Twentieth century science has achieved the historical transition leading from the chaos of post-Darwinian debates to an established field of research in evolutionary biology. The most recent of its disciplines, genomics, constantly makes use of evolution to track the relationships among genes in the hyperspace defined by sequence homologies between macromolecules across species. Here we are in a universe which Darwin could not imagine, since he could only access the macroscopic and superficial phenomena which made up the diversity of life. However, Darwin seemed confident in the capacity of science to eventually overcome any possible difficulty. At no time did he seem to doubt the success of a method based on an interaction between theory and observation. He acknowledged that he did not know the laws of heredity, but he collected data among pigeon-breeders and even became one of them. He carried out meticulous enquiries to understand artificial selection as it was practiced by professional stock-breeders and horticulturists. Every morning of the week was devoted to his correspondence with a number of informants all over Britain and the British Empire, from whom he gathered information about problems that were important to him. Among the information they supplied were data from birth registers, which Darwin used to document the ratio of male to female births in humans. During his work on carnivorous plants, he would painstakingly investigate the mechanisms of digestion of insects by plant leafs (yet we know that nobody could suspect the existence of enzymes in his time). We may never know whether all of his investigations were linked by the logic of a great plan, but we can admire the deliberate protocols of Darwin's studies on so many classes of phenomena.

This special issue of the *Comptes Rendus Biologies* is the outcome of a conference which was conceived as an invitation to read Darwin again, and take into account the non-obviously "Darwinian" aspects of his work, "Darwinian" being taken in the sense of the scientific tradition of evolutionary thinking that developed between 1859 and the present. Breaking with common practice, we brought together historians and biologists, who were allowed to evaluate each others' readings of Darwin from both a historical perspective and from the vantage of Darwin's heritage in contemporary science. We are happy that this conference led them to publish papers which benefited from the discussions held at the meeting.

Our objective has been to bring into focus works that are unduly considered as "minor" in Darwin's scientific achievements. The studies published in this issue are hardly consistent with the common view of Darwin as a unitary thinker. For this reason, the contents follow a graduation from more specific studies to ones that relate to the difficult question of the place of human beings

Table 1
Chronological landmarks simplified from de Beer [18].

Born at Shrewsbury	12 February 1809
Beagle sails from Plymouth	27 December 1831
Visits Galapagos Islands	September 1835
Beagle lands at Falmouth	2 October 1836
First *transmutation* Notebook	July 1837
Elected Fellow of the Royal Society	24 January 1839
Marries his cousin Emma Wedgwood	29 January 1839
Structure and Distribution of Coral Reefs	1842
Unpublished *Essay*	1844
Geological observations	1844–1846
Monographs on Cirripeds	1851–1854
Joint paper with Wallace	1 July 1858
Origin of Species by Means of Natural Selection (1st edition)	24 November 1859
Dimorphism in Primula	1862
On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects	1862
Variation of Animal and Plants under Domestication	1868
Descent of Man and Selection in Relation to Sex	1871
Origin of Species by Means of Natural Selection (6th and last edition)	1872
The Expression of Emotions in Man and Animals	–
Insectivorous Plants	1875
Climbing Plants	–
The effects of Cross- and Self-Fertilisation in the Vegetable Kingdom	1876
Formation of Vegetable Mould through the Action of Worms	1881
Dies at 73 at Down House	19 April 1882

among other species. We start with Darwin's interests in palaeontology [4], geology [5], and the anatomy of cirripeds [6]. These are followed by three studies based on his works on plants. Whereas the study of climbing plants [7] is a genuine experimental study, conducted with an admirable empirical sense, his books on orchids [8] and fertilisation [9] inspire the contributors to question his methods and the purpose of his research. With Darwin's theory of heredity through pangenesis [10] and his work on sexual selection [11–13], we are led to consider the consistency – or inconsistency – of his central enquiry on evolutionary mechanisms, his own position on the debates of naturalists about humans, and the prejudices of his day about women. It is striking that no unity can be found in his studies on humans and behaviour [14–17], and we can wonder how it is possible that his book on the expression of emotions in humans and the other animals was written with so little regard to their common descent. The invited editors of this issue feel deeply indebted to the contributors for having raised so many long-neglected issues in the field of classical Darwinian studies.

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