The Secrets of Darwin's Greenhouse
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Retreat to The Garden?

In 1862, Darwin published his first book after the Origin of Species (1859). Many had, no doubt been expecting him to finally tackle the vexed question of human evolution (which he had done his best to duck in the Origin), but instead he produced a book with the jaw-breaking title On the Various Contrivances by which British and Foreign Orchids are fertilised by insects, and on the good effects of intercrossing. Darwin explained the while some might criticise him for publishing over 400 pages of comprehensive, technical illustrations of exactly how different orchid species were fertilised, he felt its length was justified: "Having been blamed for propounding this doctrine [natural selection] without giving ample facts, for which I had not sufficient space in that work, I wish here to show that I have not spoken without having gone into details".

Nobody could complain that Darwin had failed to go "into details" with his orchid book (at one point he even acknowledged that he had explained something "perhaps in too much detail…"). Some interpreted the orchid book as a retreat from the controversy that had greeted the Origin; when the Saturday Review reviewed the orchid book, they suspected it would "escape the active, and often angry, polemics" that Darwin's previous work had aroused.

As I suggested in the first lecture of this series, working in his garden and greenhouse was undoubtedly a pleasure for Darwin, which took him away not only from public controversy, but perhaps also from the grief he felt at having to watch three of his children die (Charles and Emma's third child, Mary, died just a few weeks after her birth in 1843; their daughter Annie died in 1851, when she was just ten years old; and their last child, Charles Waring, lived for less than two years). However, I want to suggest that Darwin's greenhouse and garden were far more than just a peaceful retreat. The greenhouse was primarily Darwin's laboratory, where he tested his theory of natural selection. The six botanical books that he produced were crucial to demonstrating to his fellow men of science that he had tested his ideas thoroughly – and that they could to the same. As other men of science began to do their own experiments, modelled on Darwin's, support for his ideas grew among the scientific community.

Darwin's botanical work demonstrated how the theory of evolution by natural selection could open up new avenues of investigation, new experiments and new ways of looking at the natural world. He admitted that anyone who decided to tackle a book such as Orchids would need "a strong taste for Natural History". However, he was confident that those willing to make the effort would find that explanations based on evolution, were every bit "as interesting" as the explanations offered by those who were convinced that "every trifling detail" of each orchid's structure was "the result of the direct interposition of the Creator." Darwin was modest (and careful) enough not to say his approach was superior to earlier ones, but he was nevertheless attacking the long-standing tradition of natural theology – the claim that to study nature was to study God. If, as Christianity claimed, every living thing had been created by God, natural history was much more than a pleasant recreation. Sunday afternoons spent messing about in duckponds and tide-pools, catching butterflies or pressing flowers did as much to bring you closer to God as a Sunday morning spent in Church. At least they could, as long as one viewed the adaptations of plants and animals as "contrivances", divinely

designed mechanisms that had been planned to allow the organism to survive, thrive and reproduce. As the Reverend William Paley, the most prominent exponent of natural theology in the nineteenth century, had put it:

> "We admire the flower; we examine the plant; we perceive the conduciveness of many of its parts to their end and office: we observe a provision for its nourishment, growth, protection, and fecundity… For the contrivance discovered in the structure of the thing produced, we want a contriver" (Natural Theology, 1809 edition, p.54).

Darwin was as willing as Paley to admire the flower, examine the plant and acknowledge the apparent ingenuity of its structure. But Darwin, of course, saw no need for a "contriver". He was convinced that natural selection explained how it was that nature seemed to provide evidence of design, despite the absence of a designer.

Orchids

The mysteries of pollination and fertilisation – the sex-lives of plants – were what first drew Darwin to botanical research. He later recalled (in his autobiographical fragment, "Recollections of the Development of my mind & character") that his research had begun "During the summer of 1839, and, I believe, during the previous summer" – around the same time as his marriage to Emma. He was particularly interested in the question of whether or not inbreeding was harmful – in part, because he had married his cousin. His marriage was an experiment whose results he would have to wait to discover. In the meantime, he took common flowers such as Red Campion (Silene dioica) to perform simple experiments, such as counting the numbers of seeds produced by flowers that had been fertilised with their own pollen, and comparing the results with others which had received pollen from another plant. The results varied from one species to another, but in the vast majority of cases, the cross-pollinated flowers produced more seeds. And more of the cross-fertilised seeds germinated successfully. In later experiments, Darwin also proved that cross-pollinated plants were almost always hardier than self-fertilised ones (as the autumn drew on and his garden got colder, Darwin took plants each out of his greenhouse put them in the garden; in every case, those whose parents had been cross-pollinated survived longer).

