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Chapter 2
Passiflora gracilis: Inside Darwin's greenhouse

A rainforest ought to be paradise for a plant: but like all desirable neighbourhoods, it can get overcrowded. Although the forest is wet and lush, a newly germinated seed usually finds light is in short supply. One way to reach it is to grow into a gigantic tree, with a thick trunk hundreds of feet high, supporting massive branches that expose the plant's leaves to the sun. But it takes time to grow such a trunk, and for every seedling that makes it, thousands fall by the wayside. An alternative strategy is to be a vine, producing a thin, rapidly growing stem that clambers up someone else's trunk – thus getting the leaves into the light with a minimal expenditure of time and energy.

Passionflowers are typical rainforest climbers: they have specialized tendrils that will cling to almost anything; they can sense light and grow rapidly towards it; and, once there, they devote themselves to the ultimate end of any organism's life – reproduction. The delicate, showy flowers from which they derive their name attract various pollinators – bees, bats, butterflies, moths or birds – that fly from flower to flower, spreading the plant's pollen as they go. Once fertilized, the ovaries swell to form passionfruit, whose bright colours and sweet taste help attract animals, especially birds and primates, which eat the fruit and so spread the plant's seeds.

Like many South American primates, brown capuchin monkeys (*Cebus apella*) are fond of passionfruit. Capuchins get their name from their brown bodies and the white fur around their faces, which reminded European travellers of the brown and white robes of Capuchin monks, who wore a distinctive white hood or *capucize* over their brown robes (cappuccino coffee gets its name from the same visual analogy). Unlike the monks, Capuchin monkeys live in sexually active social groups in rainforest canopies and eat more or less anything they can get their hands on. Brown capuchins are noisy, destructive feeders: they move from tree to tree, tearing apart fruit, cracking nuts, and leaving half-eaten plants, seeds and droppings wherever they go. The droppings provide an ideal fertilizer for germinating passionflower seeds, allowing them to begin a new scramble towards the light.

In 1553, the passionflower's strategy of attracting primates to eat its fruit and spread its seeds paid off handsomely when a member of the primate species *Homo sapiens*, known as Pedro de Cieza de León, published the first account of these exotic flowers and fruits. His story helped persuade other members of his species to spread the passionflower all over the world; the sour-sweet, egg-shaped passionfruit in your local supermarket are evidence of how well the passionflowers' primate-based strategy has worked.

León's *La Chronica del Perú* included a description of a fruit 'that is very delicious and fragrant called granadilla' (meaning a small pomegranate or *granada*). However, it was not the fruit that attracted his readers, so much as the flowers; a later Spanish writer described the flower as 'very similar to the flower of a white rose and it appears to have been carefully made to show the representation of the passion of Jesus Christ'.[1]

In 1609, Giacomo Bosio, a member of the Knights of Malta, was gathering stories about Christ's cross and the legends and miracles associated with it. Knowing of his interest, a Mexican-born friar showed him drawings of a 'stupendously marvellous' flower from the Americas that seemed to bear the symbols of Christ's Passion. Bosio was initially struck by the flower's outer ring of corona filaments, typical of most passionflowers. He interpreted this as symbolizing Christ's crown of thorns, because the species he saw depicted had seventy-two filaments – the traditional number of thorns in Christ's crown. He took the five

stamens (the male parts of a flower) to represent the scourges used to beat Christ, and the five blood-red spots at the base of the specimen Bosio saw gave the plant its Spanish name, *La Flor de las cinco Llagas* ('the flower of the five wounds', i.e. Christ's four stigmata and the spear-wound). The flower also had three carpels, the female reproductive organs on the tops of which the pollen is deposited. Bosio interpreted these as representing the three nails used to nail Christ to the cross. And finally, the pollen-receiving female parts grew from a single column, which was seen as symbolizing the pillar that Christ was tied to during the flagellation.[2] The fame of the plant spread, usually in pictures that simplified its botanical features in order to make their religious significance clearer. The miraculous passionflower was soon growing in gardens across continental Europe.

In August 1612, just three years after Bosio's account had appeared, passionflowers were blooming in Paris, and at about the same time, Captain John Smith, President of Virginia and Admiral of New England – best known for his relationship with the Indian 'Princess' Pocahontas – recorded in his diary that 'The Indians plant also Maracocks, a wild fruit like a lemmon' ('Maracock' was the Algonquian Indian word for the passionfruit). It was from the British colony in Virginia that passionflowers made their way to Britain; they are mentioned in John Parkinson's *Paradisi in sole Paradisus terrestris* (1629), the first English gardening book. Parkinson called the plant 'the Virginian climer', or the 'Jesuites Maracoc', but – perhaps because of the charged religious atmosphere of the eve of the Civil War – he found it politic to reject a specifically Catholic symbolism for the plant.[3]

Nevertheless, Charles I was sometimes referred to as 'the passionflower' by English Catholics after his execution, or – as they saw it – his martyrdom. This association may have prompted John Tradescant the younger to popularize the plant to British gardeners, since Tradescant, like his father, was head gardener to the King after the Restoration. He also travelled, collected and sold exotic plants. He made several trips to Virginia and his catalogue of new plants (published in 1656) included a passionflower, which he called *Amaracock* or *Clematis Virginiana* ('clematis' simply means 'vine-branch', and was then used to describe any climbing plant). As a result of Tradescant's work, passionflowers were soon being cultivated in Britain; the Duchess of Beaufort's gardeners were growing the blue passionflower in 1699.

The great Swedish naturalist, Carl von Linné, or Linnaeus, gave the passionflower its modern Latin name: he simply translated 'passionflower' into Latin and called it Passiflora. Famously, he also standardized the way plants and animals were named, by founding a system that is still in use. Each species has a two-part name, or binomial: the second name is that of the species itself; the first is that of the group of closely related species, called a genus (genera is the plural), to which it belongs. The annual or crinkled passionflower is *Passiflora gracilis*, the blue is *Passiflora caerulea*, and so on. Modern botanists classify the genus Passiflora into a family called Passifloraceae, which consists of several other genera of tropical climbers, including Basananthe and Adenia, all of which are forms of passionflowers.

Linnaeus's botanical works were soon translated into English and his naming system became especially popular in Britain, but although the name Passiflora was soon well known, passionflowers themselves were not widely grown in Britain until the nineteenth century. And while they owed much of their popularity to their striking colours and shapes, their progress was also aided by a change in the tax laws, by the impacts of imperialism and industrialization and, in particular, by the effects of industrial pollution.

