PART II

Model Organisms

STUDIES IN THE HISTORY OF HEREDITY AND REPRODUCTION

This section assembles four case studies spanning the time from the end of the nineteenth century to the end of the Second World War. They reach from the establishment of classical genetics to the dawn of molecular biology in Germany. The scientists involved, from Carl Correns and Max Hartmann, to Alfred Kühn, and to Georg Melchers and his colleagues, were all housed at one time or another at the Kaiser Wilhelm Institute for Biology in Berlin-Dahlem, founded in 1911. This institute was one of the few and prominent places in which genetics took shape in the early decades of the twentieth century in Germany.

The four case studies describe four experimental systems, each with a different model organism. In the case of Carl Correns, it was a hybridization system based on the garden pea *Pisum sativum*; in the case of Max Hartmann, a cellular propagation system based on the unicellular green alga *Eudorina elegans*; the flour moth *Ephestia kühniella* served as the experimental model for Alfred Kühn and his group as they developed a system for studying gene actions, in particular in eye pigment formation; Georg Melchers and the virus group concentrated their efforts on tobacco mosaic virus. Each group used its model organisms in different ways, testifying to the role their experimental systems played in generating unprecedented knowledge. But the focus of each group was also different. The case study on Correns examines the micro-dynamics of a particular experimental reorientation. The case study on Hartmann looks at the experimental narrowing of a biological function. The chapter on Kühn focuses on the productive interaction of model organism and experimental system. And the study on the Dahlem virus group fore-grounds the institutional dynamics of research. Together with my case study on the history of protein synthesis research in the test tube after the Second World War (Rheinberger 1997), the studies of this volume amply demonstrate the role of experimental systems as historical actors for the life sciences in the first half of the past century.

4. Pisum

Carl Correns's Experiments on Xenia, 1896–99

Classical genetics as a discipline was born around the turn of the twentieth century. The standard history of genetics has long included the particular circumstances of its birth. Yet despite considerable historiographical effort the question why Gregor Mendel's experiments took more than thirty years to find a wide audience remains unanswered.[1] It is still debated how the so-called "rediscovery" of Mendel's laws came about around 1900.[2] As is well known, the conventions of scientific writing in general and priority disputes in particular can obscure the way certain findings were historically obtained and certain conclusions were historically drawn. In Mendel's case, his "rediscovery" occurred at least three times, making far more complicated the usual story of belated scientific recognition.[3] In what follows, I reconstruct the story by referring to Carl Correns's unpublished research notes on his hybridization experiments with *Pisum sativum* and *Zea mays*. The resulting picture is of a scientist who initially seeks to solve a particular problem, finds himself struggling with his experimental material, and finally arrives in the course of his experiments at an epistemic regimen in which previously incidental observations and considerations suddenly acquire new significance. The whole account is a textbook example of the impossibility of rationally reconstructing the birth of a science, since neither its origins nor its critical turning points, the hallmarks of scientific success, are easy to discern. The magnifying glass of Correns's research protocols sharpens our view of the hesitations and delays constitutive of empirical scientific work. His research notes also give us an idea of the intricacies and material peculiarities of his hybridization experiments and their effect on his conclusions.

This case study is based on protocols housed in Berlin-Dahlem,[4] which means that they must have accompanied Correns on his itinerary from Tübingen by way of Leipzig and Münster to Berlin, where they survived the Second World War. This was lucky, since as Correns's biographer Emmy Stein informs us most of Correns's archive was destroyed early in 1945.[5] What remains are primarily observations and lists of findings noted on loose sheets roughly arranged according to experimental object and order of experiment. Unfortunately, Correns did not date all of his notes and Stein, who worked on the archive during the last years of the war, did not always keep the files in the original condition.

With Hugo de Vries[6] and Erich von Tschermak-Seysenegg,[7] Carl Correns is one of the three botanists credited with the rediscovery of Mendel's laws. Robert Olby remarks that of the so-called three rediscoverers and the several other plant breeders who published Mendelian ratios in and around 1900, "Correns showed the deepest understanding," and assumes that he arrived at the "correct explanation" without knowing about Mendel's paper.[8] But the story is more complicated.[9] In the following pages, I retrace Correns's path to the segregation law. His first publication on peas (1900) offers this formulation of it: "The hybrid produces sexual nuclei that bring together the dispositions [*die Anlagen*] of the parents in all possible combinations, with the exception of those of the same character pair. Every combination occurs with roughly the same frequency."[10]

A Short Biographical Note

Carl Erich Correns (1864–1933) was born in Munich, where he studied with Carl Wilhelm von Nägeli toward the end of the latter's life. He completed his dissertation, entitled "Über Dickenwachstum durch Intussusception bei einigen Algenmembranen" (On Thickening by Intussusception in the Membranes of Several Algae) in 1889, two years before Nägeli died.[11] From 1889 to 1892, he worked as an assistant to Gottlieb Haberlandt in Graz, Simon Schwendener in Berlin, and Wilhelm Pfeffer in Leipzig. He obtained his *Venia legendi* (authorization to teach) at the University of Tübingen in 1892, when Hermann Vöchting granted him his habilitation for the work "Über die Abhängigkeit der Reizerscheinungen höherer Pflanzen von der Gegenwart freien Sauerstoffs" (On the Dependence of Excitation Phenomena in Higher Plants on the Presence of Free Oxygen).[12] Correns spent the next ten years in Tübingen, where he performed his first hybridization experiments (with peas and corn, among other plants) in the small botanical garden of that South German university town. He also cultivated experimental plants on the truck farms of commercial gardeners in the Tübingen area.[13] He continued to carry out extensive breeding experiments to the end of his career, which led him to Leipzig as an associate professor in 1902 and to Münster seven years later as a full professor and director of the botanical garden. In 1913, he was appointed director of the newly founded Kaiser Wilhelm Institute (KWI) for Biology in Berlin-Dahlem, where he pursued his research until his death in 1933.

