**Mendel in and after his time.**

**Abstract**

Although Gregor Mendel’s crosses with peas are a recognised foundation stone of genetics, science historians argue that he himself had been looking into issues of hybridisation, and that the genetical implications were incidental. They attribute the main fabric of Mendelian genetics to geneticists who took up the subject after the rediscovery.

This article offers a more pragmatic view, looking into immediate circumstances that could have influenced Mendel’s aims and scientific choices, and assessing connections with the rediscovery. It also draws comparisons with later genetical milestones, in particular the operon.

**Introduction**

Darwin’s 1859 monograph on The Origin of Species and Mendel’s 1866 Experiments in Plant Hybridization are the 19th century’s most influential contributions to biology. Both have attracted a large amount of secondary literature, but, while documentary sources for Darwin include extensive unpublished notes and a voluminous correspondence, as well as published books and articles, those for Mendel consist of 10 letters to Carl Nageli (professor of Botany in Munich University), some family correspondence that doesn’t mention science, and a few published papers. It’s hardly surprising that there are widely differing views on Mendel’s scientific interests and aims.

Most Genetics texts credit Mendel with having founded the science of heredity, and conflate his results and arguments with work done 30 years later, when biologists were better equipped for the Mendelian approach than their mid-19thC forebears. However science historians point out that Mendel’s text has been given meanings that are not in fact there, and press their point by arguing that he had not been studying heredity at all, but hybridisation. 4, 9, 41, 43The Versuche refers to hybrids in its title and throughout the Results and Discussion, while the letters to Nageli deal mainly with hybrids. 36 Furthermore, placing Mendel within the hybridising tradition solves the long-standing problem of why his theory of heredity was overlooked for so long. He had not been dealing with heredity, so there was no gap.

Nevertheless, if geneticists have read too much into Mendel’s paper, historians might have read too little. Mendel himself is curiously absent from their discussions of species, evolution, plant breeding, and other issues at the forefront of the mid-19thC biological scene. The solitary gardener of earlier accounts now comes across as a sort of team member, who applied methods in use at the time and saw the results as contributing to contemporary debates. He is no longer a founder of 20thC genetics but a 19thC forebear.

But Mendel’s immediate circumstances, and his approach to scientific research, must have played a role. This article looks into how these might have influenced his motives and interpretations.

**Hybridization and Botany**
The species hybridising school in Botany, which arose in the 18thC, has a rather low profile, perhaps because ideas about species were, to some extent still are, so vague as to make it hard for hybridizers to decide on precise aims. Previously hybridisation had been confined to the animal kingdom, where the mule was the most obvious example, and the term was also applied to humans with mixed parentage, more commonly known as half-breeds. Since sex in plants was not recognised, at least as far as Western academic circles were concerned, until the German botanist Camerarius offered clear evidence in the late 17thC, plant hybrids were not even suspected.33

The first formal report was in the early 18thC, when the English horticulturist Thomas Fairchild came across a hybrid between a Sweet William(Dianthus barbatus) and a carnation (Dianthus caryophyllus);his finding became known as Fairchild’s mule but seems to have been only regarded as a curiosity. 30 In Sweden Carl Linnaeus compiled evidence for hybrid plants in the wild, and in 1759undertook the first artificial hybridization by crossing pink and yellow-flowered species of goats beard (Trapogon porrifolius x pratensis). The progeny had flowers of an intermediate shade and Linnaeus claimed that hybridizaton could produce a new species. But when Gottlieb Kolreuter undertook an extensive program of crosses he found that many hybrids were infertile, and those that were fertile did not perpetuate a new type, but produced a highly variable second generation; he concluded that hybridization did not lead to new species, though he went on to show that variation could be transferred from one species to another through backcrosses. Kolreuter saw the abundant variation as part of the species essence, and supposed that it blended in crosses. He was followed by Felix Gartner, who undertook an even more extensive program of crosses in which he also noted the association between hybridisation and variation, but he differed from Kolreuter in seeing a role for hybridisation in speciation, and in following individual characters through crosses. He did however remain committed to the indivisible “essence”. 41 Less prolific hybridizers included Ernst Wichura, Henri Lecoq and William Herbert, who also thought in holistic terms. These practitioners of hybridization did not follow identical paths, and had different opinions about what might be going on, however they had one thing in common. They were all committed botanists. Botany did not exist as a profession at the time and those mentioned had taken their university degree in some other subject; Linnaeus, Kolreuter and Gartner in Medicine, Wichura in Law and Herbert in Arts; Lecoq had qualified in Pharmacy. Nevertheless they had all pursued the subject from youth, and maintained a lifelong interest.

Mendel’s father was a tenant farmer who could ill-afford to pay for his son’s education. 45 However the teacher at the village school spotted Mendel’s ability, and means were found to send him to High School. There the science curriculum covered only Physics and Mathematics, so Mendel had no formal introduction to Botany during his early years. But his father grew fruit trees and kept bees on his small holding, and the local parish priest, J. Schreiber, was skilled in the new methods for improving crops, which he passed on to the local peasantry, introducing new varieties and teaching the basics of grafting. The young Mendel was among Schreiber’s pupils. He did not start academic studies in Biology until he joined St Thomas’s Monastery in Brno, where he began teaching himself, not entirely successfully (at least as far as the academic hierarchy was concerned) since he failed the Biology paper in Vienna University’s external degree. The failure was actually rather fortunate as it led to his being sent to the university, where his first formal tuition in biology included Botany lectures from the dynamic and up-to-date Professor Unger. Unger took the line that species undergo change (which almost cost him his post), 18 and we know that Mendel bought Gartner’s book, which detailed more than ten thousand crosses 47, during his time in Vienna. He was finally confronted by the latest ideas about species hybridization. But his arrival at the subject was so different from his predecessors and contemporaries that it is hard to see him as part of the tradition.

Mendel’s university subjects were not, of course, confined to Botany. He also attended lectures in Physics, which he had studied at school and which he taught throughout his teaching career in Brno; he did not see himself as a botanist, but as a Physics teacher. 36Many authors have drawn attention to how Physics must have underpinned his use of mathematics in analysing the pea data, and very likely his experimental approach.

Some of his pupils left an informative snapshot of everyday Mendel, who had been, they said, so fond of numbers that he gave one to every member of the class, according to their position; when he wanted to carry out a test he did a quick calculation, and called out the pupil with the number he had arrived at. 45 This little game suggests someone who had always been in the habit of making counts and playing with numbers. Maybe the teenage Mendel had observed regularities among the plants on his father’s farm, and had counted them. Maybe the numbers had aroused his curiosity.

