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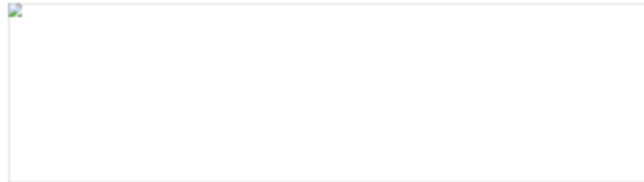
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Darwin the botanist

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David Kohn

French title: Darwin le botaniste

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Summary

In his theory of evolution, Charles Darwin proposed that living beings were “all netted together” through a common ancestry. Yet one branch of the tree of life, the plant kingdom, was Darwin’s most enduring focus. He was a major field collector, a consummate and sustained observer of plant life, a rigorous botanical experimentalist, and the high theorist of plant evolution.

Botany played a pivotal part in each phase of Darwin’s life. As an undergraduate, he collected specimens for his botany professor’s herbarium while on a geological expedition in Wales. Voyaging for five years aboard the HMS *Beagle*, he collected plants along with fossil bones and bird skins. Preparing to write *On the Origin of Species*, botany became critical to the growth of his evolutionary theory. Ultimately, he turned his home and the surrounding countryside into a botanical field station.

Darwin’s six botanical books would recast large areas of plant science. His studies on the fertilization of orchids, on insectivorous plants, and on the climbing and other plant movements were each a beautifully

articulate example of how evolution could solve the traditional mysteries of natural history. Through his work, Darwin laid foundations for modern botany that remain firm to this day.

Darwin's botanical formation

Darwin was heir to a rich botanical tradition, one that often resonated in the specific botanical topics and viewpoints he was to adopt. His grandfather Erasmus Darwin, for example, was an evolutionist and spread the Linnaean doctrine that plants, just like animals, have sexes. Darwin's first botanical exposure was in his father's ample garden at The Mount in Shrewsbury where young Charles played among apple trees bred by Thomas Andrew Knight, President of the Royal Horticultural Society. However, the foundations of Darwin's formal education in botany were laid at Cambridge by his dynamic professor John Stevens Henslow (1796-1861) who later opened the way for Darwin to participate in the *Beagle's* scientific cruise around the world.

The Beagle voyage

The Beagle expedition concentrated on certain regions of South America: coastal Brazil, Patagonia, Tierra del Fuego, the Andean coast as far north as Lima and the oceanic Galápagos archipelago.

Plants came before birds in the birth of Darwinian evolution. Darwin did not become an evolutionist on the Galápagos, but the basis for a profound shift in his understanding of species was established there – and it began with plants. When the *Beagle* arrived in the Galápagos in September 1835, Darwin immediately observed that the flora appeared unique. Thereupon, he collected “all the plants in flower”. This we know from a pocket field notebook that Darwin kept when he was in the archipelago. Darwin's Galápagos plant specimens, numbering well over 200, constitute the single most influential natural history collection of live organisms in the entire history of science. Indeed, Darwin's plants represent the foundational collection for the entire Galápagos flora. Settled back in London in 1837, he sketched his first evolutionary tree and began firmly applying the idea of descent with modification to all of natural history.

In 1856, Darwin put ink to blue foolscap and began to steadily write. His seminal book, *On the Origin of Species*, was finally published in November 1859.

Preserving priority

Once the *Origin* was published, botany became the central focus of Darwin's research for the remaining years of his life. This botanical work was highly original, not only because of the quality of his observations, but because it was the first attempt to apply the principles of evolution to plants.

Darwin's crucial contribution to botany was his understanding of and ability to demonstrate that the flower is a product of evolution. By the 18th century, botanists were convinced that flowering plants have both male and female parts, and assumed that most plants self fertilise or inbreed. This erroneous and deeply ingrained view of the flower continued until Darwin began publishing on the biological meaning of flowers in the 1860s. The prevalence of cross-pollination was Darwin's single most important botanical truth.