These results of these straightforward experiments were the starting point for most of Darwin's botanical research (and, as we shall see in the final lecture, his thinking on many other topics, including the desirability of cousin marriage between humans). The most important point was that cross-pollinated plants produced more seeds (and those seeds were both hardier and more fertile). So, any variation which made cross-pollination more likely would spread – all those hardy, fertile seeds would spread it. And of course, each plant that sprang from them would exhibit the same variation (and thus the same, slight advantage) as the parent plant. Darwin fully admitted his ignorance of why plants and animals varied, but – like every gardener, farmer and parent – he knew that they did. Offspring never looked exactly like either of their parents. He realised that variations were random, in that harmful and beneficial variations were equally likely. But Darwin's principle of natural selection relied on the fact that their survival was not: what made a variation beneficial was that it increased the plant's chances of surviving and therefore of reproducing – which ensured that the beneficial variation was passed on. So, any variation that increased the chance of self-fertilisation – however slightly – was harmful (it would result in a plant that produced fewer, less-fertile seeds). But a variation that increased the odds of cross-fertilisation was beneficial: it would lead to slightly more seeds, each slightly more vigorous and hardy than those of plants without the variation, and thus the new variation would spread.

(As a write this, the analogy with the current Covid-19 crisis is, sadly, obvious and unavoidable: the virus mutates – to use the modern term – producing many new variants. Some are more effective at spreading, while others are less, but those that spread more easily will – by definition – become more common in the population.)

Thanks to the careful studies he conducted in his garden, Darwin realised that the differences between these varieties of plants would initially be minute, almost undetectable, but over time they could transform the species – and nature had all the time in the world to play with. Darwin's friend and mentor, the geologist Charles Lyell, had established that the earth was unbelievably ancient – many hundreds of millions of years old. As he gazed into this vast abyss of time, Darwin realised that even the tiniest advantage would mean that over almost countless generations, the plants that possessed an advantage would spread and become more common. And in each generation the process of random variation would be repeated, giving rise to further variants, some of which might be even more successful – for example, by further increasing the chance of being cross- rather than self-fertilised. Any such variant would become slightly more common. And the process would go on gradually accumulating tiny advantages over countless millions of years. This gradual accumulation of minute changes would produce better-adapted flowers (more able to survive and reproduce) and eventually completely new species. This was natural selection: it produced contrivance without a contriver.

Darwin had outlined this argument in the Origin of Species, and concluded that the offspring of cross-fertilised plants "gain so much in vigour and fertility over the offspring from long-continued self-fertilisation, that they will have a better chance of surviving and propagating their kind". But – as we saw – he had been criticised for not providing the full scientific details that had led him to his conclusion. The orchid book was a long, detailed, response to such critics. Most of its chapters had a similar format: Darwin described each species' structure in detail, with the help of a diagram or two, and then explained how the delicate machinery of the flower promoted cross-fertilization. He commenced with Orchis mascula, the common British Early Purple orchid, which he probably collected himself from a place he called Orchis Bank, a site near his home in Kent where he and Emma loved to walk. At the bottom of the orchid's flower is the enlarged petal known as the lip or labellum (from the Latin labia, a lip) and, as Darwin noted, it "forms a good landing-place" for insects, who are attracted by the flower's colour and scent, which promise a sip of nectar (although, not all orchids make good on this promise). To reach the nectar, the insect pushes its head into the flower, brushing against the plant's pollinia (the pollen masses); this triggers a protective pouch to rupture, allowing the sticky pollinia to become firmly glued to the insect's head. Darwin encouraged his readers to try imitating the process for themselves, by inserting a sharp pencil into an orchid's flower; it would emerge, as he illustrated, with the pollinia firmly stuck to it.

