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Chapter 4
Hieracium auricula: What Mendel did next

A tiny seed, weighing only a fraction of a gram, floats in the air. It is suspended from a little parachute of fluffy bristles; the slightest puff of wind will carry it away from its parent plant to find somewhere new to grow. This is the seed of *Hieracium auricula*, commonly known as the pale hawkweed. Like most hawkweeds, *H. auricula* has small flowers, pale yellow in this species, and looks rather like its close relative, the dandelion. Both dandelions and hawkweeds are considered a nuisance by many humans, especially gardeners. They will soon take over a lawn if not dealt with; that tiny parachute, the pappus, is an adaptation that helps the seeds spread. Once they land, they germinate quickly and are soon producing new flowers and seeds, enabling them to spread still further.

Wind-blown seeds are not the only characteristics that make hawkweeds and dandelions efficient weeds. Both have flattened leaves that hug the ground, so that if a passing animal eats the flowers before they can set seed, the plant survives to produce new flowers. Happily for the flowers, these leaves also make them resistant to another major predator: gardeners armed with lawnmowers. When a lawn is mown, the plant's leaves are flattened further but not destroyed; soon, new stalks and flowers will appear. Getting rid of hawkweeds or dandelions requires pulling them up, which reveals another of the plant's survival mechanisms – a long, strong single root, like a miniature carrot, which is called a tap-root. Unless that is pulled up, destroying the flowers and leaves will not get rid of the plant; the root stores enough energy to grow new ones.

Hawkweeds are not just a nuisance to gardeners. Although native to Europe, they have now spread across much of the United States, where they have become invasive weeds. *Hieracium auricula* is known in Montana as meadow hawkweed and is classified by the state government as a 'Category 2' noxious, or harmful, weed; in Oregon, where the same species is usually called yellow hawkweed, it is also a designated weed, and in Washington state it is a 'Class A noxious weed' – the locals hate it so much that it has become known as yellow devil hawkweed. Hawkweeds are also a problem in Canada and in New Zealand, where a closely related species, *Hieracium pilosella*, or mouse-ear hawkweed, has been so successful at invading pasture land that it forms dense mats of leaves which exclude other kinds of vegetation. Mouse-ear hawkweed is edible, at least if you are a sheep (which the majority of New Zealand's mammalian inhabitants are), but it is not as nutritious as the plants it displaces and so is reducing the productivity of the country's pastures.

Obviously, even the lightest wind-blown seeds could not have enabled hawkweeds to get from Europe to New Zealand; it was, of course, the humans who are now struggling to control them who brought the plants to these new territories in the first place.

In Britain, the medicinal properties of hawkweeds were first described in the mid-sixteenth century by William Turner, sometimes referred to as the father of English botany. His *New Herball* became famous because the plant descriptions of his earlier books were complemented by superb woodcut illustrations. Turner informed his readers that 'The nature of Hawke wede is to coule [cool] and partly to binde' (that is, to cure diarrhoea).

Turner's work was copied and improved on by later English herbalists and physicians, such as John Gerard, John Parkinson and Nicholas Culpeper (or Culpepper), over the late sixteenth and seventeenth centuries. Culpeper described hawkweeds in his book *The English Physician* (1652), better known as *Culpeper's Herbal*, which included a detailed list of Britain's native medicinal plants

and the diseases they would cure. Culpeper noted that hawkweeds 'hath many large hairy leaves lying on the ground', which looked like those of a dandelion. He also described how its 'small brownish seeds' were 'blown away with the wind' as the plant 'flowreth & flies away in the Sumer Months'. Drawing on the work of the ancient Greek botanist Dioscorides, Culpeper gave the plant's 'Vertues and Use', which included the fact that the juice, if taken with a little wine, 'helpeth digestion' and thus is good for removing 'crudities abiding in the stomack'. It also 'helpeth the difficulty of making Water'. And when applied to the outside of the body 'it is singular good for all the defects and diseases of the eyes, used with some womens Milke'.[1]

It was their supposed efficacy in treating eye diseases that gave the hawkweeds their name. The Roman historian Pliny the Elder, writing nearly 2,000 years ago, recorded the plant in his *Natural History*, his fabulous compendium of fact, myth, observation and hearsay on every aspect of the natural world. Pliny mentions a kind of lettuce 'with round, short leaves' that was 'called by some *hieracion* (hawkweed), since hawks, by tearing it open and wetting their eyes with the juice, dispel poor vision when they have become conscious of it'. Following the lead of the short-sighted hawks, humans had investigated the plant and found that 'With women's milk it heals all eye-diseases'.[2] Medieval falconers used the plant to treat birds that seemed to be becoming short-sighted.

Culpeper's distinguished predecessor, John Parkinson (who first described the passionflower in English), also produced an immense herbal, which he called the *Theatrum Botanicum* (1640). Among almost 4,000 plants included in its 1,755 folio-sized pages was *Hieracium pilosella*, which he called 'mouse-ear', suggesting that you should give it to your horse before visiting the blacksmith so that it 'shall not be hurt by the smith that shooeth him'. He also observed that shepherds were careful not to let their sheep feed in pastures where the plant was growing 'lest they grow sicke and leane and die quickly after' (which perhaps underlies the New Zealanders' hostility to the plant).

The first European settlers in America brought books on herbal medicine with them or printed their own; one of the first medical books to be produced in America was an edition of *Culpeper's Herbal* (1708). But settlers soon discovered that many European medicinal plants were not to be found in the new world, so they imported the plants' seeds. Concerned, no doubt, for their horses, eyes and digestions, humans brought hawkweeds to the Americas, among dozens of foreign plants also imported for their medicinal uses. (Many more came accidentally after their seeds arrived mixed in with newly disembarked animal's fodder.) Dandelions were spread in the same way as hawkweeds: the scientific name of the common dandelion is *Taraxacum officinale*; 'officinale' comes from the Latin *officina*, meaning a shop, because dandelions were sold for medicinal purposes (many medicinal plant species have this same 'second', or specific, name for this reason). In America, Europe and the countries Europeans colonized, plants were the source of most medicines until well into the nineteenth century; in 1881, the *American Journal of Pharmacy* noted that *Hieracium venosum* (rattlesnake weed) could be used to treat tuberculosis; 'at least', the *Journal* continued, 'it seems to have a well-deserved reputation for that disease among cattle'.[3] Hieracium seeds for medicinal use can still be bought from herbal medicine sites on the internet, although most sites are responsible enough not to ship the seeds to Oregon, which has an anti-hawkweed quarantine.

With human aid, hawkweeds spread around the world, but it was in their native Europe that they first attracted the attention of botanists. As Culpeper had noted, 'there are many kinds of them', thousands of species have been described since his day, and it remains uncertain exactly how many species there are, partly because classifying living things is a complex business. In some cases there are very clear and obvious differences between species: no one could confuse a hawk with a hawkweed, any more than they could confuse one with a handsaw, but distinguishing one kind of hawkweed from another is much harder. Hawkweeds share this property of being hard to classify with plants such as brambles (the genus Rubus) and dandelions (Taraxacum). The fact that

these groups are both difficult to classify and also pernicious weeds is, as we shall see, not a coincidence.

Lumpers and splitters

By the mid-nineteenth century, hawkweeds, brambles and dandelions were at the centre of a botanical war in which 'lumpers' faced off against 'splitters'. These two factions brought two very different philosophies to bear on one of the most contentious scientific subjects of the day, the classification of life. In essence, they disagreed about how many kinds of living things there were in the world, an issue that was fundamental both to important scientific and religious questions.

Beginning with the discovery of America, European knowledge of the incredible diversity of the world's animals and plants had been growing rapidly – and at an increasingly rapid pace. Initially, Europeans tried to fit the plants of the New World into the categories they had inherited from the ancient Greek authorities. For centuries, naturalists had been following in the tradition of authors like Pliny, compiling and writing commentary on ancient wisdom, but from the Renaissance onward Europeans were forced to recognize that there were more plants and animals in the world than even the wisest Greeks had dreamed of. These new plants and animals needed new names and new classifications. Within 100 years of Columbus's arrival in America, the Cambridge Professor of Botany, John Ray, observed that while the ancient Greek botanist Theophrastus had recorded just 500 species of plants, his own *Historia Plantarum Generalis* contained 17,000 species.