**Hybridization and Variability**

During most of the 18thC plant hybridization was an academic activity, but in 1799 Thomas Knight reported a cross between peas that produced a distinctive variant, and regretted that: “those who have made the science of botany their study, should have considered the improvement of those vegetables which, in their cultivated state, afford the largest portion of subsistence to mankind and other animals, as little connected with the object of their pursuit.” 31

Plant breeders were not slow to respond, and by the mid-19thC hybridization was yielding a steady stream of new varieties, though, naturally, from crosses that were fertile. Major character changes were regularly utilised, but breeders had no clues as to their origins, which were murky. Rare new variants had long been a problem for biologists faced with the task of reconciling observation with religious views on the fixity of species, and their uncertainties are reflected in terminology introduced in the 18thC, when a stock that produced abnormal or irregular forms was described as ”sporting” , that is, as in sport, therefore not to be taken too seriously; the variants themselves became “sports”.46 By the mid-19thC the idea that variation was not quite kosher had receded, at least as far as most biologists were concerned, but “sporting ” remained in place, now implying a happening outwith understandable biological processes. Explanations of sports mostly invoked environmental causes as set-out by Lamarck, who had summarised a generally accepted view though, contrary to popular opinion, he did not propose a theory for heredity. 8In fact it was not all that long since “heredity” had been applied only to such things as inheritance of property and other material goods; the term was not extended to biology until the late 18thC, when it encompassed a variety of issues. 42

Hybridizations between varieties distinguished by abnormal characters were in striking contrast to crosses between parental plants that had no such differences, and which mostly preserved the status quo, other than minor fluctuations that were hard to distinguish and which some biologists dismissed as not heritable. Variation was essential for studying heredity and hybridization was an obvious tool, which played a role well into the 20thC. In England William Bateson and his followers crossed varieties of garden plants and of poultry breeds.1 In the US a flourishing school of mouse genetics, which would make a major contribution to cancer research, had its beginnings in the fancies that were popular as pets, mouse breeder Abbie Lathrop was such a good source that she became known as the Mother of Mouse Genetics.53Plants, poultry and mice were soon outpaced by the fruit-fly, which did not emerge from a hybridising tradition. But looking for variation among flies incarcerated in milk bottles was an arduous task that kept Thomas Hunt Morgan and his fly group busy for years - fruit-fly “sports” were indeed infrequent.38 It was not until the 1920s that Hermann Muller succeeded in measuring the slow rates of change and “sporting” finally gave way to the much more respectable mutation, and, importantly, amenable to scientific analysis.39 When X-rays were found to increase mutation rates, geneticists no longer had to rely on what turned up.

Mendel did not, needless to say, go into the question of variation, other than dismissing the idea that growth conditions were responsible for cultivated plants having more observable variation than their wild relatives. But the opening paragraph of the section on The Reproductive Cells notes that crosses among normal species yield constant forms, not variants: “constant forms can only be formed when the egg cells and fertilizing pollen are of like character, so that both are provided with the material for providing quite similar individuals, as is the case with normal fertilization of pure species”. Although some historians claim that Mendel was only interested in hybrids this passage does not suggest indifference to constant forms, it simply draws attention to the fact that generations of similar individuals give no information. Experimental research depends on the availability of suitable material. Mendel could have been attracted to hybrids because they were a source of variants.

**Mendel’s Introduction and Discussion**

There is, of course, no doubt that The Versuche’s Introduction and Discussion put hybridization at the paper’s centre. The Introduction states the aim as “to determine the number of different forms under which the offspring of hybrids can appear”, and mentions Koleuter, Lecoq, Wichura and Gartner. The Discussion applies the law of segregation to data from hybridizations. What could be clearer?

But Introductions and Discussions are not a reliable guide to an author’s motives and interests. Introductions are usually written last, and might or might not give an accurate account of the reasons for the experiments. When Morgan published his pivotal paper on Drosophila’s X-linked white-eyed mutation he did not say why he had been looking for mutations.37The search had been a response to Hugo de Vries’s report of frequent major changes in Oenothera, which De Vries called mutations and claimed were evidence for speciation by jumps; 57he didn’t know that Oenothera was in a permanently hybrid state, maintained by a combination of chromosomal structures and lethal mutations, and that the apparently frequent visible mutations were simply being revealed when the system broke down.54Neither De Vries nor Morgan agreed with Darwin’s argument that Natural Selection acts mainly on numerous minor changes, but while the Oenothera changes seemed a promising alternative, more evidence was needed; Morgan thought he would look for some in the animal kingdom and fruit-flies, which produce numerous progeny at fortnightly intervals, looked like a good model system. When a white-eyed mutation eventually appeared in a male fly it was hardly an incipient species change, nevertheless Morgan crossed the fly with a normal red-eyed female and found a sex-related inheritance pattern. He realised that the mutation was on the X chromosome and promptly abandoned speciation in favour of fruit-fly genetics. The introduction to the paper merely refers to a pedigree culture that had been running for nearly a year. When Jacob and Monod published their influential Operon model, half a century later, they did not mention Monod’s earlier studies on growth, which had led him to enzymes, and finally to genes. They certainly didn’t mention that Monod had not been at all interested in genes during that earlier period 24. Mendel’s Introduction should be treated with caution.

The Versuche’s Discussion is more convincing. Here Mendel uses his theory to calculate putative outcomes for variable hybrids, comments on possible examples of constant hybrids, and makes a few cautious remarks that might, or might not, hint at his views on evolution. He has indeed entered into the hybridiser tradition - but did he focus on it as narrowly as many historians believe?

Few analyses of the Discussion take into account the possible influence of the Brno Natural History Society. This had recently split off from the Brno Agricultural Society, which had a strong practical bent whereas the naturalists were interested in pursuing pure science, such as species hybridisation. Mendel first presented his results in the form of two lectures, and although his notes have not survived, several newspapers published reports. Unsurprisingly these give no insights into the scientific issues, nevertheless they offer useful background. Zhang et al recently used them to make a convincing reconstruction of the lectures, and they draw attention to the fact that Mendel opened the second lecture with a short review of plant reproduction in general, which did not mention hybrids.62 We know from the Nageli letters that the response to the lecture was divided, and Zhang et al go on to suggest that when writing the Versuche Mendel restricted his law to hybrids because the audience had expressed doubts about its general application. This is very plausible. And, of course, Gartner’s book was a treasure trove of examples to which Mendel could apply his theory.