Steam, smoke and glass

An 1845 editorial in the weekly newspaper the *Gardeners' Chronicle* celebrated the Prime Minister Sir Robert Peel's decision to abolish the tax on glass. 'All duties on glass are to be extinguished,' the paper's editor proclaimed, 'and every man who has a greenhouse, a Cucumber frame, or even a window, owes [Peel] a debt of gratitude.' The editorial claimed that 'There was not, in the whole list of excisable materials, an impost so oppressive as the

glass duty.' The paper was particularly outraged because the tax had converted 'A beautiful substance . . . costing little except labour and skill . . . into a material which could only be enjoyed, even by those in easy circumstances, on the most indispensable occasions'.[4]

With Chartist agitators marching through the streets of London, starvation in Ireland and revolution brewing across Europe, the cost of a cucumber frame might not appear momentous, but the abolition of the glass tax had implications for Britain's landscape that are still with us.

At the time the tax was repealed, window glass was still hand-blown: a balloon of molten glass was pressed flat on one side, like the flat bottom of a hand-blown glass vase. As it cooled, sheets of glass could be cut from this flattened surface. The process was not only highly skilled, time-consuming and expensive, it also could not produce sheets larger than around two by three feet (60 × 90cm). But according to another popular middle-class publication, *Chambers's Edinburgh Journal*, the end of the glass tax promised to change all this: 'it is impossible to foresee to what useful purposes glass will be put', their editorial prophesied, nor 'how cheaply it will be possible to obtain it'. The journal's writer believed that abolishing the tax would give 'an elasticity . . . to the trade' because 'new enterprisers will embark in it'; and sure enough, in 1847, the abolition inspired a young man from Sunderland, James Hartley, to patent a system for making rolled plate glass.[5] Hartley machines made glass sheets that were bigger, stronger and cheaper than anything that preceded them; he became Britain's largest glassmaker and his glass was exported all over the empire. Without it, the great Victorian railway stations, with their vaulted iron and glass roofs, could not have been built, nor could the huge shop windows that displayed the dizzying proliferation of consumer goods that Britain's burgeoning industries were producing. But from the passionflowers' perspective, the most important thing about Hartley's invention was that it made possible large, cheap greenhouses.

Greenhouses had begun getting bigger before Hartley's invention. In 1816, the Scottish-born garden designer and journalist John Claudius Loudon had patented a new kind of wrought-iron glazing bar for greenhouses. This permitted curved roofs for the first time, which let in more light; the older, wooden sashes blocked much of it. Loudon's bars made it possible to erect structures like the Great Conservatory at Chatsworth; designed by Joseph Paxton and completed in 1840, it was then the largest in the world. Mass-produced wrought iron allowed the great Palm House at the Royal Botanic Gardens, Kew, to dwarf even Chatsworth. But only governments or the very wealthy could afford to build on such a scale. In 1872, *Beeton's Book of Garden Management*, a product of the publishing empire built on the fame of Mrs Beeton's *Cookbook* and the *Englishwoman's Domestic Magazine*, commented that: 'Glass structures of even the smallest kind would, a very few years ago, have been considered a piece of great extravagance for any but the affluent.'[6]

To become affordable, greenhouses had to be mass-produced, which required increased demand. A sense of where that demand came from can be gleaned from *Chambers's Edinburgh Journal*'s celebration of the abolition of the glass tax:

> It is impossible to foresee the advantages of cheap glass which will be reaped by horticulturalists. Conservatory frames and other glazed implements of their art are so serious an item of expense that recent insurance companies have thought it worth their while to afford insurances against hail – a severe storm of which has been known to ruin many a struggling gardener.[7]

In a similar vein, the *Gardeners' Chronicle* commented that 'To men with whom glass was necessary for their purposes of their trade, the excise duty was a most grievous burthen.'[8]

Both publications were thinking primarily of the market gardeners who fed the inhabitants of Britain's rapidly expanding cities. The biggest problem they faced was smoke – every house and office was then heated by coal fires while steam-powered factories had to be near their workers, so their chimneys added to

the pall. And on top of that, 6,000 miles of railways were built in Britain between 1830 and 1850, by which time coal production had hit 49 million tons a year – rising to 147 million tons over the next thirty years.

The Victorians applied their much-vaunted ingenuity to the problem of smoke, and various ideas were proposed to clean up the air, including a scheme to pump fresh air in pipes from Hampstead Heath into the heart of the City of London (which, perhaps unsurprisingly, was never implemented). It was not until 1851 that a more practical solution presented itself. In order to house the Great Exhibition, Joseph Paxton decided to out-do even Kew's Palm House by building the world's largest glass building; before it had even been finished, it had earned the affectionate nickname 'the Crystal Palace' from the satirical magazine *Punch*.

Others were less impressed. The art critic John Ruskin called it a 'cucumber frame' and *The Times* referred to it as 'a monstrous greenhouse' and campaigned against its being built, especially since its construction was to involve cutting down several of Hyde Park's beautiful old trees. To overcome such opposition, Paxton came up with an ingenious solution to the problem of the trees – he built around them. As a result, there were fully grown elms inside the building; the *Gardeners' Chronicle* observed that 'while the dirty, half-starved Elms, growing as if wild in the open park, made shoots at most a foot long on the average, the well-fed, well-cleaned, well-lodged trees under the [Crystal Palace's] transept, made shoots from 6 to 7 feet long'.[9] The 'monstrous greenhouse' had demonstrated to the public what horticulturalists already knew – greenhouses could address the problem of smoke. Glass buildings became so popular that in 1877 it was even suggested that a vast neo-Gothic-style conservatory be built over London's Albert Memorial to protect it from air pollution.

Industrialization made mass-produced greenhouses both practical and necessary; the smoke belching from the glass- and iron-making factories made it almost impossible for city-dwellers to grow plants out of doors. Because horticulturalists had to rely on glass to make a living, as Britain's cities grew, so did the demand for greenhouse glass. The editorial writer in *Chambers's Journal* had also foreseen that 'Private individuals also will be able to have conservatories.'[10] And, indeed, hundreds of thousands of Victorians left the Crystal Palace determined to have a greenhouse of their own. Paxton boasted that he had cut the cost of the Palace by building from standardized parts, manufactured in bulk. He took advantage of his new fame to launch a range of affordable, modular greenhouse kits, based on the same principles. Mass production made greenhouses cheap and popular; soon there was a size and price to suit everyone. Greenhouses varied from simple glazed but unheated structures to what was known as a 'stove', in which a furnace kept the interior hot enough to grow tender tropical plants – such as passionflowers.

For those who could not afford a full-sized greenhouse, or did not have a garden to put it in, there was the Wardian case, a miniature greenhouse that could sit on a table or windowsill. These were named after an enterprising gentleman, Nathaniel Bagshaw Ward, who claimed to have invented them but had in fact simply improved an existing design and then promoted it in a book with the characteristically imaginative Victorian title, *On the Growth of Plants in Closely Glazed Cases*. Ward had a passion for gardening and botany and gradually converted his London home into a verdant, social centre for London's botanists and their visitors from abroad. The gardening writer John Loudon visited Ward's home and described the planter boxes that were to be seen 'along the tops of all the walls of his dwelling house, of the offices behind, and of the wall round the yard, even up the gable ends and slopes of lean-tos'.[11] Ward held scientific soirées and took every opportunity to promote his glass cases: they were ideal for growing ferns and helped spark a fern craze; he also recommended them to botanists and nurserymen as an ideal way to bring living plants from across the empire to British gardens.