It was largely because of this massive expansion of knowledge that – in the century after Ray's book appeared – the Swedish naturalist Linnaeus carried out his massive reform of classification. Part of the trouble was that naturalists, botanists, farmers and florists all gave plants their own local names: *H. auricula* is not merely known as pale hawkweed, yellow hawkweed and yellow devil hawkweed, it is also known as kingdevil hawkweed and as the smooth (or in Connecticut, 'smoothish') hawkweed. And it has other names in Canada and New Zealand, as well as obviously many more in many different languages across the world. Even worse, different species may have the same common name in different countries. This confusion of common names was one of the reasons Linnaeus introduced standardized scientific names: he named the hawkweed genus Hieracium in his *Species Plantarum* ('Species of Plants', 1753) identifying and naming almost thirty different species, from *H. alpinum* to *H. venosum.* Today, the *Index Kewensis*, one of the most authoritative databases of botanical names, lists over 11,000 species of Hieracium. But in the intervening years, names have come and gone.

The almost endless details of the history of biological naming are not important to our story; suffice it to say that the proliferation of names and the renaming of species led to chaos. When naturalists wrote to each other discussing, comparing or exchanging specimens they – quite literally – did not know what they were talking about. One naturalist would decide that a particular plant was so different from those already named that it had to be considered a new species, and so it had to be given its own name. A second botanist would find the differences less significant than the similarities and decide that the plant merely represented a variety, and thus did not deserve a new name. Meanwhile a third might decide that both the similarities and differences were significant, and so classify the plant as a subspecies, which meant adding a third name to go with the other two; as recently as 1999, Linnaeus's original *H. alpinum* gained a new subspecies, *Hieracium alpinum augusti-bayeri,* discovered in northern Romania.[4] And, if that were not sufficient confusion, some twentieth-century botanists have proposed moving many species out of Hieracium into the genus Pilosella.

Back in the nineteenth century, some naturalists decided that this proliferation had gone too far: they accused those who continued to name new species of focusing too narrowly on insignificant differences between plants, of splitting hairs, and thence of being 'splitters'. The outraged splitters fought back, dubbing their opponents 'lumpers', for wanting to lump together

as a single species plants that were obviously not the same. The first recorded use of these terms is in an 1857 letter of Charles Darwin's, where he told his friend Joseph Hooker that 'It is good to have hair-splitters and lumpers.'[5] Hooker would undoubtedly have disagreed, but was too busy to respond immediately: his wife Frances gave birth to their fourth child, Marie Elizabeth, the week Darwin's letter arrived. However, a couple of years earlier, Hooker had published his views on the subject, arguing that it was better to 'keep two or more doubtful species as one', and that by doing so 'we shall avoid the greater evil' – the endless proliferation of species. The 'hair-splitters' who maintained dubious species by preserving their separate names were simply causing chaos; if his readers doubted him, Hooker invited them to 'witness the state of the British Flora with regard to Willows, Brambles, and Roses'.[6] Willows and brambles, like hawkweeds, are notoriously difficult to separate into clearly defined species.

The question of exactly how many species of a particular plant there are might seem trivial, especially when the plant in question is a worthless weed, but to botanists it was an absorbing problem. Classification was much more than a matter of mere list-making: it touched on one of the biggest issues in nineteenth-century science: what were species and where did they come from? Like most of his contemporaries, Linnaeus had been convinced that species 'reckon the origin of their stock in the first instance from the veritable hand of the Almighty Creator', and that God, 'when He created Species, imposed on his creations an eternal law of reproduction and multiplication within the limits of their proper kinds'.[7] Only God could create a species, and once he had done so, it could not change; yet within twenty years of making this unambiguous assertion, Linnaeus was not so sure. His uncertainty was prompted by hybridization. His garden at Uppsala, like other botanic gardens across Europe, contained plants from all over the world. Sometimes pollen from one species landed on plants of another species and – very occasionally – these accidents created new hybrid varieties. These unplanned experiments led curious gardeners to start making deliberate ones, in an effort to produce attractive or productive new varieties. Most of these crosses failed: either the offspring were sterile or the hybrids quickly reverted to the parental type, but now and again a hybrid appeared that seemed to breed true. Confronted with examples in his own garden, Linnaeus had to admit that these stable hybrids 'if not admitted as new species, are at least permanent varieties'.[8]

In 1759, a few years after Linnaeus had made his concession, the Imperial Academy of Science in St Petersburg offered a prize of 50 ducats (well over £5,000 in modern British money) for an essay that would finally settle the old question of whether or not plants really had separate sexes. Linnaeus entered the competition and won it. His essay cited various examples of plants that did not set seed unless both male and female plants were present and argued that hybrid plants were proof of plant sexuality, since the characters of both parents were combined in the hybrid offspring. But Linnaeus clinched his argument by sending with his essay the seeds of a hybrid goatsbeard (Tragopogon), a kind of edible plant, also known as salsify, that is related to hawkweeds and dandelions. Linnaeus had crossed two kinds of goatsbeard in his garden and found that his hybrid form bred true. It therefore counted, in his view, as a new species and he named it *Tragopogon hybridum*.

Linnaeus's prize-winning essay concluded that 'It is impossible to doubt that there are new species produced by hybrid generation' and that where there were 'many species of plants in the same Genus' they 'have arisen by this hybrid generation'.[9] But he was still convinced that God had originally created all living things, so he proposed that an original set of parent plants had been directly created and that the profusion of families, genera, species and varieties were produced by mixing together God's original types. Linnaeus did not believe new types of plants could have arisen in any other way, nor could humans make new species at will; most human-made hybrids would, he argued, prove infertile or revert to their parental types. Nonetheless, he did challenge the long-standing view that *all* hybrids were necessarily sterile.

The apparently natural production of hybrids was what made

groups like hawkweeds so complicated, and which attracted the attention of some botanists. The nightmarish difficulty of classifying them suggested that in these groups of plants, the boundaries between species and varieties were blurred; some took this messiness as evidence for theories of transmutation, or evolution, arguing that plants like hawkweeds were in the process of evolving into new species. Furthermore, studying such groups might produce evidence as to how evolution worked: what was the mechanism that changed one species into another? Others disagreed profoundly, insisting that God had created all species exactly as we see them now, and that species had not – indeed, they could not – change. To suggest otherwise was blasphemous; if humans could not classify hawkweeds, it was because they had not yet understood the perfect plan of God's creation.

As these debates raged, the hawkweed seeds drifted silently on the wind. Some came to rest in a priory garden in the town of Brünn (modern Brno), where they caught the attention of a man called Gregor Mendel.

Mendel was obscure in his lifetime, but today most people are aware that he was a simple, uneducated Austrian monk who, while playing around with pea plants in his garden, discovered the basic laws of modern genetics. Yet his breakthrough was ignored, partly because he was cut off from the scientific world of his day, but also because the one famous scientist he contacted, the botanist Carl von Nägeli, sent Mendel off on a wild goose chase to investigate the genetics of hawkweeds. Nägeli may even have done this deliberately: jealous of his younger rival's brilliance, he set poor, innocent Mendel to work on a famously intractable group of plants, confident that the monk would never be able to sort them out. Frustrated by his failure, Mendel died in heartbroken obscurity. One final ironic twist to the story is added by the fact that Mendel supposedly sent a copy of his paper on peas to Charles Darwin, who never read it. Darwin found German difficult, so Mendel's paper survives alongside Darwin's other papers in Cambridge's University Library, its pages still uncut. If Darwin had only known what it contained, he would doubtless have abandoned his pangenesis theory, adopted Mendel's, and saved the biological world from having to rediscover Mendel in the twentieth century and re-establish the science of genetics.