**Mendel’s Preparation**

The time that Mendel spent sorting through characters and varieties has aroused few comments, other than noting his unusual care. He must have already given the matter some thought before he purchased likely varieties from seed merchants, then he spent two years making checks. Maybe three years in all, a long preparation by any standards. No new methodology was involved, on the contrary historians point out that Mendel’s procedures came from an established tradition, and that he used established breeds. Indeed, in a recent review Sandor Gliboff provides an extensive list of hybridizers and breeders who were doing similar crosses and reporting on variation among the progeny, and highlights their likely influence on Mendel.19So why did Mendel devote so much time to preparation?

We get a surprising insight from a paper written in 1902, by Raphael Weldon. 59Weldon was interested in continuous variation in natural populations, and his painstaking measurements of shells of the snail Clausilia laminata gave the first demonstration of natural selection in action. 58He also took a keen interest in heredity. He was a follower of Galton’s Theory of Ancestrian Heredity in which, as the name implies, ancestral lineages feature 8, and Weldon took these seriously.

Weldon accepted Mendel’s findings but thought that three generations were insufficient for a complete understanding of heredity. The variation that he was familiar with did not fall into neat Mendelian classes, and he ascribed the confusing real-life picture to influences from remote ancestors, who had no place in Mendel’s theory.

Weldon pointed out that when he looked for green and yellow peas he found 6 colour groups on a continuous scale - he identified no fewer than 50 shades, far in excess of Mendelian pairs. He then looked into the breeding history of several common pea varieties and found that ”the hybrid Telegraph produced seeds of various colours at the time of its origin, and now more than five-and-twenty years after its introduction, it does so still”. He also quoted from a paper that Laxton had published in the same year as the Versuche, which had summarised many years of work: ”... the colour of the immediate offspring or second generation sometimes follows that of the female parent, is sometimes intermediate between that of and the male parent, and is sometimes distinct from both ... in shape the seed frequently has an intermediate character but as often follows that of neither parent. ”In sum, Weldon drew a vivid picture of the chaos outside Mendel’s greenhouse.

The standard story is that Mendel succeeded because he chose well-defined differentiating characters, eschewing the continuous variation that did not lend itself to unpicking basic laws of heredity. However Weldon’s litany of complaints highlights the fact that major characters are not always swell-defined. It looks as though Mendel had had to decide which characters were indeed major, and that meant overlooking all the minor variations that Weldon records so painstakingly. Most of these would eventually be accounted for by invoking modifier genes; and since modifiers vary between lineages they solve Weldon’s concerns about ancestry.

Making decisions on what to focus on, and what to ignore, is central to experimental design, but historians rarely give it much attention. Maybe it is just too difficult to appreciate what unsorted complexity looked like before it was disentangled and a route hacked through. William Bateson had been crossing poultry breeds, and struggling to make sense of how several major characters were inherited, when he heard about Mendel; but he does not mention his failure in a report to the Royal Society, a year after the rediscovery: “ The literature of breeders teems with facts now palpably Mendelian. Gartner, Godron, Laxton, even Darwin himself, must have been many times on the brink of discovery. ... Looking now at such experiments as those of Rimpau with wheat, etc, of Laxton with Pisum, Godron with Daturea, of Darwin with Antirrhinum, and sweet-peas, we can hardly understand how such a conclusion was missed”. 1Bateson had himself been carrying out such crosses, and had forgotten rather quickly that he too must have been on the brink of discovery!

Plant breeders Knight, Goss and Sageret followed clear-cut characters through several generations, and it has often been suggested that they would have arrived at Mendelian laws if they had counted offspring. 33 But they worked before the cell theory and the reproductive cycle were fully established, so even if they had found Mendelian ratios they would not have been in a position to explain them. The reproductive cycle did feature in species hybridizer Naudin’s explanation of segregation, but since Naudin did not invoke intracellular elements, and supposed that several pollen grains were needed for fertilization, he was not well-placed to pursue possibilities. 32And although his publications were widely read no-one seems to have paid much attention to segregation.

In short, 19thC crossing procedures, whether in species hybridisation or in plant breeding, provided Mendel with methods and varieties, but fell far short of his insightful 8-year analysis. Which raises the question of how much methods contribute to scientific breakthroughs. Can traditional methods suffice, or is new technology the key? While both scenarios occur, many biological breakthroughs have emerged from existing methods, applied with greater rigour than the norm and greater awareness of key aims, or adapted to address a completely new aim. For example when Hermann Muller discovered that X-rays cause mutations and damage chromosomes he was following other attempts to exploit radiation, and he made use of fruit-fly mutants that had been in the public domain for some years.40Several decades later the operon model emerged from crosses and enzyme assays that were no different from what many other groups were doing. 24It is odd to find Mendel being put into the hybridising tradition because he used methods from that tradition.

**Mendel’s Explanation to the Brno Natural History Society.**

Since Mendel first presented his results and conclusions in two lectures to the Society, we need to ask who might have been in the audience. Orel’s biography describes the Society’s members as actively pursuing scientific aims, but, like all such societies, they were a mixed bunch. While several professors were at the head of affairs, Orel also mentions a practicing pharmacist and a clerk; the pharmacist would have been qualified in botany, with an emphasis on medicinal uses, the clerk was presumably an amateur. No doubt many members were amateurs, professional botany being still in its infancy. In short, Mendel could not have expected an audience that was up to speed on cells and the reproductive cycle.

J Heimans was one of the first to question Mendel’s ideas about heredity, and was particularly doubtful about whether Mendel had had any concept of ”the gene” .He based his argument on Mendel’s terminology: “Mendel occupied himself only with phenotypic differences, that is, with directly recognisable characters, for which he almost invariably used the term “merkmal” (features). Occasionally he chooses the words factor, character or element, and in one place speaks of “die invere Beachaffarheit der Pollen und Kemzellen” (the internal nature of the pollen and germ cells). There is not a single passage which proves that he regarded characters as individually linked with a separate material carrier.... A careful consideration of these and some other expressions in Mendel’s work confirm us in our conviction that Mendel, although he undoubtedly assumed that each character is transmitted in a distinct and unalterable form, saw the transmission exclusively in its phenotypic aspect, and that the idea that each character must be bound to a separate material character did not enter his mind.” 22 Many historians have taken Heiman’s view. For example Olby draws attention to a passage in which 'traits united through fertilization' instead of ‘elements united.’