Before Ward's cases, transporting live plants on slow-moving sailing ships had been a risky business; if the salt spray did not kill them, the shock of being moved through several different climates

often did. The new cases were not foolproof: one arrived in London that had been packed by someone whose anxiety about its safety clearly exceeded his knowledge of plants; he had 'painted the glass over, then covered it by way of protection with broad battens of wood and lastly nailed a thick piece of tarpaulin over the whole'. Not surprisingly, the plants arrived dead in their dark coffin.[12] But despite such setbacks, Wardian cases helped to make thousands of new types of plants available in Britain.

In its domestic setting, the Wardian case served as an elegant ornament, its living plants bringing a little colour and life to the often airless Victorian drawing-room, while attesting to its possessor's taste and interest in scientific matters. The shipboard cases brought samples of the empire's exotic fruits, flowers and vegetables to fill Britain's greenhouses, helping the plants to reach new habitats.

In addition to cheap greenhouses, the Victorians invented those other indispensable features of the British Sunday afternoon, the lawnmower and the garden centre, and they also gave us the ever-popular solution for what to do when the rain makes gardening unappealing – the gardening magazine. The steam that powered Victorian Britain's railways also powered its printing presses and churned out cheap, machine-made paper. The country experienced a massive boom in newspapers, magazines and books and as dozens of new publishers began chasing after new readers, they soon spotted gardeners as a potential market; the *Gardeners' Chronicle* was just one of a number of magazines launched to take advantage of it.

This new audience also helped resurrect the *Botanical Magazine*, which printed descriptions of new plants illustrated by beautiful hand-coloured plates. It had been published for nearly forty years when it was taken over by William Jackson Hooker, Regius Professor of Botany at Glasgow University, in 1826. He worked to increase its scientific content, but also took advantage of the exotic plant boom to reach a new audience, using connections around the world to get new plants to illustrate. In the 1830s he made contact with John Tweedie, a Scottish gardener who had emigrated to Buenos Aires some years before, hoping to obtain work designing and landscaping for wealthy Argentinians. Patrons were rarer than he had hoped, so Tweedie began to explore the country's interior looking for new plants to satisfy British gardeners' growing lust for novelties.

Tweedie's plants were soon being described and illustrated in the *Botanical Magazine*. In 1839, for example, Hooker gave a new passionflower the name *Passiflora nigelliflora* (meaning that its flowers resemble those of nigella, the plant that the spice black cumin comes from), telling his readers that 'it was discovered, in 1835, by Mr Tweedie, on his way from Mendoza to Tucuman'. Hooker described its botanical characteristics for the benefit of his more scientific readers, but gardeners were the major audience – Hooker explained that the new plant 'flowered in the Glasgow Garden in September, and seems to require the heat of the stove'. Among Tweedie's other discoveries were *Passiflora tucumanensis*, which was described as 'a free grower, and flowered copiously the second year in the stove of the Glasgow Botanic Garden'.[13] Tweedie was typical of the collectors who gathered plants and sent them home to England. In both Britain's colonies and her trading partners, gardeners, missionaries and colonial officials, naval officers and soldiers, convict supervisors and paid plant collectors were all at work trying to satisfy both commercial demand and the curiosity of men of science. Some worked for money, or for the glory of gardening, God or empire – but many were simply eager to contribute to botanical science.

The garden and greenhouse boom turned plants into big business. In the 1840s, new species of passionflower were being sold through gardening magazines for a guinea (£1.05) each. At that time, a domestic servant earned between £20 and £60 a year, so these were clearly not plants for the masses. However, by the 1850s, prices had fallen to 16s. 6d. for the showier types, down to just 2s. 6d. for the more common varieties. These plummeting prices show how much demand had increased; passionflowers were now being grown or imported in huge numbers, making them more affordable. At the same time the railways, whose

smoke continued to cause city gardeners such problems, also allowed garden materials, equipment, building materials and plants to be moved quickly and cheaply around the country, all of which fostered the gardening boom. Thanks to collectors like Tweedie, commercial nurseries and the opportunities (and difficulties) created by industrialization it became remarkably easy to obtain exotic plants in Britain.

Among the *Botanical Magazine*'s rivals was the *Botanical Register*, edited by John Lindley (also editor of the *Gardeners' Chronicle*), Professor of Botany at University College London. In one issue he described a new flower he called *Passiflora onychina*, or 'Lieut. Sulivan's Passion flower' because it had first been collected by the naval lieutenant Bartholomew Sulivan, who had 'procured the seeds, with others, from the Botanic Garden at Rio de Janeiro, in 1827'.[14] A few year's after his trip to Rio, Lieutenant Sulivan was reassigned to a small surveying vessel, HMS *Beagle*, commanded by Robert FitzRoy. It set sail for South American waters again in December 1831. Alongside FitzRoy, Sulivan and the other officers and crew was a feckless young man of no fixed ambitions but with a burning enthusiasm for natural history collecting, Charles Darwin. He was to play an important part in the passionflower's story.

Sterility, marriage and the passionflower

The *Beagle* spent more than half its five-year voyage in South American waters, and while its crew were busy with the ship's real work, producing accurate maps for the British navy, Darwin was free to go on long inland journeys, sometimes for months at a time, exploring the pampas, the mountains and the rainforests. In his published journal, now known as *The Voyage of the Beagle*, he described seeing 'Numerous cottages . . . surrounded by vines', some of which were almost certainly passionflowers, since most passionflower species are native to South America. Darwin collected two unfamiliar species of passionflower while the ship was in the Galápagos: his dried, faded specimens are still in the University Herbarium at Cambridge. Sadly, he was there in

September and October, when the plants were not in flower, but his specimens still have their climbing equipment attached – slender, fragile tendrils that would come to fascinate Darwin. Indeed, since John Stevens Henslow, the Cambridge Professor of Botany who had taught him as an undergraduate, had urged his former pupil to concentrate on plants in flower, Darwin's Passiflora specimens suggest he may have already been interested in their climbing habits.[15]

After the *Beagle*'s return to Britain in 1836, Darwin distributed his specimens to various experts, in order to have them properly identified and named. At this stage in his career, his main expertise was in geology, not botany, so the passionflowers went with the rest of the Galápagos plants to his old friend Henslow. Unfortunately, Henslow was too busy with his university duties and his parish work (he became vicar of Hitcham, Suffolk, in 1837) to work on his former student's plants. They languished, neglected, for many years.