Unfortunately, almost every word of the previous paragraph is incorrect. Strictly speaking Mendel was not Austrian, he was a German-speaking Moravian; Moravia was then a province of the Austro-Hungarian empire and is now part of the Czech Republic. (Nor was he in fact a monk; the Augustinian order, to which Mendel belonged, are friars.) Far from being a simple, uneducated man, Mendel had studied both biology and mathematical physics at the University of Vienna, where he had been taught by some of the best-known men of science of the day. Nor did he discover anything by accident; he performed carefully planned and well-designed experiments. The scientific society he belonged to had many distinguished members and its journal was widely read, so his work was not entirely ignored – although there are good reasons why it did not make quite the impact he hoped it would. (Nor is it strictly true to say that Mendel's work was 'rediscovered' in the twentieth century, but that is a story for the next chapter.) And Mendel never sent a copy of his paper to Darwin; at least, no such copy exists and there is no record of it ever having existed. But even if he had done, Darwin is unlikely to have found it of much interest, as we shall see. Finally, the story of Nägeli and the hawkweeds is also entirely inaccurate; the actual history helps us to understand what Mendel was doing and why, and – most surprising of all – it shows us why, despite the enormous importance of his work, he neither discovered modern genetics nor invented its basic laws.

In a Moravian monastery garden

Mendel's father, Anton, was a farmer and his mother, Rosine, was a gardener's daughter. He grew up in Moravia's rich farming country, amid vineyards and sheep, with a garden that had beehives tucked in-between the fruit trees. Anton had to spend half his week working for his landlord; the Austro-Hungarian

empire, like much of Europe, was still run on essentially feudal principles. Young Johann Mendel (Gregor was his name in religion, once he became a friar) learned his first lessons about plants and plant-breeding by watching people like his parents, who had been struggling for generations to improve their crops and incomes. But by the time Mendel was born in 1822, the proverbs and folklore that had once guided farming communities were being rapidly displaced by the new scientific methods. Anton worked with the town's parish priest on a project to improve the yield and hardiness of fruit trees by grafting and breeding; together they produced nearly 3,000 trees which were distributed among the local farmers. Mendel's work is perhaps best understood as an attempt to carry on his father's efforts to make their land more fruitful.

As we have seen, humans had been improving crops and animals for thousands of years before Mendel's time. By the eighteenth century, breeders like Robert Bakewell knew how to produce bigger, fatter sheep; his fellow Englishman Thomas Knight applied similar techniques to plants. Knight was the first president of Britain's Horticultural Society and was one of the first to publish information about these new techniques. The first step was establishing which two individual plants had actually been crossed: instead of leaving this vital business to the wind, birds or bees, Knight investigated how to fertilize flowers artificially – pioneering the techniques Darwin would later use on his passion-flowers. Knight's hope was that new kinds of fruit trees could be created by crossing varieties that had desirable characteristics, but trees take so long to mature and bear fruit that it would take several lifetimes to discover if an experiment had worked. So he hit on the idea of first trying out his techniques on rapidly growing annual plants; after much consideration, he chose the common pea (*Pisum sativum*) for his experiments, 'not only because I could obtain many varieties of this plant, of different forms, sizes, and colours', but also because of 'the structure of its blossom', which prevented stray wind-blown pollen from getting into the flowers – much like Darwin's orchids. If a bee failed to visit the pea flower at exactly the right time, the flower's shape ensured that it would be self-fertilized, a fact which, as Knight commented, 'has rendered its varieties remarkably permanent'.[10] By simply netting the plants to keep insects away, Knight could fertilize the plants by hand, and so know which plants had been cross-fertilized by which.

Knight began his pea experiments in 1787 and a dozen years later was able to publish his results in the Royal Society's *Philosophical Transactions*. His paper was translated into German the following year and soon became well known among continental breeders. However, the anonymous German translator of Knight's paper added a footnote, observing that the techniques of artificial fertilization it described were already well known in German-speaking Europe thanks to the work of Joseph Gottlieb Kölreuter.

Kölreuter was the first naturalist to carry out systematic experiments on hybridization, partly – as we shall see – because he was interested in Linnaeus's question as to whether hybridization could create new species. But his plant-breeding research had a more pragmatic purpose; as Kölreuter wrote, he hoped that he 'might one day be lucky enough to produce hybrids of trees, the use of whose timber might have great economic effect', especially if, as he hoped, such hybrids might be faster growing, enabling them to reach maturity 'in half the time' it took their parent species.[11] This was what attracted the interest of people like Moravia's farmers, the promise of new, improved animals and plants, rather than resolving what was or was not a new species. In Moravia, this goal was furthered by Christian Carl André, who came to Brünn at the end of the eighteenth century to promote the natural sciences in the region.

André seems to have had an enthusiasm for founding scientific societies with unfeasibly long names. He began with the 'Moravian Society for the Improvement of Agriculture, Natural Science, and Knowledge of the Country' (which later changed its name, presumably to save time, to the Agricultural Society). He was intrigued by Bakewell's techniques and founded another

society – the 'Association of Friends of, Experts on, and Supporters of Sheep Breeding' – to promote and develop scientific sheep-breeding, a major concern since Brünn was then the centre of the Hapsburg empire's textile industry. And when André heard about Knight's work with fruit trees, his first thought was to found a 'Pomological [fruit-scientific] and Oenological [wine-scientific] Association'. It also eventually changed its name – to the Pomological Association – and among its members was the newly appointed abbot of the Augustinian priory in Brünn, Franz Cyrill Napp, an enlightened man, dedicated to ensuring that the friars should provide both practical and spiritual guidance to the local people. With this in mind, he set up an experimental nursery garden; Mendel was one of the young friars who worked in it.

Despite his humble background, Mendel was well educated: unlike most peasant children, he had attended a *Gymnasium* (secondary school), which had a small natural history museum attached – founded at André's suggestion – that helped foster Mendel's interest in nature study. Unfortunately, while Mendel was still in his teens, his father was injured in an accident that left him unable to work, leaving the family unable to pay young Johann's school fees. From the age of sixteen he had to support himself by tutoring other pupils. He hoped to become a school-teacher, but since his family could not afford to send him to university, he entered the Augustinian priory of St Thomas as a novice in 1843.

Despite it not having been his first choice of career, the priory suited Mendel. Napp encouraged the friars to study science, especially agricultural and horticultural subjects. This was not purely for the benefit of the local people; the priory had considerable debts when Napp took over and he hoped that modernizing its farms and fields would help pay them off – like their neighbours, the friars bred sheep and sold the wool at a profit. As he worked to get the priory's finances back in order, Napp took a close interest in Bakewell and Knight's techniques and encouraged the friars to study them as well.

After a year's probation, Mendel began to study theology. After rising at 6 a.m. and attending Mass, he studied in the priory library, which contained scientific books as well as religious ones, or worked in its garden, learning how to hand-pollinate plants to create improved varieties. Many of his fellow friars shared his interests and he found himself in the midst of a stimulating community, full of lively conversation about science, its uses and its religious implications.

Mendel began to study for the priesthood in 1848, a year when revolutions briefly convulsed much of Europe. The nature of these revolts and the demands they made varied widely, but there were widespread calls for an end to the types of semi-feudal ties that bound people like Mendel's father. Another common claim was for improved education, to allow the newly emancipated peasants to join the modern world. In Brünn, Napp was a prominent supporter of these reforming demands; he demonstrated his solidarity by publicly saying Mass for students who had been killed in the fighting. Although the new Austro-Hungarian emperor, Franz Josef I, quickly emasculated the newly created parliament, effectively ending the revolt, the abolition of feudal labour and the educational reforms survived.

As the revolution fizzled out, Mendel completed his theological studies and became a priest, but his health was often poor and it was clear that he was ill-suited to regular parish duties. With Napp's support, he was appointed to a full-time teaching post at a *Gymnasium*. However, one of the reforms that had been introduced after 1848 was a new education act, which required all teachers to take university exams. Although Mendel was a gifted – and by now, experienced – teacher, he did not have the now vital qualification, so in 1850 the school's headmaster despatched him to the University of Vienna. Mendel failed, partly because his examiner seems to have been prejudiced against members of monastic orders working as teachers, but also because no one had coached him in how to prepare appropriately for university exams.