But Heimans and Olby have not considered the difficulties of introducing an entirely new concept to an unprepared contemporary audience with diverse backgrounds, never mind the fact that cell interiors were still so vague that separate material carriers could only be speculative. One report on the second lecture describes Prof Niessl coming in at the end with illustrations of fertilization in mosses, algae and ferns. 45 This confirms the suspicion that many of those present would have not have been familiar with microscopy’s latest findings.

Mendel had to present the Pisum crosses through visible characters, because if he had introduced the reproductive cells while explaining the experimental findings, he would have lost his audience. His explanation in terms of cells therefore came after the results, and his cautious suggestion of intracellular material that forms uneasy liaisons came right at the end. That idea would have been entirely new to everyone. It’s hardly surprising that he did not always make a clear distinction between visible characters and hypothetical elements.

Olby has argued that Mendel was mainly interested in applying algebraic series, but this view does not sit well with the circumstances of the Brno lectures. Mendel explained to Nageli that he had given the lectures because data were needed from other species, and he hoped to persuade other members of the Society to obtain them. It is unlikely that he was expecting a mixed group of natural historians to take up algebra.

**Mendel’s working methods.**

Revisionists stress that Mendel does not specify paired elements that might correspond to genes. Nor, when he eventually introduces the intracellular elements in hybrids, does he consider what they might be. His reticence is often seen as something of a failure, and, along with his supposed lack of interest in pure-breeding strains, led Olby to point out that Mendel had not been Mendelian in the 20thC sense. That is not an unreasonable assessment of a scientist working in the mid-19thC.

However when Mendel describes his methods in a letter to Nageli, responding to the latter’s doubts over whether the Discussion goes beyond what could be deduced from observation, an explanation for his non-committal attitude emerges:“...it is shown in an experimental manner, that if 2 or 3 differentiating characters are combined in the hybrid, the developmental series is a combination of two or three simple series. Up to this I don’t believe I can be accused of having left the realm of experimentation. If then I extend the combination of simple series to any number of differences between the two parental plants, I have indeed entered the rational domain. This seems permissible however because I have proved by previous experiments that the development of any two differentiating characters proceeds independently of any other differences”

Mendel worked from evidence. Hybrids yielded evidence for pairs of elements from crosses, constant forms did not. And since the “elements” were out of sight, there was no visual evidence as to what they might be. Olby thought Mendel should have proposed looking inside cells for possible physical manifestations, and saw the omission as supporting his argument for algebraic series being the main focus. It is a lot more likely that Mendel would have known that cytological methods in the mid-19thC could not yield information on countless minute pairs, let alone connect the pairs to characters.

When Mendel introduced the “elements”, proposing that hybrids arise when gametes with different elements fuse, and that when the hybrids self cross gametes with different elements and gametes with identical elements fuse at random, he seems to imply that constant forms have two; and his earlier assumption that similar systems operate in constant and hybrid forms could also be construed in this way. But he does not spell it out, and nor does he discuss separation during reproduction. Historians are right to credit the rediscovery with the standard Mendelian picture of pairs in constant and hybrid forms, which separate and then fuse randomly.

Mendel was hardly unique in failing to arrive at the complete picture from a breakthrough experiment. Again the Operon offers a comparison. When Jacob and Monod were discussing possibilities for a repressor molecule they had recourse toa wealth of information that 19thC scientists could not have dreamed of, nevertheless they had to make a guess, and although they took known facts into account, their guess was wrong. The repressor is a protein but the original paper proposed RNA. Nor did Jacob and Monod pin down the all-important promoter at first, or even second, attempt, and the only hard evidence for unstable messenger RNA, on which the model depended, came from a very recent experiment in a completely different system.

The Operon was proposed at a time when a lot was known about molecules and cells. Mendel faced a very different scene. The 19thC saw the unstoppable rise of molecules, but how these operated within organisms was largely conjectural; and although microscopy was yielding information about cells, there was a long way to go. Schleiden and Schwann are credited with the Cell Theory, which states that cells are a universal component of organisms, however their success story is marred by the supposition that cells emerge de novo during development; Schleiden saw the cell as arising from the omnipresent, and very visible, nucleus, like a crystal growing from a seed; Schwann had a slightly different, but equally erroneous, theory. 20 The theories did not persuade everyone and sceptics included Franz Unger, who taught Mendel, but it was not until the 1850s that cells were generally recognised as permanent structures. In the words of Rudolph Virchow, “every cell is derived from a pre-existing cell”.

Virchow did not go into the mechanics of cell division, cells and their contents were assumed to split in half; when the biological mass became too big. Nuclear division followed suit, and the arrival of chromosomes on the scene did not immediately shift opinion; it was not until the 1880s that mitosis provided a mechanism for ensuring accurate division and accurate distribution of components to daughter nuclei. 8 Mendel was working on his theory when simple splitting was still in vogue. His proposal of elements that form liaisons in hybrid cells, which hold together in the plant body but break down into component parts during reproduction, and segregate with precision, seems rather remarkable when viewed in this context. It is hardly surprising that he did not attempt to extend the idea to all cells.

**Elements and particulate inheritance**

Everyone agrees that particles and particulate inheritance are a cornerstone of Mendelism. Since Mendel didn’t mention them, where did they come from?

Particles were in fact ubiquitous in 19thC theories of heredity, 8so much so that their absence from the Versuche adds weight to the argument that Mendel confined his interest to hybridization. Herbert Spencer is credited with being the first to think in terms of self-reproducing particles, which made their appearance in 1863. He named them physiological units, making it clear that he was considering how organs and tissues might arise from a single fertilised cell, as well as how characters might be transmitted to the next generation. He proposed that the physiological units were identical, but capable of assembling into a wide variety of larger structures that oversaw development of body parts. Assemblies of physiological units look like a sort of premonition of large organic molecules.

Two years later Charles Darwin published his theory of pangenesis, which also depended on self-reproducing particles, in this case called “gemmules”. Gemmules differed from physiological units in not all being identical, each trait having its own group; within a group gemmules could change from being active to latent, and vice versa, according to requirements, Darwin’s idea was that gemmules were shed by body parts and travelled freely round the body, and, in due course, to the reproductive tract. The reproductive tract provided a direct route to the progeny, where the gemmules recreated the body parts.

It wasn’t long before 19thC theories were moving towards systems in which heredity and character development were more independent. Francis Galton had a strong interest in continuity between generations, which was central to his Theory of Ancestrian Heredity, and he proposed material devoted to heredity in this context. He called it “stirp”. He did not take much interest in the physical nature of stirp. He initially presented Ancestrian Heredity in terms of statistics, and although he added particles later he did not go into details.