In 1843, seven years after the *Beagle*'s return, Darwin finally got tired of waiting for Henslow and offered the Galápagos plants to William Hooker's son, Joseph Dalton Hooker. Joseph had just returned from a remarkable voyage of his own – four years spent circumnavigating the Antarctic on another British naval vessel, the *Erebus*. It and its sister ship, the aptly named *Terror*, had braved icebergs and storms to sail further south than any ships had before, trying to determine the exact position of the southern magnetic Pole. Although the ships' hulls had been strengthened to help them resist the pack ice, no wooden sailing vessel could survive the Antarctic winter. As the days closed in and the ice began to extend its grip, the *Erebus* and *Terror* retreated north and wintered in Australia, New Zealand or South America, carrying out repairs and re-supplying. During these respites, Joseph Hooker went exploring and collected plants. Although he was only an assistant naval surgeon (while Darwin had paid his own way as a gentleman companion to the captain), having a father with a famous name in botanical circles opened doors for Joseph. He contacted his father's correspondents wherever he went.

Although his ship did not take him to Buenos Aires to meet Tweedie, Hooker met many similar men in Australia and New Zealand whose love of botany had led them to collect for his father, who had recently become director of Britain's national botanic garden at Kew.

On his return to Britain, Hooker decided to write not merely a description of his travels but a comprehensive flora of all the countries around Antarctica. By comparing and contrasting the plant life of different countries, he hoped to discover how plants had arrived in their present habitats. Apparently aware of his interest in distribution, Darwin offered the *Beagle* plants to Hooker, including the passionflowers. Darwin's published journal of the *Beagle* voyage and his publications on geological and other topics had made him a celebrated figure and Hooker was both surprised and flattered by his attentions. Once the plants had arrived, he wrote to tell Darwin that they 'are far more xtensive [*sic*] in number of species than I could have supposed' and that even though he 'was quite prepared to see the xtraordinary difference between the plants of the seperate [*sic*] Islands from your journal', he was nevertheless surprised by his observations of the actual specimens, which he realized would force him and other botanists to rethink their ideas about plant migration.[16] Three years later, Hooker described Darwin's passionflowers in the *Transactions* of London's Linnean Society; convinced they were new species, Hooker named them *Passiflora tridactylites* and *Passiflora puberula*.[17] Darwin's gift, including the passionflowers, began a lifelong friendship with Hooker; their regular letters and visits were invaluable to both men, and Hooker's observations and his knowledge of botanical matters were to shape Darwin's work over many decades.

After his return from the *Beagle* voyage, Darwin started trying to work out the implications of what he had seen. He did not, of course, come up with the idea of evolution as soon as he saw the Galápagos: it took years to develop and test his theories, and passionflowers were to play a small but vital role in that work. Among Darwin's surviving papers is a notebook marked

'Questions & Experiments', which he scribbled in during the first few years after his voyage. It is full of obscure jottings, which he made purely to jog his own memory; they are hard to read and even harder to interpret. Among them is a single, cryptic reference to passionflowers, which his father cultivated: under the heading 'Figs, flower', Darwin listed plants whose fertilization he wanted to investigate, including, 'Passion Flower. (as it is required to impregnate it artificially.)'.[18]

Darwin evidently knew that cultivated passionflowers need artificial pollination to produce fruit. He is likely to have read about the difficulties of growing them in the gardening magazines, the same ones where Paxton's do-it-yourself greenhouses were advertised and Tweedie's new passionflowers announced. Among these was the *Cottage Gardener*, which first appeared in 1848 and proudly described itself as 'a practical guide in every department of Horticulture'. Darwin not only read it, but wrote to it on many occasions, hoping its readers might help answer his botanical questions and supply him with fresh facts.

The *Cottage Gardener* featured regular columns on such topics as 'Greenhouse and Window Gardening'; in 1849 one Donald Beaton wrote an introductory guide to the plants that he felt should be in everyone's greenhouse. First on the list was the Sweet-scented Mandeville (*Mandevilla suaveolens*, commonly known as the Chilean jasmine), another of Tweedie's introductions. Beaton's article continued, 'After the Mandeville, I would recommend a passion flower', listing some of the hardier and more vigorous varieties that would grow outdoors or in an unheated greenhouse.[19]

Donald Beaton was a Scot by birth, who had worked to improve the spectacular gardens at Shrubland Park, Suffolk. He was an expert on plant hybridization and on bedding schemes, another Victorian response to industrial smoke – flowers grown outdoors in polluted cities died so quickly that gardeners developed the technique of raising masses of flowers under glass, planting them outside when they were in flower and replacing them as soon as the first crop faded. This technique also allowed

the creation of the elaborate geometric and other designs that became known as carpet bedding, which can still be seen in some old-fashioned parks and gardens.

The year after Beaton promoted the passionflower in the *Cottage Gardener*, another of its writers, Robert Errington, contributed an article on the 'Culture of the Passifloras for the Dessert'. The opportunity to serve exotic fruit to dinner guests was a major reason to own a hothouse. In Jane Austen's *Northanger Abbey*, Catherine Morland is shown around the Abbey's gardens, in which 'a village of hot-houses seemed to arise'. It is clear that this 'village' had one main purpose: General Tilney, the garden's owner, 'though careless enough in most matters of eating . . . loved good fruit', yet despite 'the utmost care [he] could not always secure the most valuable fruits. The pinery had yielded only one hundred in the last year.'[20] A pinery was a hothouse devoted to producing pineapples, so that men like General Tilney could impress their neighbours with a display of conspicuous consumption. Passionfruit were grown for the same reason.

However, exotic plants would only impress if they could be persuaded to bear fruit and that – as Errington acknowledged – was not easy. In his advice to growers he noted that 'Another point too, and an all important one, must have strict attention – the flowers must be "set" by hand as they open. Without this, the crop can by no means be relied on.' The procedure was simple enough: 'take one of the anthers, when burst, about eleven o'clock in the forenoon, and merely rub the point of the stigma with it', but he was unsure why it was necessary. Perhaps, he speculated, it was because in most passionflowers, the anthers (where the pollen is produced) hang downward, so that when they ripen and burst, the pollen falls away from the receptive stigmas, which – as we have seen – are raised up on a central column above the stamens. Errington observed that the benefit of this arrangement to the flower is 'not very apparent' and suggested that his fellow columnist, Beaton, 'could doubtless throw some light on this curious economy'.[21]

Beaton responded in the following issue. Pausing only to mock 'the old story about the Spanish monks having mistaken this arrangement for emblems of the crucifixion' as being 'mere moonshine', Beaton claimed that despite the apparently impractical arrangement of the flowers, when they are fertile, the carpels bend to meet the stamens. He patronizingly commented that it was 'No wonder . . . that honest men like the Spanish monks and our friend [Errington], should be deceived and puzzled by "such fancies." However, we must give Mr Errington credit for wishing to clear away all impediments to such mutual understanding.'[22]

Beaton failed to answer the question of why the flower was arranged in this peculiar way, and the information he gave was largely wrong.[23] Most passionflowers are incapable of self-fertilization in the way that he describes; instead, they depend on an insect, a bird, a bat (or a gardener) to carry their pollen from one flower to another – without such assistance, they cannot reproduce.