Fortunately, the educational reforms also had a positive effect on Mendel's life. The Hapsburg government had decided that the

rapidly industrializing country needed new types of schools, technical schools, which would emphasize practical studies such as science, engineering and mathematics in order to equip students for the new world. With Abbot Napp's enthusiastic support, schools of this kind were established in Brünn, which was an increasingly industrialized city, but teachers for these modern subjects were in short supply. Despite his exam failure, Mendel seemed to possess talents his country would need, so one of his examiners in Vienna suggested he be given the opportunity for further study. Napp agreed, and the priory paid for Mendel to return to Vienna to continue his studies.

Back in Vienna, Mendel studied physics with Christian Doppler (after whom the Doppler effect is named, i.e. the way the frequency and wavelength of something like a sound appears to change when its source is moving relative to the listener), who emphasized the importance of designing elegant experiments and taught the most advanced mathematics of the time, statistics and probability. Although physics was Mendel's first love, he also studied chemistry, palaeontology and plant physiology. The latter was taught by Franz Unger, who shared Doppler's interest in experimental design; this emphasis on hands-on practical work was another legacy of the post-1848 educational reforms.

Unger was probably the most influential teacher Mendel had. He introduced his young student to the latest scientific ideas, especially to the then radical new cell theory. Back in 1663, the English natural philosopher Robert Hooke had looked at cork, a tree-bark, through an early microscope. He observed the regular, empty spaces in the cork, which reminded him of the rows of tiny rooms in which monks lived, so he dubbed them 'cells'. The name stuck, but it was only in the mid-nineteenth century, as better microscopes were mass-produced, thus becoming cheaper, that proper investigation of these cells began. By the time Mendel was studying at Vienna, using a microscope was a standard part of his course.

In 1838, two German naturalists, Theodor Schwann and Matthias Schleiden, had discussed cells over coffee. Schleiden described how every single plant cell he examined possessed a dark central core, a nucleus (it was first described and given this name by the English botanist, Robert Brown, after whom Brownian motion is named, i.e. the random movements of particles suspended in a fluid). As he listened, Schwann realized that he had observed something similar in the animal cells that he studied; a year later he published a book – *Mikroskopische Untersuchungen über die Übereinstimmung in der Struktur und dem Wachstum der Tiere und Pflanzen* ('Microscopical Researches on the Similarity in the Structure and Growth of Animals and Plants', 1839) – which became the founding document for an important new biological theory (despite his failure to mention Schleiden's contribution – or anyone else's). Schwann argued that cells are the basic building blocks, the atoms, of all living things – they are not only the simple units from which every physical structure is built, they also form the cogs, gears and engines that make organisms work. Every living process, from digestion and respiration to circulation and reproduction, depends on a precise arrangement of specialized cells. And yet, despite their tight interconnections, cells remain separate entities within the bodies they belong to. The new theory presented a new picture of organisms, as colonies of separate, living machines. Initially, Schleiden and Schwann believed that cells formed like crystals, new ones coalescing within the body as an organism grew. However, experimental work in the 1850s proved them wrong, and gradually most biologists accepted that cells always came about through either the fusion or division of other cells. This became the central dogma of cell theory: every cell comes from another cell. Schleiden was one of Unger's scientific heroes and it was probably his encouragement that led Mendel to acquire a copy of Schleiden's crucial book (*Grundzüge der wissenschaftlichen Botanik*, 'Basic Principles of Scientific Botany', 1842–3), which he read closely.

Cell theory played a vital role in ending the long-running biological debate about what exactly happened during sex. Were male and female influences mixed, or did the action of sperm or pollen on ovum simply stimulate a preformed organism to

develop? A belief in some kind of mixing was becoming increasingly widespread, but its proponents still had to explain how this mixing happened. Plants presented a further complication, which was that the pollen settled on the stigma, some distance from the plant's ova, which developed in the ovary at the base of the carpel. Since there was evidently some kind of male influence, how did it travel down to the ova?

As they tried to understand these questions, many naturalists assumed that male and female influences were contained in two kinds of fluid, which were blended during fertilization. Even plant fertilization, which seemed to be a pretty dry business of dust-like pollen grains settling on a flower, was assumed to involve fluids in some way; Kölreuter, for example, argued that once the pollen was ripe, the grains it contained liquefied and were squirted out on to the flower's stigma. He suggested that the ways in which male and female elements were mixed in their offspring was best understood in chemical terms, just as acids and alkalis combined to form new substances with new properties. If he was right, perhaps the male fluid simply seeped down to the ova.

Gradually new, improved microscopes allowed botanists to peer more closely into the flower's private life. In 1827, the French botanist Adolphe Brongniart observed that grains of pollen grow when they land on the stigma of a flower; they produce a tiny pipe, the pollen tube, which slowly develops until it reaches the plant's ovary. This is how the male influence is transmitted; Brongniart argued that the pollen grain appeared to contain what he called a 'spermatic granule', very similar to an animal's sperm; it was this tiny parcel, not some mysterious fluid, that carried the male's contribution to the new plant. His observations brought botanists into a controversy already well-established among the zoologists: did the sperm actually penetrate the egg, or did it merely stimulate the egg to develop?

This was the question the new cell theorists aimed to settle. Schleiden and Schwann argued that the plant and animal kingdoms were united at their most fundamental level, the cell. Every plant and animal was made of cells, all of which had nuclei, and all new cells were formed from existing cells. In which case, Schleiden argued, the pollen tube could not be transporting 'a pre-existing embryo'; instead, it must carry a single cell which fuses with the female cell to form a new cell – the first cell of a new plant body. Schleiden was convinced that he had driven the last nail into the coffin of preformationism (the idea that the embryo was preformed in either sperm or ova); not everyone agreed, but his theory proved very popular in German-speaking Europe. Unger was one of Schleiden's supporters and argued that it was now clear that both parents contributed to the character of the new plant.

With his head full of these new ideas, Mendel returned to his priory in 1853 and, thanks to his university education, was able to get a decent teaching job. He also began to experiment with plant-breeding, applying what he had learned to the old problems his parents and grandparents had addressed before him: how to produce better crops. Some of his students were also farmers' children, and they later remembered being taken to the priory and shown Mendel's garden. Gardening spilled over into the classroom too, and Mendel would sometimes demonstrate the techniques he used for his experiments, showing the students how to make little paper caps with which to cover the flowers to prevent unwanted pollen entering them. The spectacle of a celibate friar explaining the sex lives of plants inevitably led to occasional schoolboy titters, at which Mendel would exclaim crossly, 'Do not be stupid! These are natural things.'[12]

Mendel's experiments had a distinctly practical purpose; one of his first scientific papers concerned a species of weevil that was devastating pea crops in Brünn. Peas were important: like their peasant neighbours, the friars grew them to sell and to eat. They grew several varieties, some of which were easy to shell, which saved time, but were not as sweet-tasting as other varieties. Some of the sweet varieties, on the other hand, grew on very tall plants, making them harder to pick and vulnerable to storm damage. If only, Mendel thought, one could take the most useful characters of each variety and combine them. The obvious solution was to

cross-breed the sweet – but tall and hard-to-pick – varieties with the bushy, easy-to-pick, short ones, but how could he be sure that the improved varieties would not revert back to one or other of the original forms after a few generations? Mendel knew, both from his parents and his teachers, that this was an old problem, so as he began his experiments, he read what other people – particularly Knight, Kölreuter and Carl Friedrich von Gärtner – had done before him. He had already read some of their work in Vienna and it is clear from his notes in the margins of Gärtner's book, which still survives, that he read them closely and thought carefully about their ideas.

Hybrid species?