The Early Tübingen Years

Correns investigated *Pisum* in his years as a *Privatdozent* (untenured lecturer) in Tübingen (1892–1902). A glance at his extant notes of the 1890s shows that he cultivated a wide range of interests in this period. He pursued his work on the morphology and growth of the cell membrane, subjects already taken up in his doctoral dissertation;[14] explored, in the wake of his *Habilitationsarbeit*, the physiology of movement in plants, especially the physiology of tendrils;[15] carried out extensive research on the vegetative reproduction of mosses, publishing the results in a book in 1899;[16] undertook a systematic study of algae and cyanobacteria (the *Oscillatoria*);[17] and collected and published his findings about alpine flora.[18]

Correns's academic training had been centered on physiology, morphology, and systematics. He started to do breeding experiments only around 1894. In a short, undated autobiographical sketch, he says: "In my ten years as a *Privatdozent* in Tübingen, my works and publications tended to follow beaten paths. . . . However, as soon as I obtained the habilitation and gained access to a botanical garden, I started to conduct, in addition, a wide diversity of experiments that we would today call 'genetic,' experiments that I had long had in view."[19] At first, Correns's crossing experiments seem to have had no real impact on his research questions, which were still physiologically oriented: these experiments were in any case limited in scope and rather unsystematic. They were manifestly carried out as assays designed to elucidate problems of developmental physiology, such as the formation of adventitious embryos in *Hosta* (Funkia), a problem Correns vainly tried to solve through hybridization. In his autobiographical sketch, he himself characterizes his early breeding experiments as "*fooling around*."[20] However, as we shall see, they moved ever closer to the center of his concerns as the years went by. Yet it was not until he had finished his book on the vegetative reproduction of mosses in fall 1899—a book with no direct bearing on questions of heredity—that problems of breeding assumed a commanding position in Correns's work, occupying him for the rest of his scientific life.[21]

Xenia

Correns's interest in maize was aroused when he looked into Darwin's observations on xenia. Xenia are characters of a pollen-giving plant that appear directly on the mother plant, especially its seeds and fruits, and not just in individuals of the next generation. When Correns began his investigation of xenia in 1894, there was no valid explanation for the phenomenon. By the time he completed it six years later, Sergej Navashin in Kiev and Léon Guignard in Paris had discovered and published the basic explanation for it: a consequence of double fertilization in angiosperms, leading to the embryo on the one hand and the endosperm, the early nourishing tissue of the embryo, on the other.[22] Correns carried out his first crosses with *Zea mays* in 1894, and maize remained his most important experimental object for studying xenia. But he also combed the literature on other plants for references to xenia. Over the next few years, he added *Lilium, Matthiola*, and *Pisum* to the list of his experimental plants.

In a folder containing Correns's notes taken between 1896 and 1900, there is a page dated "15/IV," entitled "Gaertner's experiments with *Pisum*."[23] The reference is to Carl Friedrich Gärtner's *Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich* (Experiments and Observations on the Creation of Hybrids in the Plant Kingdom).[24] There is every reason to suppose that this page of notes dates from the early period when Correns had just started experimenting with peas—it was probably written in 1896—since the remarks in which he summarizes his observations indicate that he was working on the question of xenia in peas at the time of writing: "Thus—as G. himself also emphasizes, a very striking influence on the fertilized seed (not the fertilized fruit!). Very striking that *all* the seeds in the same pod, or perhaps even all the pods of a single cross (c. 5) usually attested this influence! Does the coloration of the seed depend on that of the cotyledons? This would make it possible to explain the result, understood as an *intermediary formation*!"[25] Another undated note on *Pisum* summarizes a paper of Wilhelm Rimpau's, singling out Rimpau's observations of "reversions": "Rimpau easily achieved several crosses, all showed a great inclination to reversions, several not constant even after 6 years."[26]

The biggest surprise in this folder is a note titled "Mendel (66)" dated "16. IV. 96" (fig. 1).[27] The note is transcribed in Table 1, below. We must conclude that Correns read Mendel's paper in April 1896, his later recollections notwithstanding. In the autobiographical sketch already mentioned, he says:

> It was in a sleepless November night, near daybreak, that I suddenly hit upon the explanation for the observations of *Pisum* and *Zea*. But it was only when I sat down to prepare the publication that I systematically reviewed the literature. It was then that I realized, thanks to Focke's Pflanzenmischlinge [1881], that Mendel had already discovered and published all this thirty-five years earlier. . . . If I had found the explanation earlier, I would

Table 1

16. IV. 96

Mendel (66) distinguishes:
dominant and recessive characters. For our

cases is	dominant:	recessive:
—form of seed	round	angular
—seed coat: ("albumen")	grey to brown	*white*.
—cotyledons:	yellow	pale yellow, *green*
—pod:	smoothly rounded	wrinkled
— :	green (unripe)	yellow (unripe)

The dominant and recessive characters are expressed from the first generation on in such a way that the former are present in 3 individuals, the latter in 1.

| The hybrid form of seed shape and cotyledons develops immediately, directly through fertilization |