Carl Nageli set out his theory of heredity towards the end of a long career exploring a wide range of botanical topics. He too recognised hereditary material as an independent entity but, unlike Galton, was explicit about what it might be, and he provided a detailed program of actions. He set aside some protoplasm that he called “idioplasm”, and drew on his own measurements of starch molecules when describing structures within idioplasm; these had a hierarchical organisation, but were so versatile that they could change when need arose, for example, like gemmules they could combine to form bigger units.

August Weissmann made a convincing case for the hereditary material being in the nucleus, and when chromosomes appeared, and were seen undergoing the indirect division that ensures accurate distribution to daughter cells, he devised a chromosomal theory of heredity. The theory did not dispense with particles. Weissmann put them onto the chromosomes and proposed a hierarchy that was reminiscent of idioplasm, and had an equally elaborate set of functions.

19thC hereditary particles took a variety of forms, and occupied a variety of locations, but had one thing in common. They were all created in order to account for the kinds of things that biologists supposed must be going on insideorganisms. While some of the suppositions were surprisingly prescient, and explorations of possibilities raised important issues, the theorists did not have a shred of evidence for particles, let alone for what they might do. It would be decades before methods capable of detecting minute intra-organismal particles were developed.

In 1889 Hugo de Vries became interested in heredity and devised the last of the19thC particle-heavy theories, which he called Intracellular Pangenesis, in honour of Darwin. De Vries was a plant physiologist who saw plant interiors as mosaics of particles engaged in different functions, so the idea of particles being responsible for heredity was attractive. He called his particles pangenes and proposed that, like other hereditary particles, they could reproduce themselves, he assigned different pangenic groups to different traits and, like his predecessors and contemporaries, gave them dual responsibility for developing the plant body and for transmission; in a significant step towards Mendelism he stressed that the groups were inherited independently, rather than being part of an indissoluble whole. Group sizes were not fixed, which allowed the number of pangenes to affect the strength of a character. They could therefore account for some of the natural variation that Weldon drew attention to subsequently.

By 1889 the nucleus was accepted as the likely seat of heredity, and De Vries duly placed pangenes inside it. But cell functions took place in the cytoplasm which meant that pangenes had to move between nucleus and cytoplasm. Pangenes in the nucleus were latent while those in the cytoplasm were active, though cytoplasmic pangenes could relapse into latency when not needed.

Intracellular Pangenesis in its original form was yet another attempt to explain heredity by surmise, but De Vries saw the need for evidence. He had noted the likelihood of characters being inherited independently, and during the following decade he set up numerous crosses, counting progeny and applying Galton’s new statistical methods; the pangenes gradually decreased in number and by 1900 had reduced to Mendelian pairs. De Vries insisted that he arrived at pairs independently, but he had in fact already seen the Versuche 6, 55 so it very likely played a role. It’s often easy for a scientist to overlook input from others.

Regardless of what route De Vries took to Mendel’s theory, he fully appreciated its significance. Carl Correns had also been giving some thought to heredity, and arrived at Mendelism via pea crosses that had originally been aimed at a different problem 10, while the more junior Tschermak followed shortly after with a somewhat shakier understanding, which was also obtained from pea crosses set up for another purpose. De Vries’s first Mendelian publication concentrated on segregation of single characters 56, while Correns, who had emphasised assortment of independent characters, noted the 9:3:3 1 ratio. The two outcomes became the 1st Law of Segregation and the 2nd Law of Assortment. The fact that Mendel did not draw attention to 9:3:3:1 is sometimes cited as evidence that he did not appreciate the full implications of his theory; but since the ratio is only one of a number of possibilities, depending on dominance relationships and gene interaction, it is arguable whether it should in fact occupy such a prominent place in any critique.

De Vries went further than laws, he defined genes as units. And the units were descendants of pangenes, albeit with modifications:“ According to the principles which I have expressed elsewhere (Intracelluläre Pangenesis, 1889), the specific characters of organisms are composed of separate units. One is able to study, experimentally, these units either by the phenomena of variability and mutability or by the production of hybrids. In the latter case one chooses in preference hybrids from parents which are distinguishable from each other by only a single character (the monohybrids) or by a small number of well delimitated characters, and for which one considers only one or two of the units and leaves the others aside.... The totality of these experiments establishes the law of segregation of hybrids and confirms the principles that I have expressed”.

The units became particles, and particles explained Mendel’s theory very nicely. They made it easy to envisage a one to one relationship between genes and characters, and to understand why partners remained separate from each other and from other partnerships. Gametic purity was an obvious outcome and accounted for characters that emerge unchanged after being hidden for generations, finally seeing off the problems inherent to blending inheritance. Particulate inheritance became part of the fabric of Mendelism, despite equivocation from Bateson and outright opposition from Wilhelm Johannssen. When the particles turned out to be embedded in chromosomes they were simply converted into beads on a string.

The wide acceptance of genes as particles disguises the fact that Hugo de Vries did not cite any evidence. There was none. He had of course thought carefully about likely requirements for the hereditary material, and some of his ideas seem to anticipate molecular mechanisms. But a comparison between pangenes and nucleic acids reveals a large and unbridgeable gap.

Particles lent themselves to the idea of the gene as an autonomous unit in charge of its own function. While there was plenty of evidence that gene products interact, the genes of classical genetics were seen as atomistic. When they turned out to be divisible it became possible to make intragenic maps, but while the maps uncovered an internal structure, they offered few clues as to how genes function. Some curious instances of gene expression being affected by chromosome rearrangements raised questions,but were not amenable to detailed analyses. Then in the 1950s microbial genetics and biochemistry formed a highly productive partnership that effectively despatched the particulate gene.

In fact the first hard evidence came from classical crosses in maize, when Barbara McClintock discovered a transposable element that was able to switch on its new neighbour. 34 The evidence was, inevitably, short on molecular detail, and since a transposable element is an intruder it is not an ideal source of information about standard genomes. McClintock herself supposed that she had interrupted normal development, and was never fully reconciled to the fact that she had disturbed a transposon. The caveats do not apply to the Operon model, which emerged some years later. 24

Jacob and Monod worked with E coli, and used the panoply of methods available for microorganisms to identify regulation of enzyme production by a repressor and, crucially, to locate the site at which the repressor acted. It mapped upstream of the coding genes, and Jacob and Monod called it the operator. The Operon model introduced the important concept of two types of gene, structural genes that are concerned with cell functions, regulator genes that determine how and when the structural genes operate, acting as sensors for external influences. But arguably the operator site, where the regulator took action, was the most significant breakthrough.