As we have already seen, edible peas, *Pisum sativum*, were one of the species that Knight had used in his experiments, which would have been another reason for Mendel to re-read his work. Gärtner also performed some experiments with edible peas. Among their attractions to a researcher was that pea-growers sometimes found several different-coloured peas in the same pod; that made it easy to see at a glance whether you had a pure-breeding strain. However, Gärtner was interested in more than creating sweeter peas; the question of creating stable new varieties of hybrid peas was also a way of investigating Linnaeus's old problem of whether or not hybridization could create new species. As Mendel read and experimented, combining his practical skills with his university education, he too became intrigued by this question.

At the time when the St Petersburg Academy of Science announced its prize competition, Kölreuter was in charge of the Academy's natural history collection. He had hoped to win the prize himself, but missed the deadline and was probably somewhat unhappy about Linnaeus's triumph. He planted Linnaeus's hybrid goatsbeard and found that – contrary to Linnaeus's claims – the seeds did not all come up true. Although he fully accepted Linnaeus's case for the sexuality of plants, Kölreuter refused to accept that hybridization could create new species.

The year after Linnaeus won the Academy's prize, Kölreuter published what would have been his entry, a book describing his many experimental crosses: altogether about 500 different hybridization experiments involving over 100 species. Like Knight, Kölreuter understood that experimenting with trees was impractical, so he had spent many years crossing tobacco plants, (Nicotiana). Kölreuter was sceptical of Linnaeus's claims because in his own experiments he found that hybrids always reverted to the parental form. Especially if the original form was growing nearby; the parental pollen always seemed more potent than the hybrid pollen, so Kölreuter concluded that any hybrids that occurred in the wild could never be stable. Yet, despite his enormous hard work, he never received the recognition he deserved.

Kölreuter's problems were exacerbated by his circumstances. He was not wealthy enough to devote himself to his research full-time; he had to work for a living. His position in St Petersburg lasted only a year before he returned to Germany. Subsequently he moved around, taking whatever short-term positions he could find, until finally becoming Professor of Botany at the University of Karlsruhe. For many years Kölreuter had to perform his experiments on potted plants that he carted around with him on his travels. Even when he was settled in an institutional position, he found that the gardeners were often incompetent or deliberately unhelpful and would forget to water his plants or attend to the experiments in progress.

It would be difficult to find a greater contrast between Kölreuter and Carl Friedrich von Gärtner, who was probably the most famous expert on plant breeding in the German-speaking world during the nineteenth century. While Kölreuter's father had been a humble apothecary, Gärtner's father was Professor of Botany at St Petersburg. Carl planned to follow a medical career and began as an apprentice at the royal pharmacy in Stuttgart, going on to study medicine and chemistry at some of the nineteenth century's leading universities. Having a famous botanist for a father was just one of Gärtner's many advantages over Kölreuter. When his father died, Gärtner became wealthy

enough to devote himself to botany full-time. As a young doctor, he took advantage of his father's money to travel across Europe, meeting its leading naturalists. It was soon after he returned that he first read Kölreuter's book (Gärtner's father, Joseph, had known Kölreuter). Young Carl was fascinated and decided to devote himself to plant hybridization. To assist him with his experiments, Gärtner had a large private garden and a diligent paid staff.

As we have seen, Kölreuter had accepted Linnaeus's proof that plants were indeed sexual beings and he was confident that his own experiments had proved once and for all that in plants, both parents were essential to the production of offspring (even if he was not quite sure how this mixing of parental characteristics was effected). He wrote that 'even the most stubborn of all doubters of the sexuality of plants would be completely convinced' by his work; if they were not, 'it would astonish me as greatly if I heard someone on a clear midday maintain that it was night'.[13] Yet shortly after Kölreuter's death, his work was indeed challenged by August Henschel, a German physician and botanist from Breslau who claimed that Kölreuter's results only reflected his artificial techniques. Like Knight, Kölreuter had relied on tricks such as 'castrating' plants (removing the anthers) and then dusting them with pollen from another species; such unnatural methods were, Henschel argued, bound to produce monstrosities. Henschel even regarded growing plants in pots as problematic: unnatural conditions would produce unnatural results. He argued vehemently that only natural methods could reveal nature's secrets and, as we will see, he was not the last scientist to criticize breeding experiments on these grounds.

The controversy created by Henschel's book was another factor that prompted Gärtner to focus on plant hybridization. In 1830, Gärtner was hard at work with his plants while also trying to complete the massive book on botany that his father had left unfinished when he died. As he worked, the Dutch Academy of Sciences offered a prize to anyone who could answer this question:

What does experience teach regarding the production of new species and varieties, through the artificial fertilisation of flowers of the one with the pollen of the other and what economic and ornamental plants can be produced and multiplied in this way?

It is no coincidence that the Dutch Academy should have been interested in more effective ways of creating new 'economic and ornamental plants'; then, as now, bulb-growing – especially tulips – was a major Dutch industry.

The Dutch Academy was disappointed when no one entered their competition, so they extended the closing date to 1836. Gärtner did not hear of the prize until 1835, but he submitted a hastily written summary of his experiments. The Academy gave him an extension to write them up properly, and in 1837 he was awarded the prize. His book – *Experiments and Observations on Hybridisation in the Plant Kingdom* – was initially published in Dutch, limiting its circulation, but eventually appeared in German in 1849. It contained details of 10,000 experiments on 700 species which revealed 250 hybrids; by far the largest, most comprehensive experimental study of hybridization that anyone had performed. Its sales were disappointing (Gärtner was not a scintillating writer), but Darwin owned a copy and thought it so useful that he wished it were better known. Mendel also owned a copy, which still survives at the Mendel museum in Brno; it is clear from his marginal notes and underlinings that he read it very carefully.

The ultimate conclusion of Gärtner's work was agreement with Kölreuter: Linnaeus had been wrong – hybridization could *not* produce new species. Gärtner's experiments had convinced him that only hybrids between varieties of the same species were fully fertile; any attempt to cross two different species led to sterile offspring, just as horses and donkeys produced mules. Then Mendel's old teacher, Unger, published the results of his own hybridization experiments, which discussed Gärtner and Köelreuter's work in detail. But Unger came to the opposite

conclusion and decided that new species *could* be created by hybridization. He did not suggest that this was the primary means by which new species were created, but he offered it as evidence against those who insisted that species could not evolve; Unger was a transmutationist, a believer in evolution, and his views caused religious controversy. He briefly faced the threat of dismissal for his unorthodox views, so Mendel could not have been unaware of how important – and potentially dangerous – his pea plants could be.

The results of Mendel's pea experiments might seem too familiar to need retelling, but the way they are usually described obscures one important fact: Mendel did not invent modern genetics. To see why, we need to understand what he himself thought he was doing.

By carefully keeping bees away from his plants, Mendel was able to create a series of separate pure-breeding strains. When he published his results, he explained why he had chosen peas: firstly 'interference from foreign pollen cannot easily occur', but just to be sure, 'a number of the potted plants was placed in a greenhouse during the flowering period; they were to serve as controls for the main experiment in the garden against possible disturbance by insects'.[14] In addition, there was 'the ease with which this plant can be cultivated in open ground and in pots'. As Knight had found before him, Mendel thought the pea's 'relatively short growth period' was a 'further advantage worth mentioning'; there was no need to wait years for the result. And finally, although 'artificial fertilization is somewhat cumbersome', in peas 'it nearly always succeeds'. He explained his technique: before the pollen could ripen, 'each stamen is carefully extracted with forceps, after which the stigma can be dusted with foreign pollen'.[15]

Mendel spent two years testing 'a total of 34 more or less distinct varieties of peas', which he acquired from commercial seed dealers; in this, as in other aspects of his experiments, he was more careful than any of his predecessors – Doppler and Unger's lessons on good experimental design had been well learned. Eventually Mendel selected '22 varieties that showed no variation after 2 years of testing'.[16] He separated these into seven pairs of contrasting characters: some varieties always produced yellow peas, others green; some were tall, while others were short. He began with simple crosses, such as yellow with green, but while Kölreuter or Gärtner had made use of only a few plants, Mendel made use of hundreds – he remembered the statistical methods he had learned in Vienna and knew that in order to use them he would need large samples to eliminate 'a mere chance effect'.[17] When the first generation of hybrid peas flowered and bore fruit, Mendel excitedly opened their pods and what he found stunned him: every single pea in every pod was yellow. The green trait had simply disappeared.