From both Darwin's and the orchid's perspectives, so far, so good; the pollinia are released, the function of the protective pouch and its sticky disc were clear. But the most remarkable part of the story has yet to occur. The insect (or pencil) emerges with the pollinia, "firmly cemented to the object, projecting up like horns," but if the insect were to crawl into the next flower with the pollinia in this position, they would simply brush off onto the flower's male pollinia. Unless the pollinia land on the female stigma, pollination cannot occur. However, as Darwin watched the pollinia on the tip of a pencil or insect's head, he saw another remarkable phenomenon. As the plant's "glue" dried, it contracted, causing the slender threads (the caudicles) that attach the pollinia to the disc to bend, which pushed the pollinia forward. The bending resulted in the insect's pollen payload pointing forward (instead of up) – in exactly the right position to miss the next flower's pollinia and touch the female stigma instead. And the brief delay between the pollinia attaching and the forward bending (which Darwin christened "depression"), was long enough to allow the insect to move to a new plant, making it more likely that each flower would be fertilized with pollen from a different plant. The "good effects of intercrossing" were secured by a combination of the orchid's anatomy and the insect's behaviour.

For this extraordinary mechanism to work, everything has to be just right: the positions of the pollen and stigma, the stickiness of the glue (as Darwin noted, "the firmness of the attachment of the cement is very necessary, for if the pollinia were to fall sideways or backwards they could never pollinate the flower"); the speed at which the glue dried; and the degree to which it contracted, bending the caudicles as it did. Above all, the insect and the flower had to fit one another; many orchids could not be pollinated by an insect that was either too large or too small. No wonder Darwin

argued that “the contrivances by which Orchids are fertilised, are as varied and almost as perfect as any of the most beautiful adaptations in the animal kingdom”.

One of most distinguished reviewers of Darwin’s orchid book was George Campbell (8th Duke of Argyll), a staunch promoter of natural theology who opposed Darwin’s ideas courteously but emphatically. His review commented that despite Darwin’s professed intention of avoiding supernatural explanations, Darwin seemed to embrace the language of natural theology. As Argyll commented, in the orchid book the words “contrivance,” “curious contrivance,” and even “beautiful contrivance” were “expressions which recur over and over again.” He therefore asserted that “intention is the one thing which [Darwin] does see, and which… he seeks for diligently until he finds it.” Argyll drove home his point by noting that Darwin often used human artifacts, such as spring traps, as metaphors for the parts of orchids. (He did not need to remind his readers of Paley’s familiar words: where we find contrivance, “we want a contriver”.) Argyll was one of several reviewers who thought Darwin was unable to avoid the logical conclusion: orchids (like all other living things) looked designed because they had been, by God.

However, Darwin’s close friend Asa Gray, professor of botany at Harvard university, realised what Darwin was really up to. Gray wrote to congratulate Darwin his “beautiful flank-movement with the Orchid-book”, which was gradually winning over naturalists who had been opposed to the Origin of Species just three years earlier. A delighted Darwin wrote back, “Of all the carpenters for knocking the right nail on the head, you are the very best: no one else has perceived that my chief interest in my orchid book, has been that it was a ‘flank movement’ on the enemy.” Darwin was not supporting natural theology, he was undermining it. As he wrote: “The more I study nature, the more I become impressed with… the contrivances and beautiful adaptations slowly acquired” through natural selection. Despite being produced by nothing more than random variation and a struggle for survival, such adaptations “transcend in an incomparable degree the contrivances and adaptations which the most fertile imagination of the most imaginative man could suggest with unlimited time at his disposal”. Flowers appeared to have been designed, yet there was no designer.

Killers and Climbers

Orchids was the first of Darwin’s botanical books, but he produced many others, which I would argue formed a sustained assault on the public’s understanding of plants. He later wrote that “it has always pleased me to exalt plants in the scale of organised beings”. I suspect that Darwin ‘exalted’ plants because he loved them, and wanted to share his delight with others, but even more importantly, raising the plants helped to narrow the once-unimaginably wide gap between plants and animals, thus making it easier for his readers to imaginatively bridge the much smaller distance between humans and apes. If evolution was true, then every aspect of human anatomy and behaviour had its origins in the animal kingdom; and every facet of animal behaviour – even such seemingly unique features as intelligence – must have some rudimentary counterpart in the plant world.