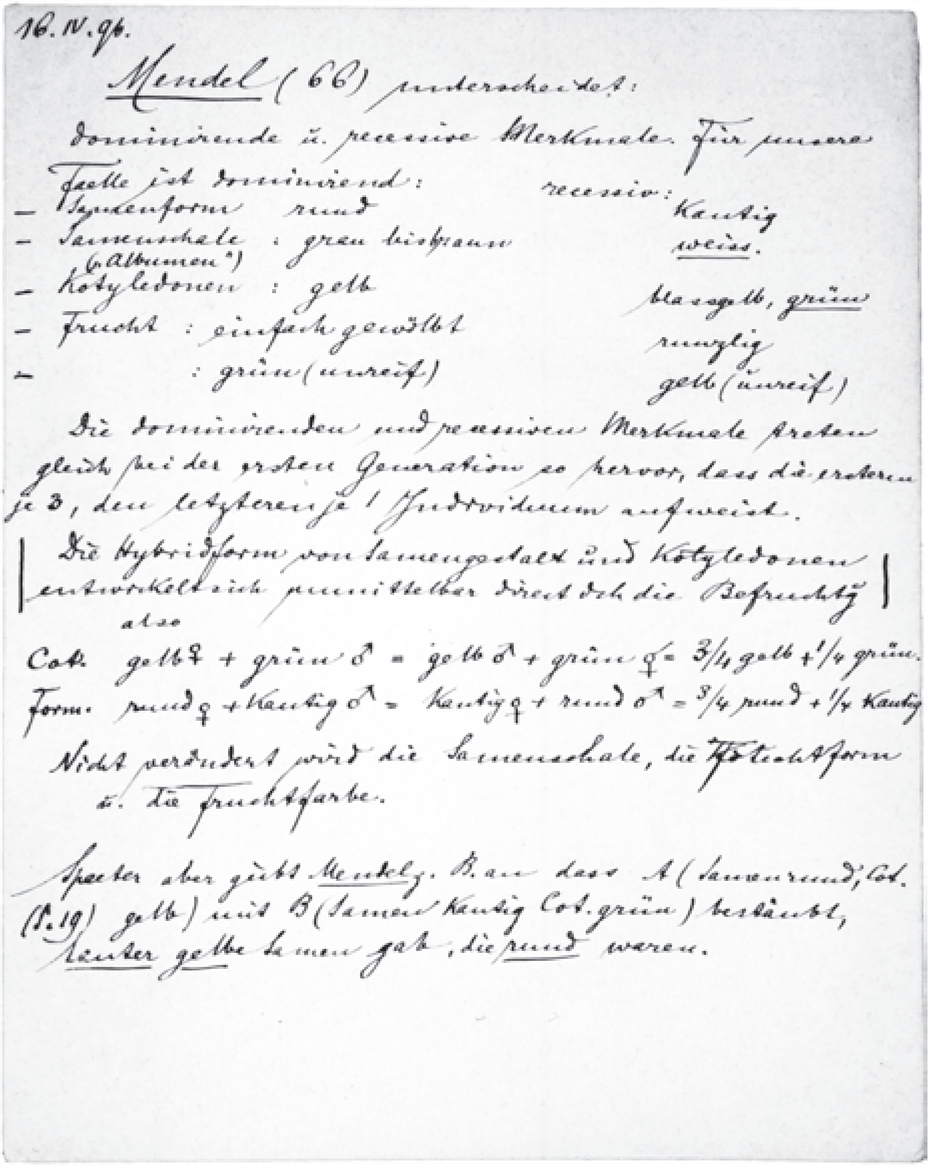
thus
Cot. yellow ♀ + green ♂ = yellow ♂ + green ♀ = ¾ yellow + ¼ green
Form. round ♀ + angular ♂ = angular ♀ + round ♂ = ¾ round + ¼ angular

The seed coat, the form of the pod, and the color of the pod do not *change*.

Later, however, *Mendel* says, e.g., that A (seed round, cot. (p. 19) yellow) pollinated with B (seed angular cot. green) yielded *nothing but yellow* seeds that were *round*.

have published it in a preliminary note, although I was at work on my book on mosses. For the significance of the results was pretty much clear to me from the first.[28]

Correns gives a similar version of events in a letter he wrote on January 23, 1925, in response to a query from Herbert F. Roberts. The indignant undertone is unmistakable: "The date of the day upon which, in the autumn (October) of 1899, I found the explanation, I no longer know; I do not make note of such matters. I only know that it came to me at once 'like a flash,' as I lay toward morning awake in bed, and let the results again run



16. IV. 96.

Mendel (66) unterscheidet:

dominirende u. recessive Merkmale. Für unsere Fälle ist dominirend: recessiv:

– Samenform rund kantig
– Samenschale (Albumen?) : grau bis braun weiss.
– Kotyledonen : gelb blassgelb, grün
– Frucht : einfach gewölbt runzlig
– : grün (unreif) gelb (unreif)

Die dominirenden und recessiven Merkmale treten gleich bei der ersten Generation so hervor, dass die ersteren je 3, den letzteren je 1 Individuum aufweist.

Die Hybridform von Samengestalt und Kotyledonen entwickelt sich unmittelbar direct durch die Befruchtg also

Cot. gelb♀ + grün ♂ = gelb ♂ + grün ♀ = 3/4 gelb + 1/4 grün.

Form. rund ♀ + kantig ♂ = kantig ♀ + rund ♂ = 3/4 rund + 1/4 kantig

Nicht verändert wird die Samenschale, die Fruchtform u. die Fruchtfarbe.

Später aber giebt Mendel z. B. an dass A (Samen rund; Cot. gelb) mit B (Samen kantig Cot. grün) bestäubt, (S. 19) lauter gelbe Samen gab, die rund waren.

1. Correns's excerpt from Mendel's paper. MPG Archive, Section 3, Folder 17, No. 115, File "Pisum-Kreuzungen 1896–1900."

through my head. Even as little do I know now the date upon which I read Mendel's memoir for the first time; it was at all events a few weeks later."[29]

This version of events has gone virtually unchallenged since. In recent years, to the best of my knowledge, only Onno Meijer has aired the suspicion "that Correns read Mendel's paper before that inspired night, that he did not realize Mendel's importance on his first reading of it, and that the paper may have made its way through his unconscious, only to re-emerge 'in a flash' later."[30] Let us see what the research protocols can tell us about this.

To begin with, we should take a more careful look at the excerpts Correns made from Mendel's paper the first time he read it. It is certain that he did not rely on the account of the paper contained in Wilhelm Olbers Focke's book on *Pflanzen-Mischlinge* (plant hybrids),[31] since he refers in his notes to the pagination of the original publication. There are indications that the offprint which Mendel had sent a correspondent of his in Munich, von Nägeli, who later became Correns's teacher and mentor, was in Correns's possession; it is probably the copy held in the offprint collection of the Kaiser Wilhelm Institute for Biology.[32] Correns's papers in Dahlem in addition contain various notes and drawings by von Nägeli.

Closer examination of the excerpt reveals that while Correns took note of Mendel's offspring ratio of 3:1 with respect to dominant and recessive characters, something else seems to have captured his immediate attention: all those seed characters that might have something to do with the xenia phenomenon he was then studying in maize. This is suggested by the fact that he framed the following sentence with little vertical lines: "the hybrid form of seed shape and cotyledons develops immediately, directly through fertilization." Correns doubtless considered this an observation relevant to the xenia problem.

It should also be mentioned that Correns was in all probability misled by Mendel's terminology. Mendel calls the second generation of crosses the "first generation of hybrids." Correns's summary reads: "The dominant and recessive characters are expressed from the first generation on in such a way that the former are present in 3 individuals, the latter in 1." At the end of his notes, however, he points—erroneously—to a "contradiction" in Mendel: "Later, however, *Mendel* says, e.g., that A (seed round, cot. (p. 19) yellow) pollinated with B (seed angular cot. green) yielded *nothing but yellow* seeds that were *round*." We can take this as evidence of a quite cursory reading.