Jacob and Monod gave a brief summary of its origin in their Discussion: “The operator tends to combine, by virtue of possessing a particular base sequence, specifically and reversibly with a certain (RNA) fraction possessing a complementary sequence. This combination blocks the initiation of cytoplasmic transcription and therefore the formation of the messenger by the structural genes.” The bracket round RNA is because, as noted above ,it was a guess. But a mutation had confirmed the base sequence upstream of the coding region, and the reference to transcription initiation seems to be the first recognition of a promoter.

At first the operator did double duty in interacting with the repressor and initiating transcription, and it was several years before the promoter was recognised as independent entity. It was originally associated with co-regulated gene clusters, however Sydney Brenner pointed out that it could also be a feature of single genes 4, and in due course all transcription initiation was indeed seen to require a promoter site outside the coding region. Somewhat paradoxically, the operator became just one of a number of regulatory devices. The original Operon model is not so much a blueprint for gene regulation, even in bacteria, as a pointer towards the kinds of situations that control function. and they convert genes from independent particles into members of circuits. 2, 16

Mendel cannot be credited with anticipating a future of genetic circuits. Nevertheless it’s worth noting that his non-committal references to elemente, or anlage, do not prejudice ideas of what these undefined entities might be. Had his text been followed maybe the particulate genes of the post-rediscovery scene would have been less self sufficient and deterministic.

**Dominance**

Regardless of whether genes were particles or members of molecular circuits, segregation and assortment were fundamental to genetic analysis. The two Mendelian laws did however undergo modification as new evidence appeared, the most significant being linkage and its use in constructing genetic maps. The fact that none of the modifications altered the fundamental theory is evidenced by molecular explanations for numerous phenomena uncovered by classical genetics.

However there was a 3rd law that added nothing to the picture, and has even been a source of confusion. This is the Law of Dominance, which states that one of the alternative characters must be completely dominant to the other. Mendel merely says that he chose seven traits in which one character was completely dominant to the other. Obligatory dominance came from De Vries.

We don’t have to look far to find that there is nothing obligatory about complete dominance - it is absent from an example of flowering time differences in the Versuche: “As regards flowering time of the hybrids, the experiments are not yet concluded. It can however be already stated that the time stands almost exactly between those of the seed and pollen parents and that the constitution of the hybrids with regard to this character probably follows the rules ascertained in the case of other characters.” Mendel said nothing further, leaving it to Carl Correns to introduce the term intermediate dominance; Correns had crossed red flowered and white flowered Mirabilis Jalapa and recovered a pink-flowered hybrid, that yielded red, pink and white flowered progeny in the Mendelian 1:2:1 ratio. 11 Correns objected strongly to De Vries’s 3rd Law of Dominance 12, but to no avail. De Vries did not retract and the 3rd Law has shown remarkable staying power, continuing to be cited in introductory texts, and debated in histories.

Why did De Vries formulate the Law? Although introductory texts imply that intermediate dominance is some kind of special case it is not in fact uncommon, so De Vries must have encountered it during his hybridisations. And he had. But he turned to the active and latent states in Intracellular Pangenesis for an explanation 51.At first active and latent had seemed equivalent to dominant and recessive, however there was a problem; the former are permanent states, the latter are relative 6.The problem was not solvable. So De Vries decided to invoke pangenesis for variability that did not give the ratios Mendel reported for the Pisum crosses. This included intermediate dominance, and complete dominance became integral to Mendelism. The third law of dominance is a sort of 19thC survivor.

Mendel summarises his theory as transmission through independent, and separable, elements, and does not include dominance and recessiveness. Nevertheless the fact that the seven differentiating characters showed complete dominance suggests that he gave it some sort of role. What might the role have been?

A striking feature of the Versuche is Mendel’s concern with accurate classification. He stresses this when choosing traits, and several times in the Results section. Since complete dominance gives clear cut classes, whereas intermediate dominance lends itself to the “more or less” situations that are harder to assign, he might have had classification in mind when he settled for complete dominance. And complete dominance not only made scoring easier, it also gave fewer classes.

**Pigmentation and the two-gene scenario**

In the Discussion Mendel applies his law to numerous character pairs in hybrids. Since that is as far as he got to considering inheritance in general, there is a good case for supposing that he was only interested in hybrids. But scattered comments in the Versuche and in the letters support a different view.

In the Versuche he describes a cross between Phaseolus multiflorus and Phaseolus nanus, which was so beset by infertility problems that there were only 32 plants in the F2. His conclusions were, naturally, cautious: “ The characters of Ph nanus which had been altogether latent in the hybrid, reappeared in various combinations, their ratio in relation to the dominant plants were very fluctuating... it is nevertheless seen by this experiment that the development of the hybrids, with regard to those characters which concern the form of the plants, follows the same law as in Pisum”.

However, when he examined flower and seed-coat colours the ratios did not merely fluctuate, they disintegrated. The flowers of Ph multiflorus were purple-red and the seeds were dark, while flowers and seeds of Ph nanus were white. The hybrid flowers were red, but too pale for complete dominance, and the Fz shades ranged from deep purple to pale violet, one plant even had completely white flowers. Since Mendel was hoping that Phaseolus would confirm his pea results, this kaleidoscope must have come as a shock; in fact it looks very like the kind of situation that led Weldon to doubt the importance of the results. But Mendel was up to the challenge:

“Even these enigmatical results, however, might probably be explained by the law governing Pisum if we might surmise that the colour of the flowers and seeds is a combination of two or more entirely independent colours, which individually act like any other constant colour in the plant...Should the colour development really happen in this way we could offer an explanation of the case above described in that the white flowers and seed-coat colour only appeared once among 31 plants of the first generation (F2 in our terminology). This colour appears only once in the series and could therefore only be developed once in the average in each 16, and with 3 colour characters only once in the 64 plants.”

This remarkable passage seems to have been somewhat under-appreciated, historians either ignore it, or are more concerned with Mendel’s symbols than with his recognition that a character could be controlled by two or more sets of “elements” - which is, of course, a vital step towards understanding more complex aspects of heredity. Maybe the fact that gene interaction, in various forms, became a regular feature of Mendelism after the re-discovery suggests that it was easy to extend the 2nd law. But the early geneticists were analysing unexpected ratios within an accepted Mendelian framework, whereas Mendel was still constructing the framework, and had to decide whether it was robust enough to accommodate the flower colour results.