The sterility of passionflowers both fascinated and alarmed Darwin because it seemed to contradict his theory of natural selection. Like the horse and dog breeders he had grown up with, Darwin knew that living things varied: children resemble their parents, but are never exactly like them. These small differences have long been referred to by naturalists and biologists as 'variations'; for any character, such as height, within a population there is a range – from the tallest to the shortest – which is referred to as the population's range of variation or simply its 'variability'. Neither Darwin nor anyone else at the time knew what caused these variations, but whatever it was, they could be inherited, as every farmer that mated a prize bull with the cow that gave the most milk understood – that was how the breed was improved. But in the years after the *Beagle*, Darwin was trying to explain how wild animals and plants might change – in the absence of any conscious direction of their breeding. The now-famous breakthrough in his thinking came as he was reading *An Essay on the Principle of Population* by the political economist Thomas Malthus. Malthus believed that without the checks of war and famine, population growth would always outstrip food production; the

only way to avoid a struggle for food was the application of 'moral restraint among the poor', in other words, people should not have children they could not afford to feed.[24] In his *Autobiography*, Darwin recorded that at the time he read this, he was 'well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants'; it therefore struck him that because of this intense struggle, 'favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of new species. Here then I had at last got a theory by which to work.'[25]

This was the essence of natural selection: organisms varied at random – some variations helped the organism survive and reproduce, but others did not. The inability of plants and animals to exercise 'moral restraint' led to an intense struggle for food, space and mates; those organisms whose variations helped them to survive would be more likely to pass on these favourable variations to their offspring. Meanwhile, those with less favourable variations would tend to have fewer offspring. And so, very slowly and gradually, over tens of thousands of generations, organisms would change and become better adapted to their environments. Eventually the descendents would be entirely different from their ancestors; a new species would have evolved.

Darwin was delighted with his theory and began to test it by seeing how well it explained his various observations and experiments; this was when plants like the passionflower became a problem. Plants obviously benefit from having both male and female parts in the same flower: they can save themselves the tedious – and often hopeless – business of finding a mate. Most flowers can simply self-fertilize and save their energy for producing and scattering their seeds. Yet not only did some plants not take advantage of this convenient arrangement, plants like passionflowers (and they are not unusual in this), seemed almost to be actively avoiding it: the flowers of many Passiflora are so arranged as to make self-fertilization unlikely (the point Errington had puzzled over in the *Cottage Gardener*), and many have the ultimate insurance against self-fertilization – if their *own* pollen falls on their stigmas, it fails to fertilize them; a phenomenon botanists describe as self-sterility. How and why did such an arrangement evolve? As Errington had wryly observed, the benefit to the plant was 'not very apparent'.

The passionflower's aversion to self-fertilization also puzzled Darwin. Ever since he had been an undergraduate at Edinburgh University, Darwin had shown a typical student's preoccupation with sex, but while his contemporaries pursued their researches in the city's bars and tea-shops, Darwin walked the beaches of the Firth of Forth, with his friend and teacher, the zoologist Robert Grant, where they collected tiny marine creatures and examined them under a microscope. Grant got Darwin interested in creatures such as corals, which are made up of hundreds of individual polyps. They seemed indecisively poised between the plant and animal kingdoms, hence Grant's name for them: 'zoophytes', or 'animal-plants'. As embryos they swim freely like animals, but then settle down to an entirely sedentary life, functioning as parts of a vast colony, almost as if they had become elements of a more complex organism, like the buds, leaves and branches of a tree.

Darwin remained interested in these questions when he was at Cambridge, where he met Henslow and heard him argue in his lectures that when plants such as strawberries propagated by sending out suckers, thus managing without sex, this was just one more entirely normal reproductive strategy, not an aberration as some of his contemporaries believed. Darwin took Henslow's and Grant's ideas with him on the *Beagle*, looking at the myriad ways that organisms procreate; some seemed to rely entirely on sex to reproduce, others managed with only an occasional coupling, while a few managed without sex at all. Among the organisms he collected on his travels were barnacles; back in Britain, he spent eight long years (1846 to 1854) studying and classifying them. He was particularly fascinated to discover that most barnacles, like flowers, are hermaphrodites – they have both male and female reproductive organs – but others have separate sexes. Perhaps the

most astonishing were strange specimens in which the male barnacles were so tiny that they lived *inside* the females' shells, almost like parasites. The males are little more than tubes of sperm; the females protect and feed them. Staggered by this discovery, Darwin wondered if these species with what he called 'complemental males' might perhaps be intermediates between the common hermaphroditic barnacles and the ones that had wholly separate sexes. They suggested a route by which separate sexes could have evolved; Darwin assumed that all organisms descended from types which were asexual or hermaphroditic, since it seemed unlikely that two independent sexes could have evolved simultaneously. But what was the evolutionary pressure that drove a self-sufficient self-fertilizer – barnacle or passion-flower – to evolve towards the complex, and potentially childless, world of two separate sexes?

Along with the other baffling problems Darwin was facing in the summer of 1838 was the question of whether or not to get married. Being a man of science, he approached the question rationally, making a list of the pros and cons. Under 'Not Marry', he listed such advantages as 'freedom to go where one liked' and 'conversation of clever men at clubs'. Not marrying would also relieve him of 'quarrelling', 'fatness and idleness', and having 'less money for books'. But marriage had its attractions, including 'Charms of music and female chit-chat'. Children feature on both lists: as an advantage of marrying, Darwin wrote 'Children (if it please God)', adding, 'it is intolerable to think of spending one's whole life, like a neuter bee, working, working and nothing after all'. But he also worried about 'the expense and anxiety of children', especially 'if many children' he might be 'forced to gain one's bread' by working for a living. Despite these drawbacks, he opted for marriage. The clinching argument being that it would provide him with a 'constant companion, (friend in old age) who will feel interested in one, object to be beloved and played with – better than a dog anyhow'.[26]

Having weighed the matter carefully, Darwin proposed to his cousin Emma Wedgwood and they were married on 29 January

1839. There were already several cousin marriages in the Darwin and Wedgwood families; they were almost becoming a tradition. However, while the Darwins and Wedgwoods were becoming an increasingly close-knit clan, not everyone was convinced such unions were a good idea. While Darwin was contemplating matrimony, he read Alexander Walker's newly published book *Intermarriage*, which claimed to describe 'the functions and capacities which each parent, in every pair, bestows on children, in conformity with certain natural laws, and by an account of corresponding effects in the breeding of animals'.[27] Walker's claim that natural laws governed the breeding of both humans and animals must surely have caught Darwin's eye; soon after he got married, he decided to test ideas like Walker's by making detailed observations of plant-breeding. One of Walker's claims was that inbreeding could cause 'deformity, disease and insanity'; over the following years, Darwin worried that his decision to marry his cousin had weakened his children, who seemed rather sickly. In 1842, he and Emma watched their third child, Mary, die just a few weeks after her birth; nine years later, their beloved daughter Annie died, just ten years old; and, their last child, Charles Waring, lived for less than two years. Darwin's garden was not merely a refuge from these sad losses, it was also where he tried to understand their causes; he spent years crossing plants with each other, trying to understand the precise effects of inbreeding.