As he counted all his yellow peas, Mendel must have wondered where the green had gone: had it gone for good, or would it reappear? For hybridizers, that was the key question. To answer it, he planted his new generation of yellow peas and waited for them to grow. As they came into flower he once again busied himself, removing their anthers and dusting them with each others' pollen, ensuring each plant only received pollen from another of the hybrids. As the pea-pods began to swell and ripen, he must have counted the days till he could open them. When he did, he had a second surprise: the green had come back, but only in some of the plants.

There must have been times when Mendel wondered whether he really needed so many plants – he recorded that his experiments had involved 'more than 10,000 carefully examined plants' – but the need for statistically meaningful results drove him on; as he carefully counted and calculated his results, his decision paid off: he found that one plant in four now produced green peas – the yellow peas occurred in a ratio of 3:1 to the green. The same ratio appeared in the other experiments with each of his seven, carefully chosen, traits.

Mendel then did a third round of experiments: crossing the plants from the second generation with the original pure-breeding strains. This revealed that the yellow peas from the second generation were not all the same: when he crossed them with the

original pure-breeding yellow strain, he still got some green peas, but not as many as in the previous generation of crosses. Clearly, some of the yellow peas from his first cross must have contained the green colour, but in a hidden form. Once again, he counted and calculated and deduced that there were three types of peas; to save time, he used letters to indicate each type: pure-breeding yellow were marked with a capital '*A*', while pure-breeding green were indicated with a small '*a*'. But there was also a green-yellow mixture, which although it came out yellow could still produce green peas in the next generation. Mendel marked these as '*Aa*'. For every pure-breeding *a* or *A*, there were two of the mixed *Aa* type: his 3:1 ratio was really a 1:2:1 ratio – one *a* to two *Aa*, to one *A*. The plants that had only the *a* (green) character produced green peas, while those with only the *A* (yellow) character produced yellow peas, and the mixed (*Aa*) forms also produced yellow peas. Because the yellow colour was able to dominate the green, Mendel christened it the dominant character, while the green was recessive, because it tended to recede or hide itself.

To anyone familiar with modern genetics, these ratios and their associated letters are familiar but slightly wrong: in current notation there are always two letters – *aa*, *Aa* or *AA*. Each letter represents what geneticists now call an 'allele', one of the possible forms that a gene can have. In this case, the gene for pea colour has two forms, the dominant (*A*) and the recessive (*a*). These come in pairs because the plant inherits one from each parent; if both its parents had the dominant form, the plant will be *AA* (and produce yellow peas); if they both had the recessive form, it will be *aa* (and produce green peas). But if one of its parents was pure-breeding green and one was pure-breeding yellow, it would get one of each and be *Aa* or *aA*, both of which produce yellow peas. If you have understood that, you may as well forget it, because that is not what Mendel concluded. If you are confused, that is excellent – because so was Mendel.

The apparently trivial difference between Mendel's notation and modern notation turns out to be both fascinating and revealing because it helps us understand how Mendel thought –

and how different that was from the way we now think. We can have a sense of roughly what it was that Mendel thought was being passed on from generation to generation from the term he used to describe the mysterious entities he had indicated as *a*, *A* or *Aa*; he called them *Anlagen* (singular, *Anlage*).

Anlage is a German word with no precise English equivalent. Mendel borrowed the term from embryology, where it refers to a primordium, the earliest stage of some part of a developing creature. If we translate *Anlage* as 'rudiment' we get some flavour of Mendel's thinking: yellow plants (*A*) passed on the rudiment of yellow colour, the tiniest seed of the peas' eventual yellowness – yellowness is, after all, all they have to pass on. In the same way, green plants (*a*) passed on the rudiment of green. Hybrid plants (*Aa*) looked yellow, because yellow was dominant, 'stronger' than green in some way, but they could pass on either the rudiment of yellow (*A*) or green (*a*) to their offspring. From Mendel's perspective, it would have made no sense to have written *aa* or *AA* for the pure-breeding lines: a pure yellow plant contains only the rudimentary form of yellow; what could be meant by saying it was yellow-yellow? It is obvious from Mendel's writings that he did not know what kind of thing an *Anlage* might be; it was – in some form or another – the quality of yellowness, but he had no idea of precisely what form it took.

Mendel conducted a lengthy series of further experiments, in which he traced two characters at once, then three. Although the maths and the notation became more complicated, the results were essentially the same: in hybrid forms, any one of the available characters could be passed on, at random. That meant that only pure-breeding strains were stable; they contained only one character, which never varied. By contrast, whatever the appearance of hybrids, they contained hidden characters and so reversion could happen at any time. He was thrilled by the ratios he had found, which reminded him forcibly of basic algebraic formulae. It seemed that he had discovered the fundamental mathematical laws that governed hybridization, but he did not think that this initial law was a universal law of heredity; Mendel

was careful to say it only applied to Pisum. Remember that his ratios only applied to the mixed *Aa* forms, the hybrids: they appeared to have no relevance to the majority of pure-breeding strains. Perhaps that is why Mendel's published 1865 paper on peas produced relatively little response. Most of those who read it were plant breeders, interested in the problem of creating new, stable hybrids. To them it seemed that – once you cleared away all the baffling mathematics – all Mendel was telling them was what they already knew: most hybrids revert to their parental type. (And that, incidentally, is almost certainly what Darwin would have thought if he had ever read Mendel's paper.) Some historians have even suggested that Mendel was as disappointed as his readers. He was trying to produce better hybrid varieties, and while the law governing reversion was fascinating, it was not really what he was after.

Hawkweeds are not peas

In an effort to generate interest in his mathematical laws of hybridization, Mendel sent copies of his Pisum paper to various notable men of science. Almost the only one who replied was Carl von Nägeli, Professor of Botany at Munich; while Mendel would undoubtedly have preferred to have had more responses, there was probably no one whose opinion he valued more. Nägeli had worked with Schleiden and done pioneering work on the structure and growth of plants. He was also highly respected by Mendel's teacher, Unger, who had described Nägeli as the man 'who has given us both ground plans and elevations of some plant structures in which each element is marked with the number its architect intended for it'.[18]

In his first letter to Nägeli, Mendel mentioned that he was continuing his hybridization experiments and had selected a few interesting plant groups for further work, including Hieracium. Mendel had already chosen hawkweeds before he made contact with Nägeli, yet the myth persists that Nägeli persuaded Mendel to tackle this obdurate group. This tale is so well known that the American novelist Andrea Barrett included it in a short story called *The Behaviour of the Hawkweeds*, a phrase that is a quotation from the first biography of Mendel (published in 1924), which began a long tradition of blaming Nägeli for wasting Mendel's time.[19]

It is clear from Mendel's first letter to Nägeli that he was already hard at work on hawkweeds. He described how artificial pollination in this genus was 'very difficult and unreliable because of the small size and peculiar structure of the flowers', but adds that 'Last summer I tried to combine *[Hieracium] Pilosella* with *pratense, praealtum,* and *Auricula;* and *H. murorum* with *umbellatum* and *pratense,* and I did obtain viable seeds; however, I fear that in spite of all precautions, self-fertilization did occur.'[20]

Mendel's choice of the intractable hawkweeds was prompted by their reputation as a complex group, hard to classify because they formed hybrids so easily in the wild. During the 1860s, several Brünn naturalists were discussing wild Hieracium hybrids and debating their relationship with the apparent parental species. And the fact that Nägeli was a well-known Hieracium specialist may well have prompted Mendel to write to him.