Having accounted for the enigmatical results, Mendel went on to suggest how his theory could be exploited: “development of colour in hybrids should be followed up by similar experiments since it might be possible to learn about the significance of the extraordinary variety of colouring of our ornamental flowers”. In a letter to Nageli he says that he himself undertook such a study in Matthiola: “The color experiments with Matthiola have lasted now for 6 years, and will probably still go on for several years. With the data already obtained, I hope finally to get to the bottom of the problem. Lack of a reliable color chart has hindered the experiments greatly. Although I had ordered from Erfurt an assortment of Matthiola annua in 36 named colors, it proved unsuitable for my purposes. I have given my special attention to this experiment, and I shall take the liberty to report on it as soon as the inspection of the 1500 specimens of this year’s culture has been completed”.

Six years of crosses, and 36 named colours, albeit not serving his purpose, mean that Mendel took the analysis seriously, though since he didn’t publish his results we don’t know whether he got to the bottom of the problem. It is not even clear what problem he was trying to solve. He could have been pursuing the idea of several elements contributing to a character. Or he could have been asking whether inheritance shed light on the complexity of pigments contributing to colour. Or both. Whatever his purpose, since colour is not confined to hybrids, and he mentions only Matthiola annua, it looks as though hybridisation was not his sole interest.

Histories of Genetics tend to emphasise the gene 29, 48 . Understandably. The gene hovered, tantalisingly, as a sort of unreachable mirage during the first part of the 20thC, inviting much speculation but nothing concrete. When it became tangible reality it delivered important insights and means for introducing new technology. It’s easy to give it pride of place. Nevertheless, the suggestion that geneticists have been solely preoccupied with the gene throughout the rise of Genetics is not entirely accurate. Mendelian crosses drew attention to the gene but could not deliver it. That only happened when bacteria arrived on the scene, replacing Mendelian laws with ad hoc systems and making it possible to extract and manipulate genes. 25Before bacteria became genetical organisms geneticists had exploited the ability of mutants to unravel complex biological systems, and to distinguish phenomena that outwardly seem very similar.

Mendel’s all-too-brief comments on flower colour suggest that he was aware that crosses could give useful biological information. In 1923 M J Sirks was undertaking an extensive analysis of Phaseolus genetics and pigments, and recognised Mendel’s pioneering work: “Mendel (1865) has already given some notes upon the results of a cross between Ph. vulgaris (Ph. nanus L.) as mother and Ph. multiflorus Willd. as the male plant...Mendel’s rather scarce materials were not sufficient for a more detailed analysis and a more conclusive exposure.”50 Sirks was not interpreting Mendel according to 20thC ideas, but treating him as a forerunner of his own experiments on pigmentation.

Uncertainties in the post-rediscovery era were not confined to genes, they extended to gene products; and since these were essential to an understanding of how genes work, there is the question of what a 19thC biologist could have envisaged happening at the molecular level. Not much. Not only were the particles in 19thC heredity theories imaginary, their activities were imaginary too. So it’s interesting to find Mendel offering an explanation that deals with solid reality, in the form of pigments which he knew could mix to give new colours. To be sure the pigments are far removed from the elements, and the explanation turned out to be wrong. The bluish-red is not put together by separate pigments, the white double mutant is in fact affected in different aspects of a single, but complex, pathway. Nevertheless it is intriguing to find tangible substances appearing in a theory that otherwise seems entirely abstract. And while Mendel was wrong about Phaseolus pigmentation, his theory does apply to fruit-fly eye colour, where a mixture of brown and bright red pigments is responsible for the wild-type dark red.

Somewhat surprisingly, this was first worked out from microscopic studies of pigment granules, not from the extensive fruit-fly genetics. In the 1930s Sewall Wright noted the absence of genetical data for some of the well-known eye colour mutants, and set his students the task of remedying the situation. One group crossed bright-red and brown-eyed flies and the F2 ratio was 9:3:3:1, with the 1/16th double mutants being white-eyed; as Mendel puts it, “once in the average in each sixteen” .61

**Sex Ratios in Lychnis**

Mendel’s penultimate letter to Nageli tells of a unexpected sex ratio in Lychnis. Lychnis (which later became Melandrium and is currently Silene) is dioecious, with an XX/XY system that, in theory, should give a 1:1 sex ratio 7 . In practice there is usually a slight excess of females. However Mendel was surprised by a cross in which female progeny far outnumbered male, and commented as follows: “Finally, let me report on a curiosity in the numerical ratios in which the male and the female plants of the hybrid Lychnis diurna+L. vespertina occur..... Is it chance only that the male plants occur here in the ratio 52: 203 or 1: 4, or has this ratio the same significance as in the first generation of hybrids with varying progeny? I should doubt the latter, because of the strange conclusions which would have to be drawn in this case. On the other hand the problem can not be so easily dismissed if one considers that the anlage for the functional development of either the pistil alone or of the anthers alone, must have been expressed in the organization of the primordial cells from which the plants developed, and that this difference in the primordial cells could possibly be due to the ovules as well as the pollen cells being different as regards the sex anlage. Therefore I do not want to dismiss the matter completely”

The passage is, of course, well known, but has not received a lot of attention, probably because Mendel had not attempted to follow up his idea, or even suggest an experimental approach. Orel’s biography points out that sex determination would not be addressed until the 20thC, and saw the letter only as an example of Mendel’s reasoning. But there seems to be more to it than that. What were the strange conclusions that caused Mendel to be doubtful about the significance of the ratio? Did he have religious qualms? Certainly the Catholic church would not have seen sex as a suitable subject for investigation; but while Mendel was a loyal and conscientious churchman, he had not joined St Thomas’s out of religious conviction. Maybe he was realising that the Pisum laws might not be limited to well-defined characters affecting appearance, but had a much wider application. That could indeed have opened his eyes to possibilities.

Whatever the reason for Mendel’s hesitation, he didn’t let it stand in his way. And when his proposal is read in the context of his time, it is rather remarkable.19thC ideas about how sex might be determined cited the environment as the major influence, so that an 1889 review by Geddes and Thomson could conclude that :“although it must be recognised that a number of factors cooperate in the determination of sex, the most important of these is nutrition, operating upon parent, sex elements, embryo, and in some cases larvae.”17 In 1905 Nettie Stevens and E B Wilson discovered sex chromosomes in Diptera, but in 1895 Wilson had written: "the determination of sex is not by inheritance, but by the combined effect of external conditions". 60

Mendel does not mention the environment, but wonders whether the ratios are comparable to what he had observed in varying progeny of hybrids. And when he thinks the implications through, he arrives at a hypothesis in which male and female plants have a different “anlage” which primordial cells distribute to the gametes, so that pollen and ovules differ as regards sex determination, and he points out that the nature of the parent plant determines the nature of the gametes, which in turn determine the sex of the offspring. This passage is clearly applying conclusions from hybridising peas to a completely different system.