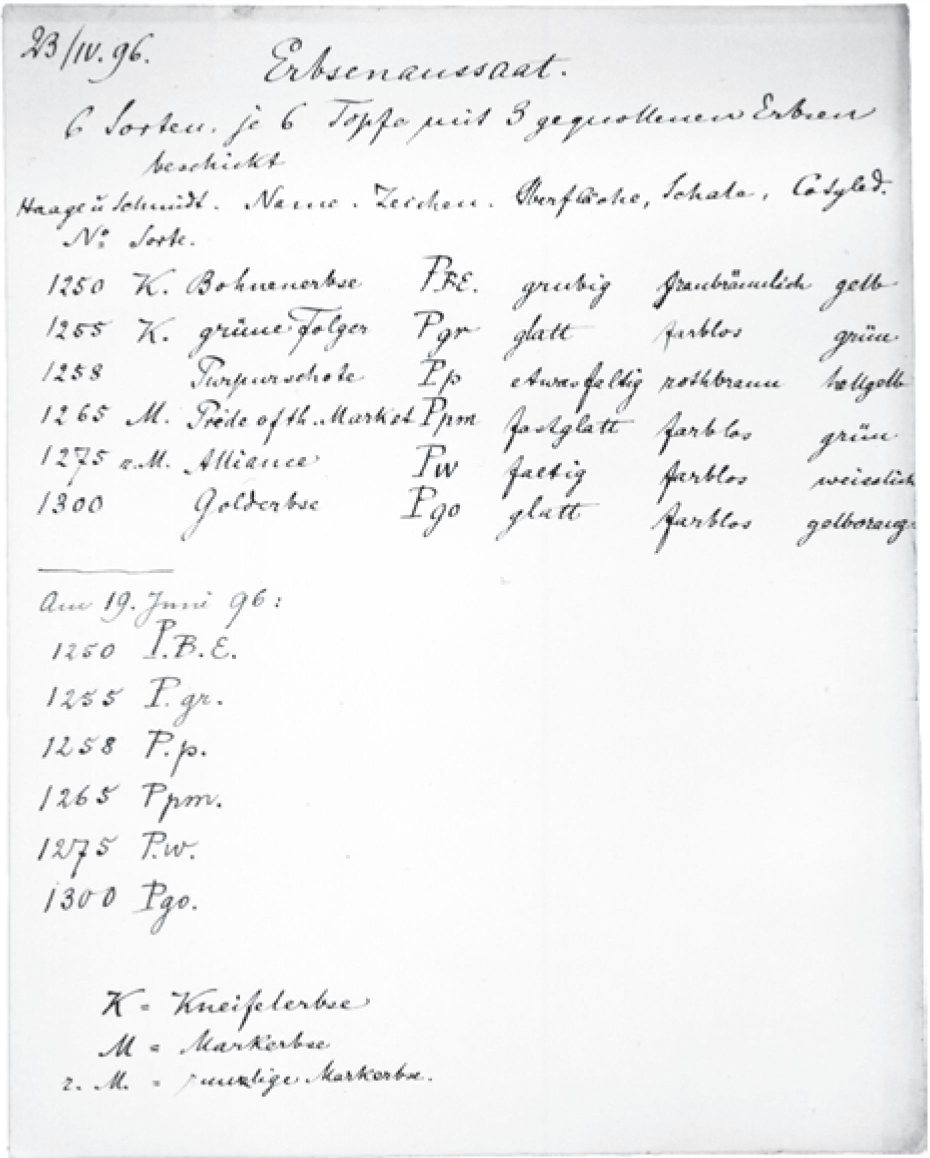
One last observation points in the same direction. In the sentence just quoted, Correns does not use the symbols A and B the way Mendel does in his paper. Mendel uses the capital letters (A and B) exclusively for *dominant characters*, whereas, in his excerpts, Correns calls the two *plant varieties* to be crossed A and B.

To judge by the notes that Correns left behind, he had very probably decided to carry out experiments with peas even before reading Gärtner, Rimpau, and Mendel, since he had already selected and purchased in April 1896 the six varieties on which he wanted to begin experimenting. This explains why he refers to "our cases" in his note on Mendel and proceeds to list five of Mendel's seven paired characters. The three characters he chose to follow were the form of the seed, the coloration of the seed coat, and the coloration of the germs (the cotyledons). A fourth character, the coloration of the seed, meant a combination of the coloration of the seed coat and that of the germs or cotyledons. If his aim was to solve the xenia mystery, all this is just as one would expect. On April 23, 1896, a week after reading Mendel's essay, Correns sowed six varieties of peas in six pots, planting three peas of each variety in each pot (fig. 2).[33]

The hard part of our reconstruction begins here. There is no reason to assume a priori that Correns was simply lying when twenty-five years later he wrote the lines to Roberts cited above or when he noted in his autobiographical sketch (undated, but also written in the 1920s) that he first read Mendel late in 1899 (that is, after he had completed the fourth generation of his pea experiments and *after* he had "arrived at the explanation" for his observations). Those who accept Meijer's conjecture and our own analysis of the note on Mendel will be more inclined to conclude that Correns had regarded Mendel's experiments from a very different angle when he first read his paper in spring 1896. He may have written his note on Mendel and given it no further thought until it resurfaced in his memory a few years later. At that point the note took its place in the experimental context that he himself had created in the meantime.

The 1896 *Pisum* Protocols

What do the protocols housed in Dahlem tell us about all this? Correns did not simply fasten on an especially clear-cut pair of characters, which is what one would expect of a "demonstrative" experiment designed to confirm Mendel's results. What he did was to cross five of the six varieties sown in April by means of reciprocal pollination. The first artificial fertilizations took place on June 19, 1896, as the plants Correns had sown began to bloom. He harvested the first seeds in late July-early August. The results are listed in the table entitled "Pollination and Yield 96" (fig. 3).[34] The


23/IV. 96. Erbsenaussaat.