Indeed Darwin realised there was a problem with plant sex immediately after discovering natural selection in 1838. If flowers perpetually self fertilised then both natural selection and evolution would be invalid, because natural selection requires hereditary variation. If there is no variation, there is simply nothing to select. Evolution stops. If flowers self fertilised for generation after generation, they would become unvarying clones. Furthermore, without variation, where did the thousands of known plant species come from? Evolution would not explain the diverse families of flowering plant genera and species. The world's flowers were just too big a part of nature for Darwin to forfeit them to the creationist position that species are immutable.

In the case of flowers, he undertook decades of field and garden observations and breeding experiments, all focused on testing and supporting one powerful hypothesis: that of natural selection.

Through his painstaking studies, such as the *Primula* example below, Darwin discovered that flowering plants have evolved elaborate structures, strategies, and relations with animals and reasoned that it was all to avoid the apparent necessity of perpetual inbreeding. Thus the Darwinian meaning of flowers became a pillar of botany and botany became one of the strongest fields supporting evolution.

Love, *Primula* style

Spring 1860 was the first flowering season following *Origin's* publication. Darwin, bursting with experimental energy, made several crucial botanical discoveries. In May, he observed two different kinds of flowers among common primulas. The style, or shaft of the female part, is either tall, protruding like a pin, or it is short. Darwin's children gathered armloads of flowers for their father, who noticed something: The two kinds of flower occur in a 50:50 ratio. To explain these two morphs, Darwin would follow the scientific method, but after his very own personal style. At first, the 50:50 ratio reminded him of a normal male-female sex ratio. So he believed the two kinds of flowers were evolving into separate sexes. That is, he thought he had witnessed one step in the evolution of separate male and female flowers. The tall-style flowers must be evolving into pure females, he surmised. Conversely, their short stamens must be losing potency. To test this he crossed the two forms. But to his surprise, the 'males' produced abundant seeds. So the experimental method forced him to abandon his first hypothesis. As Darwin once observed, his first explanations of things frequently proved wrong. The originality and breakthrough would come with thinking up the next explanation.

He now realised that the maximum fertility occurs when pollen moves from one form to the other. It was always the self fertilised flowers that had reduced fertility. Thus the two forms, each of which is both male and female, are favoured to maintain a stable population. Darwin had in fact discovered a breeding strategy that gave a clear advantage to cross-pollination and thus provided experimental support for his long-held interpretation of the meaning of flowers. To think of flowers in terms of plant breeding strategies, now that is evolutionary botany. And Darwin's primulas have been a prime example of this new way of thinking ever since.

Plant sensitivity: green adaptations

Plants don't have feet and they also don't have brains. But as far as Darwin was concerned, some plants as good as have eyes, and they do have behaviour, often expressed in the extraordinary ways these beings can move despite being rooted in the soil. Darwin's passion for working out the botanical adaptations that allow plants to stay in sensitive touch with their environment occupied him for years in physiological experiments that prefigure the biochemical and cellular studies of the early 20th century on enzymatic catalysis and plant hormones. Thus these green adaptations in leaves and stems not only paralleled Darwin's flowers, they added a new level of sophistication to the botanical bulwarks Darwin had built to support evolution and adaptation by natural selection. For example, insectivorous plants that trap and digest insects with specialised leaves fascinated Darwin. So did vines that climb up and over other plants. He saw plants as sensitive creatures whose growing tips or leaves or seedlings can track the movement of the sun. Indeed, he showed they could respond to the least beam of incident light, the pull of gravity, and the slight touch of a browsing animal.

Much of this work Darwin performed in a string of hothouses that gradually sprang up along the kitchen garden wall beginning in the late 1850s. Eventually, there were five houses heated by a boiler and offering a fair range of conditions for the array of plants that Darwin, assisted in his last years by his son Francis, wished to study.

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