After orchids, Darwin turned to the ways in which plants moved, growing climbing species such as passionflowers in his greenhouse to find out exactly how they were adapted to exploit other plants, such as rain forest trees, by scrambling up them into the sunlight. To help him with his plant researches, Darwin decided to built himself a hot house (or “stove” in Victorian terminology) to add to his existing range of unheated glasshouses. A stove would hugely increase the range of things he could grow and experiment on. He wrote to tell his friend, Joseph Hooker, “My hot-house will begin building in a week or so, & I am looking with much pleasure at catalogues to see what plants to get”. As soon as the building was done, Darwin was longing to fill it, “just like a school-boy”. He planned to start growing tropical orchids to complement the native species he had been investigating for many years, but worried over their cost. He told Hooker, who was now deputy-director of the Royal Botanic Gardens, Kew, “I dare say I shall beg for loan of some orchids… I fancy orchids cost awful sums”. Hooker responded (tongue, firmly in cheek), “You will give me deadly offence if you do not send me your Catalogue of the plants you want before going to Nurserymen”. A few weeks later Darwin visited Kew with a list of the things he most wanted and when Hooker’s gift of plants arrived,

Darwin wrote back to say he was “fairly astounded at their number! why my hot-house is almost full!”. A few weeks later, he was still crowing with delight, “I have made list of plants, 165 in number!!!”. Darwin jokingly wondered whether such a raid on Kew’s resources might lead to Hooker ending up in “the Police Court?”.

Despite his apparent love for all flowers, Darwin told Hooker that he would “keep to curious and experimental plants”, including those that moved in unusual ways. He told Hooker that “I am getting very much amused by my tendrils— it is just the sort of niggling work which suits me & takes up no time”. In fact (as is obvious from his book, On the Movement and Habits of Climbing Plants, 1865), he spent many years on painstaking experiments to discover just how and why plants climb. Some just wrapped themselves around anything nearby, but Darwin soon recognised a spectrum of increasing specialisation, marked by specific adaptations. The group of climbers that Darwin christened “tendril-bearers”, seemed to be the most specialised. As they grew, their tendrils revolved as if reaching out, exploring until they caught onto a support; they were then able to sense the light and start clambering towards it. The more experiments Darwin did, the more impressed he became. He noted that a tendril responded to the weight of “a loop of soft thread weighing 1/32nd of a grain” (0.002 grammes!) by growing towards it – a sensitivity that allowed them to detect anything they could potentially climb up. Yet the tendrils didn’t react when much heavier rain-drops fell on them, or to the wind. They seemed to be sensitive to more than simple weight. Darwin was also impressed by the speed with which the climbers reacted; after experimenting with the crinkled passionflower, Passiflora gracilis, he recorded “The movement after a touch is very rapid: I took hold of the lower part of several tendrils and then touched with a thin twig their concave tips, and watched them carefully through a lens… the movement was generally perceptible in half a minute after the touch, but once plainly in 25 seconds”. Darwin described what may have been his favourite climber, Passiflora gracilis, as exceeding “all other climbing plants in the rapidity of its movements, and all tendril-bearers in the sensitiveness of its tendrils”.

Before Darwin, most people thought (and most still do) that plants were simple, dull, motionless and insensitive; the opposite of animals. However, the orchids had shown how complex they were and the climbers revealed that plants were sensitive and mobile. Given their ability to ignore the weight of raindrops, but respond to a much lighter touch, they might even be said to possess a very limited kind of intelligence. Darwin told his son William, “My hobby-horse at present is Tendrils; they are more sensitive to a touch than your finger; & wonderfully crafty & sagacious”. The suspicion that plants possessed some limited form of intelligence (sagacity) was one that grew on Darwin as he worked. Finally, Darwin turned to the study of carnivorous plants, such as the Venus fly-trap and the sun dew, writing a book on them (Insectivorous Plants) in 1875, which caught the public’s imagination even more vividly, as it dramatized how the vegetables sometimes turned on the animals, devouring instead of being devoured. In doing so, they exhibited an extraordinary array of complex adaptations, “contrivances” every bit as sophisticated as those of the orchids. The carnivorous plants tricked and trapped and ingested their prey, and thus seemed to possess even more cunning than the climbers. As Darwin told Asa Gray, “my beloved Drosera [sundew] is a wonderful plant, or rather a most sagacious animal”; such flowers blurred the boundaries between plant and animal even further.