6 Sorten, je 6 Töpfe mit 3 gequollenen Erbsen beschickt

Haage u. Schmidt. No.	Sorte.	Name.	Zeichen.	Oberfläche,	Schale,	Cotyled.
1250	K.	Bohnenerbse	PBE.	grubig	graubräunlich	gelb
1255	K.	grüne Folger	Pgr	glatt	farblos	grün
1258		Purpurschote	Pp	etwas faltig	rothbraun	hellgelb
1265	M.	Pride of the Market	Ppm	fast glatt	farblos	grün
1275	r. M.	Alliance	Pw	faltig	farblos	weisslich
1300		Golderbse	Pgo	glatt	farblos	gelborange

Am 19. Juni 96:

1250 P.B.E.
1255 P.gr.
1258 P.p.
1265 Ppm.
1275 P.w.
1300 Pgo.

K = Kneifelerbse
M = Markerbse
r. M. = runzlige Markerbse.

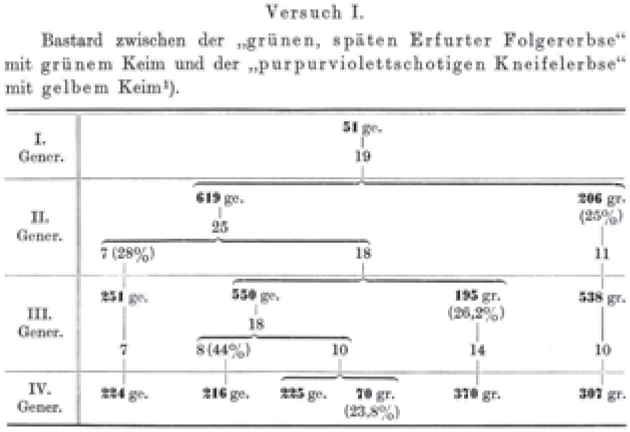
2. Page of Correns's research protocol entitled "Erbsenaussaat [peas sown]."
MPG Archive, Section 3, Folder 17, No. 115, File "Pisum-Kreuzungen, Resultate 96."

3. Page of Correns's research protocol entitled "Bestäub. u. Ertrag 96 [pollinization and yield, 1896]." MPG Archive, Section 3, Folder 17, No. 115, File "Pisum-Kreuzungen, Resultate 96."

first number at the bottom and to the right of each square represents the number of pods; the second gives the total number of seeds in each pod; the number in the center of the squares represents the number of artificial pollinations. For example, the reciprocal crosses of P_{gr} ("grüne, späte Erfurter Folgererbse," abbreviated "Grüne Folger") with P_p ("purpurviolettschotige Kneifelerbse," abbreviated "Purpurschote") yielded four and ten seeds, respectively, for a total of fourteen seeds resulting from twenty-six (7 + 19) artificial pollinations. These numbers make it abundantly clear that the crosses were not realized with an eye to the kind of statistical evaluations that Correns would surely have made had he been following in Mendel's footsteps at this point.

This non-statistical approach stands in striking contrast with Correns's statistical treatment the same year (1896) of the question of the number of pollen grains required to achieve optimal fertilization of *Mirabilis* plants.[35] In the context of these pollination experiments with *Mirabilis Jalapa* and *Mirabilis longifolia*, he conducted extensive statistical thought experiments on paper, which is to say that he was plainly already familiar with statistical methods of treating experimental data where he thought them appropriate.[36] The unpublished 1896–97 notes on *Mirabilis* also contain indications as to Correns's reading at the time, which included Joseph Gottlieb Kölreuter, Gärtner, and Charles Naudin.

In the case of the peas, Correns was obviously not planning large-scale



4. "Versuch I [Experiment I]." A cross between a "late green Erfurt Folgererbse" with a green germ and a "purpurviolettschotigen Kneifelerbse" with a yellow germ. Figure from Correns 1900a, 162.

experiments, nor did he initially set out to calculate average values. Instead, he carefully described the coloration of each harvested seed. He also compared artificial pollinations with self-pollinated samples in extensive control experiments, noted all the striking phenomena he observed, and in a few cases even measured the diameters and weight of the seeds. The last-named properties of the seeds clearly had nothing to do with the characters chosen for the crossing experiments. About the hybrids P_{pm+gr} ("Pride of the Market" fertilized with pollen from "Grüne Folger"), Correns noted laconically—as if to remind us of the question at the origin of his experiments—"all Xen [xenia] have failed."[37]

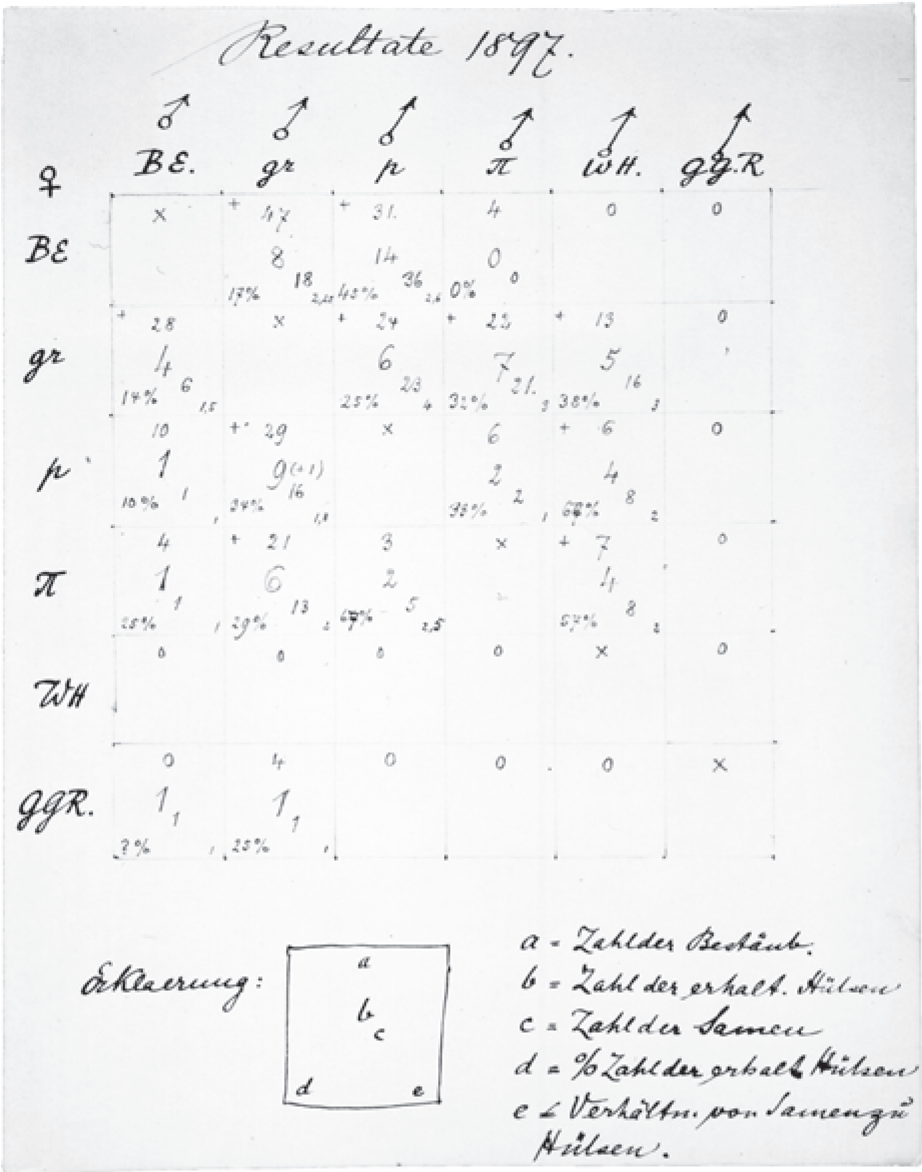
My objective here is not to provide a detailed account of all of Correns's *Pisum* crosses through the various breeding generations, let alone the parallel crosses that he carried out with maize. I shall, rather, restrict my attention to the pair already mentioned, Grüne Folger (P_{gr}) and Purpurschote (P_p), while adding pertinent information from other protocols where appropriate. The result obtained with this pair—namely, that yellow as the color of the embryo is dominant over green—is also described in "Experiment I" in Correns's first 1900 paper on *Pisum* (fig. 4);[38] we can therefore take this experiment as a reference point for the rest of our analysis. Let us retain for the time being that in describing his first-generation crosses, Correns calls the color of the seeds of the hybrid P_{gr+p} (Grüne Folger fertilized with pollen from Purpurschote) "yellow," and asserts that the pods of the reciprocal hybrid P_{p+gr} (Purpurschote fertilized with pollen from Grüne Folger) contain seeds of a "purer green" or have "conspicuously more greenish" seeds than the self-pollinated mother plant.[39]