What interested Mendel about hawkweeds was that they seemed to have a natural ability to create the true-breeding hybrid forms he was interested in: Hieracium 'possesses such an extraordinary profusion of distinct forms that no other genus of plants can compare with it'. As a result, their classification was especially complex: 'The difficulty in the separation and delimitation of these forms has demanded the close attention of the experts.'[21]

In his letters to Nägeli, Mendel discussed each of his Hieracium crosses, describing both his anticipated and actual results; from the way he describes them, it is obvious that Mendel *did not* expect to see the Pisum results repeated; in fact, he would almost certainly have been disappointed if they had been. He argued that the nature of Hieracium hybrids was an important one and, 'we may be led into erroneous conclusions if we take rules deduced from observations of other hybrids to be Laws of hybridisation, and try to apply them to Hieracium without further consideration'.[22] In his private letters to Nägeli, Mendel mentioned that now and again,

one of his Hieracium hybrids would revert to type, but he never mentioned these problems in his public reports to the Brünn Natural History Society, who were kept continually informed of the unvarying nature of the seedlings. Clearly, Mendel saw the occasional variation as the exception to the rule, probably the result of some error on his part and thus not worth reporting. The constant, unvarying hybrid progeny were what he reported.

In one letter, Mendel commented to Nägeli that 'I cannot resist remarking how striking it is that the hybrids of *Hieracium* show a behaviour exactly opposite to those of *Pisum.*' Some historians have interpreted this as an expression of exasperation at the refusal of hawkweeds to behave like peas. In fact, it is clear from the very next sentence of the letter that Mendel was far from exasperated, since he wrote: 'Evidently we are dealing here with an individual phenomena, which are the manifestation of a higher, more fundamental law.'[23] What Mendel was referring to was that when hawkweeds were crossed, the first generation varied but subsequent ones remained constant; whereas in peas, the first generation were all the same, while later ones varied. He told Nägeli how surprised he had been when he crossed the yellow hawkweed (*H. praealtum*) with a golden hawkweed (*H. aurantiacum*); as he had expected, some of the hybrids looked like a mixture of the parental species but others looked much more like the yellow hawkweed in some regards, while looking like hybrids in others. Even more remarkably, when the pale hawkweed (*H. auricula*) was crossed with meadow hawkweed (*H. pratense*), three different types appeared.

Mendel regarded the variability of the first generation Hieracium crosses and the subsequent stability of the new types as two different phenomena but, far from despairing over the unexpected result, he expanded his research to investigate it. When he published his first paper on Hieracium in 1869, he summarized his provisional findings: 'Although I have already undertaken many experiments in fertilisation between species of *Hieracium*, I have succeeded in obtaining only the following 6 hybrids, and only one to three specimens of them.' Nägeli had expected that artificial fertilization would prove completely impossible because the tiny flowers of Hieracium were so hard to work with and they self-fertilized so readily, which made it hard to cross-pollinate them deliberately. Mendel described how he had overcome this difficulty: 'in order to prevent self-fertilisation,' he wrote, 'the anther-tube must be taken out before the flower opens, and for the purpose the bud must be slit up with a fine needle.'[24] He was proud of his skill; it was difficult to produce Hieracium hybrids artificially, but he had shown it could be done. And he had shown both that at least some of these artificial hybrids were fully fertile – and that the hybrid forms were stable, as long as they were self-fertilized. Half Mendel's six hybrids involved the pale hawkweed, *H. auricula*, the most cooperative member of this unruly genus.

Mendel concluded his Hieracium paper by noting that 'the question of the origin of the numerous and constant intermediate forms has recently acquired no small interest since a famous *Hieracium* specialist has, in the spirit of the Darwinian teaching, defended the view that these forms are to be regarded as [arising] from the transmutation of lost or still-existing species'.[25] The 'famous *Hieracium* specialist' was, of course, Nägeli, who had written that 'I see no other possibility that the *Hieracia* types have originated through the transmutation of extinct or still living forms.'[26] Evolution created this confusion, but in most groups the intermediate types had become extinct, leaving a group of species with definite gaps between them, which allowed them to be straightforwardly classified. Nägeli suggested that botanists were observing hawkweeds at a slightly earlier stage in their evolution, when proliferation had begun but extinction had not yet pruned the group into distinct, comprehensible species.

Interestingly, although Mendel described Nägeli's view as being 'in the spirit of the Darwinian teaching', Nägeli was slightly sceptical about Darwin's version of evolution: he accepted that species evolved but disagreed with Darwin that natural selection was the main force driving their evolution. Like several other German biologists, Nägeli thought that living things must possess some inner drive towards perfection that created new species;

natural selection served only to eliminate unsuccessful variations. For Mendel, however, this was a minor distinction: Nägeli was a transmutationist and, despite his respect for the professor, Mendel seems to have rejected evolution altogether. His precise views are hard to ascertain, but it seems likely that he agreed with Linnaeus that hybridization could make new species by combining existing ones, but only God could create the first types of plants which subsequently hybridized to produce the full diversity of species.[27] The hawkweed experiments seem partly to have been intended to show that Nägeli was wrong about the intermediate forms; they were not new species in the process of formation, but simply an unusual kind of hybrid, one that did not revert to type. Investigating this unusual, but potentially very valuable, behaviour was Mendel's other goal – if he could work out the law governing stable hybrids, he might have found something for plant-breeders to get excited about.

In summing up his Hieracium work, Mendel commented that in Pisum the first generation of hybrids all looked the same, but their descendants were 'variable and follow a definite law in their variations'. By contrast, in Hieracium 'the exactly opposite phenomenon seems to be exhibited'; the first generation varied in unexpected ways, but then remained constant. He noted that something similar had been observed among willow trees, the genus Salix. Mendel speculated that the confusing multiplicity of intermediary species in genera like Salix and Hieracium was 'connected with the special conditions of their hybrids', which proved so unexpectedly stable, but he acknowledged that this was 'still an open question, which may well be raised but not as yet answered'.[28] Mendel wrote that in 1869, at a time when he planned to continue his work on Hieracium, but his superiors in the Augustinian order had other ideas. Abbot Napp died in 1868 and Mendel was elected as his replacement. He told Nägeli that he had a few misgivings about taking the position, since it would inevitably eat into his time, but he needed the money to help pay for the education of his two beloved nephews. His doubts were well-founded. The tiny Hieracium flowers needed to be hand-pollinated with a magnifying glass under artificial light, but by 1870, Mendel's eyesight was beginning to fail. Eventually his institutional duties intervened, his garden was neglected, and he wrote to tell Nägeli that, sadly, he had had to give up his experiments.

The hawkweeds set seed and drifted away, looking for someone else to take an interest in them. They had to wait until the twentieth century for humans to unravel Mendel's 'open question', partly because it turned out to be two questions. The first one – how do all the hybrid species of hawkweed survive – was answered in 1903, when it was revealed that not only can hawkweeds manage without sex, they almost invariably do. The ova of hawkweeds can develop into viable seeds without being fertilized – one reason why the hybrid forms that puzzled Nägeli and Mendel remained stable, even in the wild when no one was keeping foreign pollen away. Had he but known it, a major clue to this aspect of the Hieracium mystery lay under Mendel's nose: the bees in his beehives had mastered the same trick. By Mendel's day it was known that the drones, or worker-bees, in a hive developed from unfertilized eggs. This phenomenon is known as parthenogenesis in the animal kingdom and as apomixis in plants. Apomixis is common in hawkweeds, and in their cousins the dandelions (Taraxacum), as well as among brambles (Rubus). It is one of the things that makes these genera such efficient weeds; with most species, if one seed lands on a lawn, it may grow and flower, but since there is only one plant it cannot reproduce. But that single, drifting Hieracium seed has no need of a second plant to fertilize it – once it has germinated, any lawn is under threat.

Understanding apomixis would have solved one of Mendel's puzzles; why the Hieracium hybrids persisted instead of reverting to type. Modern botanists have given up on Linnaeus's puzzle as to whether these persistent intermediate forms are really true species or not, and they hedge their bets by referring to such troublesome cases as 'aggregate species' made up of many 'microspecies'. But the origins of these microspecies, of the

'extraordinary profusion of distinct forms' that first attracted Mendel's attention, has a different explanation, and it took another plant, the evening primrose, to lead us to the answer to Mendel's second question.