Although Darwin never left Britain again after the *Beagle* voyage, he conducted a vast correspondence with naturalists, gardeners and farmers from all over the world. He wrote with questions and received comments, specimens, ideas and observations. Putting these together with his garden observations, Darwin felt he could claim in *The Origin of Species* that '*close* interbreeding diminishes vigour and fertility':

> . . . these facts alone incline me to believe that it is a general law of nature (utterly ignorant though we be of the meaning of the law) that no organic being self-fertilizes itself for an eternity of generations; but that a cross with another individual is occasionally – perhaps at very long intervals – indispensable.[28]

However, some of his critics attacked this assertion, arguing that he had not provided enough evidence for it; and neither they nor he were satisfied with his 'utter ignorance' of its significance, so Darwin went back to his garden to prove it.

To help him address this problem, Darwin decided he needed to add a hothouse to the range of unheated glasshouses he had already built; a stove would allow him to compare hardy plants with more tender, tropical ones. He wrote to tell 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'.[29] He wanted to start growing tropical orchids to complement the native species he had been investigating for many years, but worried over their cost and told Hooker (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.'[30] Hooker responded, tongue-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.'[31] A few weeks later Darwin visited Kew with a list of what he most wanted and when Hooker's gift of plants arrived, Darwin was 'fairly astounded at their number! why my hot-house is almost full!' He was especially delighted to 'see several things which I wished for, but which I did not like to ask for'.[32] 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?'.[33]

The first product of Darwin's investigations into plant fertility was his book on orchids, *The Various Contrivances by which British and Foreign Orchids are Fertilised by Insects* (1862). The fantastic shapes and colours of orchids had made them another widely popular hothouse plant, which must have helped the book's sales. Darwin had been interested in orchids ever since his undergraduate days and, as with the passionflowers, he had collected some during the *Beagle* voyage. He began experimenting with plants in about 1854 in order to investigate why even those that could potentially self-fertilize actually relied on insects to pollinate them. Granted the assumption he had made in the *Origin*, that perpetual self-fertilization lowered fertility, it would still seem reasonable to assume that natural selection would have favoured a 'general purpose' flower, one that any insect could fertilize; that would surely maximize the plant's chances of reproducing, ensuring that such general-purpose flowers would become common. Yet what Darwin found was that in many species of orchids the flower was adapted so that only *one* species of insect could enter and fertilize it. Not content with having, apparently rather perversely, given up on the easy option of self-fertilization, the orchids appeared to have gone one better and evolved so as to lower their chances of reproduction even further. And yet orchids form one of the world's largest plant families.

As he worked to unravel the extraordinarily complex flowering structures of orchids, Darwin realized that this 'lock-and-key' fit of insect and flower was beneficial to both. Because other species of insect could not get at the nectar, there was no competition for the one that could. And the flower benefited because its pollen would be spread only to other members of its species, not wasted on plants the pollen could not fertilize. These mutual benefits made natural selection into a force that had slowly, over tens of thousands of generations, reshaped both the orchid's anatomy and the insect's behaviour. Insects that inherited the preference for a specific orchid might – over many generations – eventually become the only ones that visited it, as they and their orchid became adapted to each other's anatomy. Such specialized insects would face less competition and thus fare slightly better in the struggle for food; all of which increased the chance of them passing on their preference. Meanwhile orchids that varied in a way that made them 'fit' the insect better would increase their chance of successful pollination, thus spreading the improved structure more widely in successive generations. Darwin's work

revealed that what appeared to be intelligently designed – and inexplicably beautiful – structures were the products of natural selection. In each generation the most successful insects had been the ones who best fitted their flowers – together with the flowers that provided the best fit for their insects; for orchids and their pollinators, evolution was not so much the survival of the fittest as the survival of the best fitting. As Darwin put it, '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'.[34]

Moving plants

Darwin wanted more than orchids in his hothouse, but told Hooker that 'I shall keep to curious and experimental plants.' These included carnivorous ones, which seemed another example – like the minute zoophytes he had studied in Edinburgh – of organisms that blurred the boundary between plants and animals. He was delighted to discover from the nurserymen's catalogues that he could buy carnivorous 'Pitcher plants for only 10s. 6d!'; as with the falling prices of passionflowers, the nursery trade made even unusual plants affordable. Alongside the carnivorous plants were ones that seemed to possess senses: 'Mimosa & all such funny things', that reacted to touch by closing their leaves.[35] Plants were traditionally defined in contrast with animals, as being unable to sense or move, so Mimosa was another potential case of blurring the boundary. However, if Darwin was to show that it had evolved its extraordinary abilities, as opposed to being divinely designed, he needed to demonstrate that all plants possessed some ability to sense and move.

Darwin began his investigation of plant motion with climbing plants, including passionflowers. Soon after the hothouse was finished, he told Hooker (with characteristic modesty) 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, it is clear from his book, *On the Movement and Habits of Climbing Plants* (1865), that far from 'taking no time', he spent years on painstaking experiments to discover just how and why plants climb. It was obvious that some plants have highly specialized adaptations for climbing. The American cup-and-saucer vine (*Cobaea scandens*), for example, which Darwin called 'an admirably constructed climber', has branched tendrils that bear tiny hooks 'formed of hard, transparent, woody substance, and as sharp as the finest needle', which, Darwin recorded, 'readily catch soft wood, or gloves, or the skin of the hands'. This group, which Darwin called 'tendril-bearers', seemed to be the most specialized of climbers. As they grow, the tendrils revolve until they catch on a support, then they sense the light and start to clamber towards it; as he wrote to his son William, 'My hobby-horse at present is Tendrils; they are more sensitive to a touch than your finger; & wonderfully crafty & sagacious.'[36] As he worked at his hobby-horse, Darwin became increasingly impressed with the plants' 'craftiness', noting that tendrils responded to the weight of 'a loop of soft thread weighing 1/32nd of a grain' by growing towards it – a sensitivity that allowed them to detect anything they could potentially climb up. Yet the tendrils did not react when much heavier raindrops fell on them, nor to the wind.[37] Darwin was also impressed by the speed with which the climbers reacted; after experimenting with the crinkled passionflower, *Passiflora gracilis*, Darwin 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.'[38] Of all his 'crafty and sagacious' tendril-bearers, passionflowers seemed the most highly adapted; Darwin described *Passiflora gracilis* as exceeding 'all other climbing plants in the rapidity of its movements, and all tendril-bearers in the sensitiveness of its tendrils'.[39]

The remarkable mobility and responsiveness of these plants

was an evolutionary response to their environments. Darwin explained that 'Plants become climbers, in order . . . to reach the light, and to expose a large surface of leaves to its action . . . This is effected by climbers with wonderfully little expenditure of organized matter, in comparison with trees, which have to support a load of heavy branches by a massive trunk.'[40] That explained why plants climb, but Darwin still needed to explain how natural selection could have created such highly specialized plants. He noted that climbers divide into several kinds. Some, like ivy, use aerial roots to climb but there are also what he called spiral climbers, which he divided into twiners, which simply twist themselves around a support; leaf-climbers, which use their leaf stalks to attach themselves; and tendril-bearers, which have the most specialized climbing equipment.