The 1897 Protocols

The experiments performed in the next vegetation period began in spring 1897. A table provides an overview of the new first-generation crosses (fig. 5).[40] The three varieties P_{BE} ("Bohnenerbse"), P_{gr}, and P_p were crossed once again, and the three new varieties P_{π}, P_{WH}, and P_{ggR} replaced the P_{pm} ("Pride of the Market"), P_w ("Alliance weisse Zwergerbse"), and P_{go} ("Späte Golderbse") of the previous year. The information in the table resembles that summarized in figure 3, but it has become somewhat more complex. It comprises the number of pollinations, the number of pods obtained, the number of seeds contained in the pods, the ratio of the number of these seeds to the number of pollinations, and the average number of seeds in a pod. Correns obtained many more seeds this year (1897), but this multitude of numbers represents rather an efficiency control for the individual acts of artificial pollination than a representation of the transmission of characters.

While the total number of seeds from the reciprocal crosses between P_{gr} and P_p was 14 (10 + 4) in 1896, it was 39 (23 + 16) in 1897. Again, the 23 P_{gr+p} seeds all looked yellow, while the P_{p+gr} seeds looked more orange, shading toward green.[41] Thus we have a total of fifty-three seeds in the first generation. In the table "Experiment I" in his first *Pisum* paper, Correns lists, it is true, only fifty-one yellow seeds, but the discrepancy is not relevant for these results. For reasons unknown, he included only fourteen of the P_{p+gr} hybrid seeds obtained in 1897 in the count, instead of sixteen.[42] On the other hand, he counted as "yellow" the four seeds from his 1896 P_{p+gr} crosses, which he had earlier described as "greenish," because the character to be compared later was the coloration of the cotyledons, not that of the seed as a whole (where he was looking at a combination of the coloration of the cotyledons and the seed coat).

The page on which we find the list of 1897 results ("Ergebnisse 1897," fig. 6) regarding the xenia question[43] confirms the assumption that it was the failed xenia of the previous year that led Correns to repeat the first-generation crosses and even to carry out various other crosses, rather than the wish to harvest larger numbers of seeds in order to obtain reliable statistics. Clearly there were still no observations relevant to the xenia question to be had. However, the list does suggest why Correns's experiments included so many different crosses: in one case and one alone, it



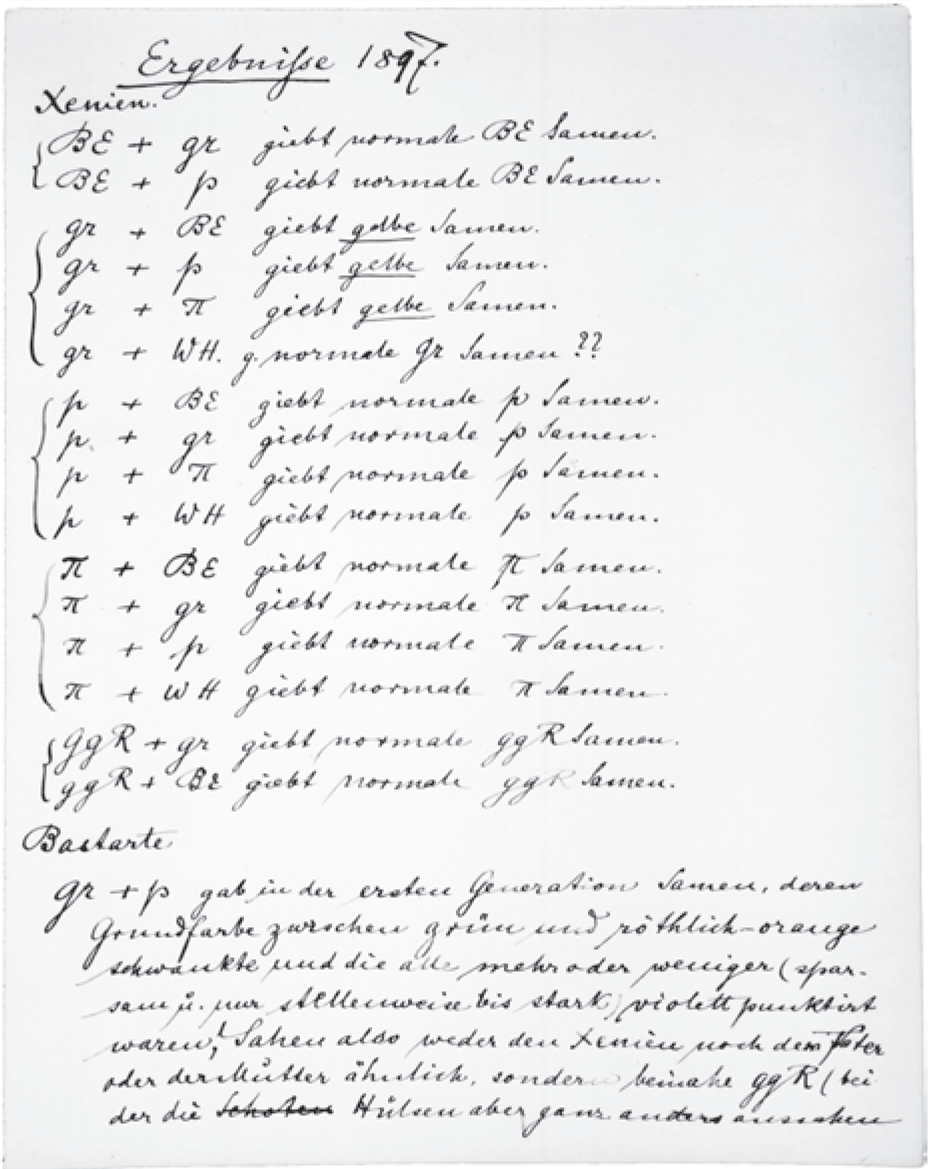
Resultate 1897.