Chapter 4: *Hieracium auricula*: What Mendel did next

Mendel published very little, and many of his papers were destroyed after his death; however, his main publications, 'Experiments on Plant Hybrids', 1865, and 'On Hieracium – Hybrids Obtained by Artificial Fertilisation', 1869, are readily available in *The Origin of Genetics: A Mendel Source Book*, (W.H. Freeman, 1966). L.K. Piternick and G. Piternick, 'Gregor Mendel's letters to Carl Nägeli, 1866–1873' (Electronic Scholarly Publishing, 1950, http://www.esp.org/foundations/genetics/classical/holdings/m/gm-let.pdf).

For **Mendel's life and scientific work**, its significance and its consistent misrepresentation by historians, the most important sources are: L.A. Callender, 'Gregor Mendel: An opponent of descent with modification', *History of Science*, 1988: 41–75; and, Robert Olby's work, particularly 'Mendel no Mendelian?' *History of Science*, 1979: 53–72; *Origins of Mendelism* (University of Chicago Press, 1985); and 'Mendel, Mendelism and Genetics' (1997, http://www.mendelweb.org/archive/MWolby.txt). I have also found Vitezslav Orel's work useful, especially *Mendel* (Oxford University Press, 1984); *Gregor Mendel: the first geneticist* (Oxford University Press, 1996); and 'Constant Hybrids in Mendel's Research', *History and Philosophy of the Life Sciences*, 1998: 291–9. Other works on Mendel consulted include: A.F. Corcos and F.V. Monaghan, 'Was Nägeli to Blame for Mendel's Choice to Work with Hawkweeds?', *Michigan Academician*, 1988: 221–33; W. George, 'The Mendel Enigma, the Farmer's Son: the key to Mendel's motivation', *Archives internationales d'histoire des sciences*, 1982: 177–83.

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Notes

1. N. Culpeper, *The English physitian: or an astrologo-physical discourse of the vulgar herbs of this nation* (Peter Cole, 1652): 62.
2. Pliny, *Natural history: in ten volumes with an English translation by H. Rackham* (Heinemann, 1968): 36–9.
3. *American Journal of Pharmacy*, August 1881, Vol 53, #8.
4. P. Mraz, '*Hieracium alpinum* subsp. *augusti-bayeri* Zlatnik in the Muntii Rodnei Mts.: an interesting taxon in the flora of Romania', *Thaiszia*, 1999, 9(1): 27–30.
5. C. Darwin to J. D. Hooker, 1 August [1857]: F. Burkhardt and S. Smith(eds.), *The Correspondence of Charles Darwin (Volume 6: 1856–1857)* (Cambridge University Press, 1990): 438. The *OED* gives this as the first recorded use of the terms, though they were already clearly familiar enough for Hooker and Darwin to use without explanation.
6. J.D. Hooker and T. Thomson, *Introductory essay to the Flora Indica* (W. Pamplin, 1855): 43.
7. Linnaeus, *Critica Botanica* (1737), quoted in L.A. Callender, 'Gregor Mendel: An opponent of descent with modification', *History of Science*, 1988: 41–75: 43.
8. Linnaeus, *Somnus plantarum* (1755), quoted in L.A. Callender, 'Gregor Mendel: An opponent of descent with modification': 43.
9. Linnaeus, *Disquisitio de sexu plantarum* (1757), quoted in L.A. Callender, 'Gregor Mendel: An opponent of descent with modification': 43. The Goatsbeard was a cross between *Tragopogon pratense* and *T. porrifolius*.
10. Quoted in V. Orel, *Gregor Mendel: the first geneticist* (Oxford University Press, 1996): 18.
11. Quoted in ibid.: 17.
12. V. Orel, *Gregor Mendel: the first geneticist*: 78, 82–3.
13. R. Olby, *Origins of Mendelism* (University of Chicago Press, 1985): 16–18, 21.

14. G. Mendel, 'Experiments on Plant Hybrids', in *The Origin of Genetics: A Mendel Source Book* (W.H. Freeman, 1966): 8.
15. ibid.: 4.
16. ibid.
17. V. Orel, *Gregor Mendel: the first geneticist*: 97–9.
18. Quoted in R. Olby, *Origins of Mendelism*: 96. See also: V. Orel, *Mendel* (Oxford University Press, 1984): 39–40; R.C. Olby, 'Carl Wilhelm von Nägeli', in *Dictionary of scientific biography*, Scribner.
19. L.A. Callender, 'Gregor Mendel: An opponent of descent with modification': 67; A.F. Corcos and F.V. Monaghan, 'Was Nägeli to Blame for Mendel's Choice to Work with Hawkweeds?', *Michigan Academician*, 1988: 221–33: 221, 23; Barrett's story is in her collection *Ship Fever and Other Stories* (W.W. Norton, 1996).
20. G. Mendel to C. Nägeli, [31 December 1866]: L.K. Piternick and G. Piternick, 'Gregor Mendel's letters to Carl Nägeli. 1866–1873' (Electronic Scholarly Publishing, 1950, http://www.esp.org/foundations/genetics/classical/holdings/m/gm-let.pdf.
21. G. Mendel, 'On Hieracium-Hybrids Obtained by Artificial Fertilisation', in *The Origin of Genetics: A Mendel Source Book* (W.H. Freeman): 50–51.
22. ibid.: 52.
23. Mendel to Nägeli, [3 July 1870]. Quoted in L.A. Callender, 'Gregor Mendel: An opponent of descent with modification': 43.
24. G. Mendel, 'On Hieracium-Hybrids Obtained by Artificial Fertilisation': 49–50.
25. ibid.: 51.
26. Nägeli, 1866. Quoted in L.A. Callender, 'Gregor Mendel: An opponent of descent with modification': 60.
27. Ascertaining Mendel's view is difficult, not least because so many of his papers were deliberately destroyed after his death, and many Mendel experts would disagree with my characterization of it. However, I'm persuaded by the arguments of L.A. Callender, in 'Gregor Mendel: An opponent of descent with modification'.
28. G. Mendel, 'On Hieracium-Hybrids Obtained by Artificial Fertilisation': 54–5.

Chapter 5: *Oenothera lamarckiana*: Hugo de Vries led up the primrose path

De Vries's own works include: 'The Evidence of Evolution', *Science*, 1904: 395–401; *Intracellular Pangenesis: Including a paper on Fertilization and Hybridization* (The Open Court Publishing Co., 1910); 'On the Origin of Species', *Popular Science Monthly*, 1903: 481–96; 'The Origin of Species by Mutation', *Science*, 1902: 721–9; *Species and varieties: their origin by mutation; lectures delivered at the University of California* (The Open Court Publishing Co., 1905).

Works by **supporters of the Mutation Theory** include: R.R. Gates, *The mutation factor in evolution, with particular reference to Oenothera* (Macmillan, 1915); D.T. MacDougal et al., *Mutations, Variations, and Relationships of the Oenotheras* (Carnegie Institution of Washington, 1907); D.T. MacDougal et al., *Mutants and Hybrids of the Oenotheras* (Carnegie Institution of Washington, 1905); and C.H. Merriam, 'Is Mutation a Factor in the Evolution of the Higher Vertebrates?', *Science*, 1906: 241–57.

For **de Vries's life and work**, my main sources were: P.W. Van der Pas, 'The correspondence of Hugo de Vries and Charles Darwin', *Janus*, 1970: 173–213; E. Zevenhuisen, 'Hugo de Vries: life and work', *Acta botanica neerlandica*, 1998: 409–17; I.H. Stamhuis, 'The reactions on Hugo de Vries's *Intracellular Pangenesis*; the Discussion with August Weismann', *Journal of the History of Biology*, 2003: 119–52.

For the **'rediscovery' of Mendelism**, see the Mendel references in Chapter 4, plus B. Theunissen, 'Closing the Door on Hugo de Vries's Mendelism', *Annals of Science*, 1994: 225–48.

De Vries's **Mutation Theory and its reception** around the world are analysed in: A.H. Sturtevant, *A History of Genetics* (Cold