Because the twiners wrapped their whole stems around the support, they used the most plant material to climb; Darwin unwrapped them, measured the stems (which were the thickest and thus the most costly part of the plant to grow), and discovered that the twiners had the longest stems. Leaf-climbers were shorter, but those of the tendril-bearers were shorter still. Reducing the amount of plant material needed to achieve the same goal showed the adaptive benefit of such specialization. By watching the plants develop, Darwin realized that tendrils were simply modified leaf or flower stalks and noted that the basic spiral movement of the twiners was essential to all three kinds of climbers. From these observations, he was able to reconstruct the probable evolutionary sequence: the twiners evolved first, with leaf- and tendril-climbers coming later. Tiny random variations in the ancestral twiners meant that some used a little more or less plant material in getting up into the light; Darwin noted, for example, that tendril-bearers can climb up the sunny outsides of bushes and trees, whereas simple twiners spent half their time in the shade. As a result, tendril-bearers could photosynthesize more efficiently and grow faster, all of which helped them conserve energy for making flowers and fruit, so they had more offspring who inherited whatever variation had benefited their parents, and so on. Gradually, generation after generation, natural selection could turn simple twiners into highly evolved tendril-bearers. In his later book, the *Power of Movement in Plants* (1880), which he wrote with his son Francis, Darwin showed that the basic movements which give plants the power to climb were found in some form in every kind of plant. Mimosa and *Passiflora gracilis* may have been exceptional, but neither was unique.

In summarizing his work on climbing plants, Darwin wrote 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'. Most plants seldom need to move, or move too slowly for us to appreciate, but in response to a particular environment they prove to be more like animals than anyone had previously noted: predatory, perceptive, responsive and swift-moving. Darwin later wrote that 'it has always pleased me to exalt plants in the scale of organised beings', to show his readers that plants were not insensible, immobile or uncomplicated, and perhaps no climbing plant was ever acclaimed more loudly by Darwin than *Passiflora gracilis*.[41]

What is the use of sex?

As well as using passionflowers in his experiments on plant motion, Darwin decided to use them (along with many other species) in his long-running series of plant-breeding experiments. These were Darwin's attempt to answer the questions prompted in part by his marriage: what was the use of sex? Or, as he put the question, in the title of his book on the topic, what were the *Effects of Cross- and Self-Fertilisation in the Vegetable Kingdom* (1876)?

Given that Darwin was partly interested in the problem of human inbreeding, it might seem surprising that he did not choose an animal species for his experiments. As we shall see in the next chapter, humans themselves make rather poor experimental organisms, but another primate, or at least another mammal, might seem a more obvious alternative than a passionflower.

However, one of the great attractions of plants for a naturalist is that it is relatively easy to control which is breeding with which. Techniques such as netting flowers, to keep out insects, and then hand-pollinating with a paintbrush made it possible to be certain which pollen had got on to a particular plant. The first plant Darwin used was the common toadflax, *Linaria vulgaris*, but dozens of other species were soon involved, both outdoors and in the greenhouse. Darwin concentrated on growing cross- and self-fertilized specimens under identical conditions to try and prove that the cross-fertilized ones really had a competitive advantage compared with the self-fertilized.

It is exhausting to contemplate the work involved in these experiments. For each of the many species he examined, Darwin had to grow dozens of plants, which had to be kept separate from each other and protected from accidental wind- or insect-pollination. Then each one had to be hand-pollinated, its growth measured, and every seed counted. And all this had to be done twice, once for the self-fertilized plants, and then again for the cross-fertilized. Small wonder that Darwin later complained in a letter that 'I have worked like a slave (having counted about 9000 seeds) on Melastomas . . . yet have been shamefully beaten, & I now cry for aid'.[42]

Fortunately, aid soon arrived. Not long after the orchid book appeared, Darwin received a letter from John Scott, a young gardener at the Edinburgh botanical gardens, who explained that 'I take the liberty of addressing you for the purpose of directing your attention to an error in one of your ingenious explanations.'[43] Scott was still in his twenties, less than half Darwin's age; it must have taken some courage (and not a little self-confidence) to correct the country's most celebrated naturalist. Fortunately Darwin was not offended by this self-assured young man; he wrote back immediately to 'thank you most sincerely for your kindness in writing to me', adding that 'Your fact has surprised me greatly, & has alarmed me not a little.'[44] Darwin worried that he might well have made further mistakes. Despite his achievements he never considered himself a real botanist; as he told Scott, 'I know only odds & ends of Botany & you know far more.' He realized that Scott could be an invaluable assistant, telling the young botanist, 'I plainly see that you have the true spirit of an Experimentalist & good observer.' These compliments had a purpose; Darwin wondered 'whether you have ever made any trials on relative fertility of *varieties* of plants', adding that 'I much want information on this head,' especially about 'Lobelias & Crinum & Passiflora'.[45]

Encouraged by Darwin's well-aimed flattery, Scott was eager to help. He told Darwin, 'I have more than one season fertilized flowers of *Tacsonia pinnasistipula* [another passionflower] in the Gardens here,' but he had encountered the same problem that so many gardeners had faced: 'I have rarely succeeded in getting any fruit to set.' But with Darwin's encouragement, Scott offered to 'commence a series of experiments on those interesting questions', using Passiflora.[46]