♀ \ ♂	B.E.	gr	p	π	WH.	GGR
BE	×	+ 47 / 8 / 18 / 17% / 2,25	+ 31 / 14 / 36 / 45% / 2,6	4 / 0 / 0 / 0%	0	0
gr	+ 28 / 4 / 6 / 14% / 1,5	×	+ 24 / 6 / 23 / 25% / 4	+ 22 / 7 / 21 / 32% / 3	+ 13 / 5 / 16 / 38% / 3	0
p	10 / 1 / 1 / 10% / 1	+ 29 / 9(+1) / 16 / 34% / 1,8	×	6 / 2 / 2 / 33% / 1	+ 6 / 4 / 8 / 67% / 2	0
π	4 / 1 / 1 / 25% / 1	+ 21 / 6 / 13 / 29% / 2	3 / 2 / 5 / 67% / 2,5	×	+ 7 / 4 / 8 / 57% / 2	0
WH	0	0	0	0	×	0
GGR.	0 / 1 / 1 / [illegible]% / 1	4 / 1 / 1 / 25% / 1	0	0	0	×

Erklaerung: a / b c / d e

a = Zahl der Bestäub.
b = Zahl der erhalt. Hülsen
c = Zahl der Samen
d = % Zahl der erhalt. Hülsen
e = Verhältn. von Samen zu Hülsen.

5. Page of Correns's research protocol entitled "Resultate [Results] 1897." MPG Archive, Section 3, Folder 17, No. 115, File "Pisum Resultate 1897."



Ergebnisse 1897.

Xenien.

BE + gr giebt normale BE Samen.
BE + p giebt normale BE Samen.

gr + BE giebt gelbe Samen.
gr + p giebt gelbe Samen.
gr + π giebt gelbe Samen.
gr + WH. g. normale gr Samen ??

p + BE giebt normale p Samen.
p + gr giebt normale p Samen.
p + π giebt normale p Samen.
p + WH giebt normale p Samen.

π + BE giebt normale π Samen.
π + gr giebt normale π Samen.
π + p giebt normale π Samen.
π + WH giebt normale π Samen.

ggR + gr giebt normale ggR Samen.
ggR + BE giebt normale ggR Samen.

Bastarte

gr + p gab in der ersten Generation Samen, deren Grundfarbe zwischen grün und röthlich-orange schwankte und die alle mehr oder weniger (sparsam z. nur stellenweise bis stark) violett punktirt waren; Samen also weder den Xenien noch dem Vater oder der Mutter ähnlich, sondern beinahe ggR (bei der die ~~Schoten~~ Hülsen aber ganz anders aussehen

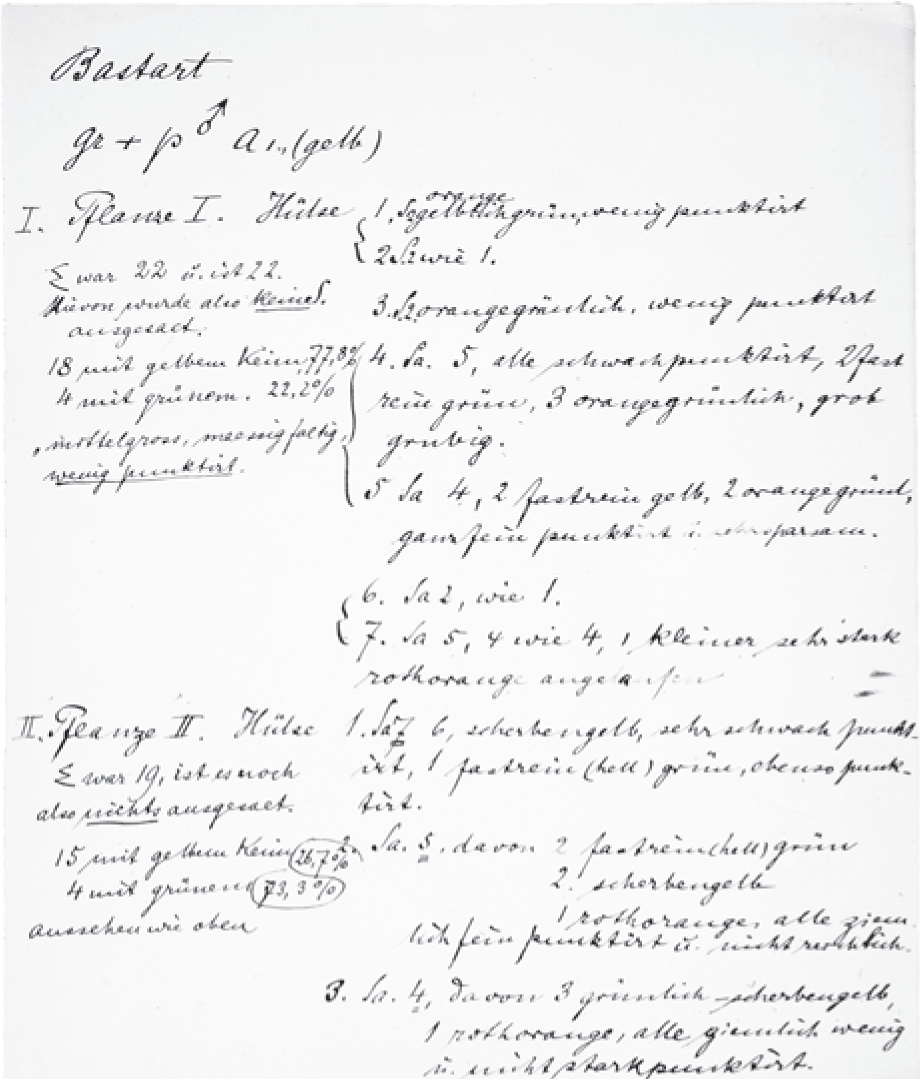
6. Page of Correns's research protocol entitled "Ergebnisse [Findings] 1897." MPG Archive, Section 3, Folder 17, No. 115, File "Pisum Resultate 1897."