Mendel does not, to be sure, consider how fertilization between male and female gametes could deliver both sexes. Nevertheless he raised the possibility of sex determination having a genetic basis some 30 or so years before it occurred to anyone else, and he was guided by the ratios from the pea crosses.

In 1904 Correns argued that sex might be genetically determined, and tested the idea by crossing dioecious with monoecious Bryonia. His suspicions were confirmed. 47

**Constant Hybrids.**

There is of course no doubt regarding Mendel’s interest in hybridisation, merely doubt regarding the extent to which he should be incorporated into the species hybridising school. But while Mendel’s ratios and clear-cut conclusions do not fit easily with the vague generalities resorted to by hybridisers, his uncertainties about later crosses with Hieracium seem in line with contemporary thinking.

Hieracium was one of Nageli’s main interests and Mendel’s letters to him are mainly concerned with the crosses, which he also reported in a short paper. His aim has long been seen as an attempt to repeat the Pisum results, and indeed he himself seems to suggest that in the first letter; however Peter van Dijk and Noel Ellis have made the interesting suggestion that the letter might be missing a page, and that the missing page gave a different intention.14 They have also pointed out that Mendel described Hieracium hybrids as bastarde, whereas his Pisum hybrids were “hybriden”. Regardless of what Mendel did or did not write to Nageli, Callendar has made a strong case for his having hoped to find constant hybrids, rather than merely a confirmation of the Pisum law. 5Unfortunately Callendar’s careful study is somewhat marred by a conviction that Mendel’s ideas were coloured by a belief in the immutability of species. This conviction seems to be based on an interpretation of a double negative. In the Versuche Mendel refers to Gartner‘s belief that species are fixed within limits, and comments: “ Although this opinion cannot be unconditionally accepted, we find on the other hand a noteworthy confirmation of that supposition regarding variability that has already been expressed”.Callendar sees the passage as saying that “Mendel gave conditional acceptance to the view, expressed by Gartner, that species are fixed within limits beyond which they cannot change”. A double negative does not necessarily mean a positive, and in this case “although” and “on the other hand” are more in keeping with a negative meaning. Maybe Mendel had in mind the Church’s rigid stance on evolution, and opted for an ambiguous statement that could be taken either way.

But Mendel’s interest in constant hybrids is clear enough. In the Versuche he cited reports in the literature, one of which he seems to have got wrong, and he preceded the reproductive scheme for the variable Pisum hybrids with a scheme for constant hybrids. At first sight that scheme has the 19thC flavour that revisionists argue for: “ If it chance that an egg cell unites with a dissimilar pollen grain we must then assume that between those elements of both cells, which determine opposite characters, some sort of compromise is effected. If the compromise is taken to be a complete one, in the sense, namely, that the hybrid embryo is formed from two similar cells in which the differences are entirely and permanently accommodated together, the further result follows that the hybrids , like any other stable species, reproduce themselves truly in their offspring. The reproductive cells which are formed in their seed vessels and anthers are of one kind, and agree with the fundamental compound cell (fertilised ovum).”

The passage reads as though Mendelwas not thinking of elements in hybrids as always in pairs, and always separating during reproduction. It is in fact hard to reconcile with the 20thC picture of mutations on chromosomes that must be similar enough to line-up during the reproductive cycle, so that they can separate in an orderly manner ,rather it seems to support Olby’s non-Mendelian argument. Mendel did not elaborate on possibilities, and when hybridisations did not lend themselves to a simple explanation, he suggested that an overall system was yet to be uncovered. In the case of Hieracium the unknown system would turn out to be facultative apomixis. 15 During the 20thC systems that could keep hybrid variants together during crosses emerged under the auspices of polyploidy.

In the 1920s Georgii Karpechenko crossed Brassica (cabbage) and Raphanus (radish) and produced the hybrid Raphanobrassica, which was mostly sterile. But its few offspring were fertile, and future generations were pure-breedng. The mostly sterile hybrid’s gametes had been diploid, and these had fused to give tetraploids in which chromosomes could pair with their usual partners. The outcome was that germ cells carried a full set of genes from both Brassica and Raphanus Karpechenko described the constant hybrid as a new species. 28

Since Mendel had no conception of ploidy and its different states, this turn of events was far beyond anything he could have imagined. Nevertheless it is intriguing that his reproductive scheme for constant hybrids fits rather nicely -the Raphanobrassica differences are indeed permanently accommodated together, as he proposed. It’s notable that Mendel, unlike most of his contemporaries, did not go into details as to how his scheme might work. His focus on bare essentials is why it fits. He was a master at honing in on essentials.

Constant hybrids were reviewed some years ago by William Stansfield, who was surprisingly dismissive of apomicts and allopolyploids, concluding that their influence is so limited as to make a search for constant hybrids largely futile 52.However molecular data are uncovering evidence of past hybridizations and chromosome doublings that had previously been unsuspected, which suggests that while events leading to constant hybrids might be infrequent, they have arisen often enough to have had a significant role on an evolutionary time scale. Maybe Mendel’s search for constant hybrids, alongside the variable type that he had analysed so effectively, was not entirely futile.

**Afterword**

Darwin did not read the Versuche, and there has been much speculation as to whether he would have seen that it provided a solution to the problem of inheritance, which he himself had more or less abandoned. Ratios and algebraic series are so different from pangenesis that it’s hard to envisage him responding positively, however a letter he wrote to the Gardiner’s Chronicle opens a different viewpoint: “ I hope that some of your readers will respond to Mr. Westwood’s wish, and give any information which they may possess on the permanence of cross-bred plants and animals. Will Mr. Westwood be so good as to give a reference to any account of the variability of the Swedish Turnip? I did not even know that it was reputed to be a cross-bred production. I am aware that this is supposed to be the case with some Turnips; but I have searched in vain for any authentic history of their origin. No one, I believe, doubts that cross-bred productions tend to revert in various degrees to either parent for many generations; some say for a dozen, others for a score or even more generations. But cannot breeders adduce some cases of crossed breeds of sheep and pigs (such as the Shropshire or Oxford sheep, or Lord Harborough’s pigs) which are now true? With respect to the Cottagers’ Kale, I was so much surprised at the accounts of its trueness that I procured seed from the raisers; but in my soil the plants were far from presenting a uniform appearance.”13

If Darwin had come across Mendel’s ideas on constant hybrids, his interest might indeed have been aroused!

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