Scott knew of Darwin's interest in passionflowers because they had been mentioned in the *Origin* as an example of a plant more easily fertilized by foreign pollen than its own.[47] Scott asked whether 'the *Passifloras* mentioned by you in Origin, [were] invariably sterile when treat[ed] with "own-pollen"; or is it a local occurrence?' and went on to discuss a couple of the species he had grown.[48] Darwin sent his evidence – inviting Scott decided to test it himself; soon the younger man was hard at work, crossing passionflowers, counting seeds, measuring growth and reporting his results to Darwin.[49] In return came praise ('What a capital observer you are!'); gifts ('if you would like to have any Book I have published . . . I sh^{d}. esteem it a compliment to be allowed to send it'); gentle criticism ('I suppose that you did not actually count the seeds in the hybrids in comparison with those of the parent-forms'); but most of all suggestions for ever more work ('I **very much** hope you will make a good series of comparative trials on the same plant of Tacsonia').[50] Scott was happy with the role of junior collaborator and asked Darwin to suggest possible experiments. 'If on reflection you would like to try some which interest me,' Darwin replied, 'I sh^{d}. be truly delighted', adding 'I

could suggest experiments on Potatoes analogous with case of Passiflora,' and suggested that Scott also repeat some of his earlier passionflower experiments to check the results.[51] To encourage him further, Darwin sent Scott copies of the *Origin* and his *Journal of Researches* (*The Voyage of the Beagle*), and in reply Scott offered his 'sincere thanks, in humble and grateful acknowledgement of the entirely unmerited kindness you have done me'. He was grateful not only for the books, but for Darwin's willingness 'to recognise the observations of one entirely unknown, a young and ardent admirer of Science'.[52]

With Scott's help, Darwin was able to show that cross-bred plants were in fact invariably taller, hardier and more fertile than self-pollinated ones. This was sufficient to explain how mechanisms to avoid self-fertilization could spread. Imagine two varieties – A and B – of an ancestral passionflower species: both can be fertilized by their own pollen, but (thanks to random variation) A is a little more self-fertile than B. Because the chances of A being self-fertilized are higher, self-fertilized offspring will be the most common. But such offspring will also be less hardy (and thus less likely to reproduce successfully in the next generation) and so will eventually produce fewer descendants than their hardier, cross-fertilized siblings. By contrast, although variety B will leave fewer offspring, more of them are likely to be the tougher cross-fertilized kind. And not only will the cross-fertilized plants pass their slight tendency to self-sterility on to *their* offspring, but there will be further random variation in the next generation, so some of the descendants will be slightly *more* self-sterile than their grandparents were. Over many generations, variety B will gradually have to rely more and more on a mechanism like insect pollination to get its pollen to another flower (which is what must have happened to the ancestors of orchids). At first it seems implausible, but as variety B – the rarer, self-infertile variety – becomes more dependent on the uncertain business of cross-fertilization, it will gradually become more common.

Given these advantages, any random variation that accidentally favoured cross-pollination is likely to become more common.

That is why even hermaphroditic plants have often evolved mechanisms – such as insect pollination – that avoid self-fertilization to some extent. The orchids' lock-and-key relationship with their particular insect is just one of a range of adaptations that encouraged cross-fertilization with other plants.

A key part of Darwin's evidence for the evolution of cross-fertilization was that nature exhibits a wide range of different degrees of fertility: the passionflowers had taught him that 'with many species, flowers fertilised with their own pollen are either absolutely or in some degree sterile', but 'if fertilised with pollen from another flower on the same plant, they are sometimes, though rarely, a little more fertile'. While whenever plants of two unrelated species are crossed, 'they are sterile in all possible degrees, until utter sterility is reached'. He concluded, 'We thus have a long series with absolute sterility at the two ends': at one extreme, the plants were too similar to breed (almost as if some mechanism prevented incestuous unions), whereas at the other end they were too different, producing sterile offspring, as when a horse and a donkey are crossed and produce a mule.[53] By the time he published *Cross- and Self-Fertilisation*, Darwin felt he had made sense of the puzzling self-sterility of the passionflowers: preventing self-fertilization guaranteed cross-fertilization, which in turn guaranteed hardier, more fertile offspring. Evolving separate sexes would be another obvious way to avoid self-fertilization, which Darwin thought might explain how barnacles had evolved from the hermaphroditic form, via transitional ones with their tiny complemental males, into distinct male and female barnacles. As Darwin wrote at the end of his orchid book, 'nature abhors perpetual self-fertilisation'; avoiding it was the ultimate benefit of having two separate sexes.[54]

Favoured races?

Darwin loved plants. The passionflowers were just one of many genera he worked with, but they are particularly interesting because he returned to them in so many different contexts: in the unfinished draft of his 'big species book', *Natural Selection*; in the

Origin (1859); and in the *Variation of Animals and Plants under Domestication* (1868). They are one of the stars of *Climbing Plants* and they played an interesting, if minor, role in *Cross- and Self-Fertilisation*. Other plants were just as important, but Passiflora provides an unparalleled glimpse of the broad range of his botanical interests.

Yet despite his enthusiasm for his greenhouse and garden, for his passionflowers and orchids, Darwin was every bit as interested in the breeding of human beings. As we have seen, he worried about his own children but he was also concerned about the future of his country and its people. It sometimes seemed that while the vigorous, energetic empire-builders he admired had made Britain rich, they had also made it comfortable – perhaps too comfortable. Would the ease with which he and his countrymen could acquire every necessity of life reduce the impact of natural selection, thus eventually weakening the race and allowing other nations to dominate them?

Darwin had carefully avoided the subject of human evolution in the *Origin*, realizing that he would have more than enough controversy to deal with. But in 1871, when he finally tackled the subject in the *Descent of Man*, he restated his belief in Malthus's pessimistic philosophy, boldly asserting that 'all ought to refrain from marriage who cannot avoid abject poverty for their children'. He noted that 'Man, like every other animal, has no doubt advanced to his present high condition through a struggle for existence consequent on his rapid multiplication; and if he is to advance still higher he must remain subject to a severe struggle'; in other words, if too much were done to help the poor and other 'inferior' members of society, the vital struggle would be mitigated in such a way as to ensure that humanity would 'sink into indolence'. It was vital, in Darwin's view, to ensure that 'the more highly-gifted men' were 'more successful in the battle of life than the less gifted' – and that they passed on their gifts to more children.[55] Darwin echoed the concern of his cousin Francis Galton over the observation that the better-educated and wealthier members of society (who must, Darwin and Galton agreed, be the most talented) were having smaller families, while the feckless poor were out-breeding them. As we will see in the next chapter, Galton had strong opinions as to what should be done about this problem.

In addition to these wider concerns, Darwin was especially worried that cousin marriage, so common among 'superior' families like his own and the Wedgwoods, would further weaken the embattled middle classes. In 1870, he encouraged an attempt by John Lubbock, his neighbour, scientific ally, and local MP, to convince Parliament to include a question on cousin marriage in the 1870 census.[56] Disappointed by the failure of Lubbock's proposal, Darwin wrote in the *Descent*, the following year, that: 'Man scans with scrupulous care the character and pedigree of his horses, cattle, and dogs before he matches them; but when he comes to his own marriage he rarely, or never, takes any such care.' In an ideal world, he thought, 'Both sexes ought to refrain from marriage if in any marked degree inferior in body or mind', but he admitted that 'such hopes are Utopian and will never be even partially realised until the laws of inheritance are thoroughly known'. As a result, 'All do good service who aid towards this end.'[57] However fascinating passionflowers might be, it was the breeding of people that Darwin's contemporaries were most exercised about.