Nevertheless, as with all the botanical books, Insectivorous Plants required a “strong taste” for natural history – and considerable patience, if the reader was to get through all the details. Given the public’s interest in these slightly sinister flowers, all kinds of writers tried producing popular works inspired by Darwin’s work on carnivorous plants. Among them was John Ellor Taylor (editor of the widely read magazine Hardiwicke’s Science Gossip), who wrote a popular Darwinian botany book with the wonderful title, The Sagacity and Morality of Plants: a sketch of the life and conduct of the vegetable kingdom (1884). One newspaper reviewer commented that many “would laugh at the notion that trees and flowers possess any sagacity or morality”, yet “those who have gone deeper into the matter know that” something akin to “a reasoning faculty, exists among plants”.

According to Taylor, botany "no longer consists in merely collecting as many kinds of plants as possible, whose dried and shrivelled remains are too often only the caricatures of their once living beauty", instead, "It is now a science of Living Things, and not of mechanical automata". Contrasting plants with automata suggested they were not governed by mechanical rules, but possessed a hint of intelligence. And the murderous habits of carnivorous plants were among the best illustrations of this. As Taylor wrote:

> "hosts of common plants constantly perform actions which, if they were done by human beings, would at once be brought within the category of right and wrong. There is hardly a virtue or a vice which has not its counterpart in the actions of the vegetable kingdom. As regards conduct, in this respect, there is small difference between the lower animals and plants."

While Taylor did not believe that plants have responsibility for their actions, he was convinced there was an unbroken continuity from the lowest plants to the highest animals. Although the book was a "charming and attractive volume", one reviewer nevertheless concluded that such things as pitcher plants were, "a tragedy of plant-life", being a "terrible example of vegetable guile in the commission of murder with malice aforethought!"

Exalted Plants

Back in 1865, Darwin had commented that "It has often been vaguely asserted that plants are distinguished from animals by not having the power of movement". This was clearly wrong; it was more accurate to say "that plants acquire and display this power only when it is of some advantage to them" (emphasis added). In the book's second edition, he strengthened that claim, writing that "The most interesting point in the natural history of climbing plants is the various kinds of movement which they display in manifest relation to their wants". And Darwin would conclude his final botanical work, The Power of Movement in Plants (1880), by asserting that since the tip of the plant's embryonic root, the radicle, possessed "the power of directing the movements of the adjoining parts" it was "hardly an exaggeration" to say that it acted "like the brain of one of the lower animals… receiving impressions from the sense-organs, and directing the several movements". The gap between plant and animal got narrower and narrower the longer Darwin thought about it.

Books such as Taylor's brought Darwin's botany to a much wider audience. One of the more unusual results was a short story by H.G. Wells ("The Flowering of the Strange Orchid", 1894). In Wells' fertile imagination, the rapid movements of plants like the passionflower was combined with the apparent guile of Drosera and the intoxicating beauty of orchids. The result was a vampire flower, which attacked human beings and sucked the blood out of them. Numerous, less-skilful imitators followed in Wells' footsteps, creating a genre of "killer plant" stories that persisted well into the twentieth century – perhaps the most surprising result of Darwin's efforts to bridge the seemingly unbridgeable gap between plants and animals.

With the help of many others – from Joseph Hooker to H.G. Wells – Darwin made a striking contribution to botany; he made people realise that plants had needs and had evolved strategies to meet them – become predatory, perceptive, responsive and swift-moving as they struggled to survive and reproduce. After Darwin, the plant world would never look the same again.

Further Reading

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