was possible that the pollen-giving plant might have influenced the seeds of the mother plant. Next to this potential exception—gr pollinated with WH—Correns put two question marks.

At the bottom of the sheet, Correns noted, by way of comment on the coloration of seeds grown from self-pollinated, first-generation P_{gr+p} hybrids, that is, the second generation overall: "gr + p in the first generation yielded seeds whose basic color fluctuated between green and reddish-orange, while all of them were more or less spotted purple (lightly, as a rule, and up to heavily only in places). Thus [they] resembled neither the xenia, nor the father, nor the mother, but almost ggR (in which, however, the pods looked completely different)."[44]

This remark suggests that we should take a closer look at the protocols in which Correns recorded his findings about the first self-pollinated hybrid generation. On April 20, 1897, he sowed seven of the ten yellow seeds that he had obtained the previous year after pollinating P_{gr} with P_p. As a control, he sowed twelve seeds that derived from the same plants but had resulted from self-pollination.[45] All the hybrid plants and all but one of the control plants grew.[46] Correns carefully noted the form and coloration of each individual seed, with the result that each one could be traced back to the individual plant and even to the particular pod from which it came. He designated the seed colors as "orange yellowish green," "orange grayish," "nearly pure green," "nearly pure yellow," and a long series of other shades. In sum, the seeds' "basic color fluctuated between green and reddish-orange." There was no sharp division between green and yellow, but, rather, a range of different shades that "resembled neither the xenia, nor the father, nor the mother."

In the protocols for the first generation, Correns kept records of the self-pollinated control plants on the left side of the page and the cross-fertilized hybrids on the right; in the protocols for the second generation in contrast, he included detailed descriptions of the seeds on the right side of the page, leaving an empty margin on the left (fig. 7). In this margin, we read, for instance, about the results for the first of the seven plants, in small, cramped handwriting: "Σ was 22 and is 22. So *none* of these seeds was sown. 18 with yellow germ, 77.8%, 4 with green, 22.2%, medium-sized, moderately wrinkled, *lightly spotted*." About plant four, we find the following note: "Σ 18, only 15 remain. So 3 are missing. Of the rest (15), 3 have green germs = 20%, 12 yellow = 80%. Otherwise like I. Sowing, yellow 2 green 1, so 14 yellow, 77.8%, 4 green, 22.2%."[47] Correns thus went back to these protocols at a later date—at the earliest, some time after the sowing season of the following year (1898). The date can be deduced from the fact



Bastart

gr + p ♂ A 1, (gelb)

I. Pflanze I. Hülse 1. orange gelblichgrün, wenig punktirt
2. wie 1.
3. orangegrünlich, wenig punktirt
4. Sa. 5, alle schwach punktirt, 2 fast rein grün, 3 orangegrünlich, grob grubig.
5. Sa 4, 2 fast rein gelb, 2 orangegrün, ganz fein punktirt u. sparsam.
6. Sa 2, wie 1.
7. Sa 5, 4 wie 4, 1 kleiner sehr starke rothorange angelaufen

Σ war 22 u. ist 22. Hievon wurde also keines ausgesaet.
18 mit gelbem Keim 77,8%
4 mit grünem 22,2%
mittelgross, massig faltig, wenig punktirt.

II. Pflanze II. Hülse 1. Sa 7 6, scherbengelb, sehr schwach punktirt, 1 fast rein (hell) grün, ebenso punktirt.
2. Sa. 5, davon 2 fast rein (hell) grün
2 scherbengelb
1 rothorange, alle ziemlich fein punktirt u. nicht reichlich.
3. Sa. 4, davon 3 grünlich-scherbengelb, 1 rothorange, alle ziemlich wenig u. nicht stark punktirt.
4. Sa. 3, davon 2 mehr grünlich, 1 mehr gelblich scherbengelb, [illegible] wie [illegible]

Σ war 19, ist es noch also nichts ausgesaet.
15 mit gelbem Keim 76,7%
4 mit grünem 23,3%
aussehen wie oben

7. Page of Correns's research protocol entitled "Bastart [Hybrid] gr + p ♂ A 1, (gelb) [yellow]." MPG Archive, Section 3, Folder 17, No. 115, File "Pisum Resultate 1897."

that he must already have used the seeds that were now "missing," an exact count of which he now belatedly tried to produce so as to be able to calculate correct percentages. And we see that he now noted the coloration of the germ rather than of the seed. The ratio was calculated on the basis of small numbers and consequently subject to considerable fluctuation. Yet as far as the dominant yellow color of the cotyledons inherited from P_p is concerned, a shift toward a segregation ratio of 3:1 is clearly discernible in the first hybrid generation. What we have here is plainly a retrospective interpretation of the 1897 results, as is confirmed by the fact that this information is recorded on a separate part of each page. Let us now turn to the protocols of the following year (1898) to see whether they contain an indication as to what led Correns to abandon his research on xenia and to reinterpret his data in the light of the segregation law.

The 1898 Protocols

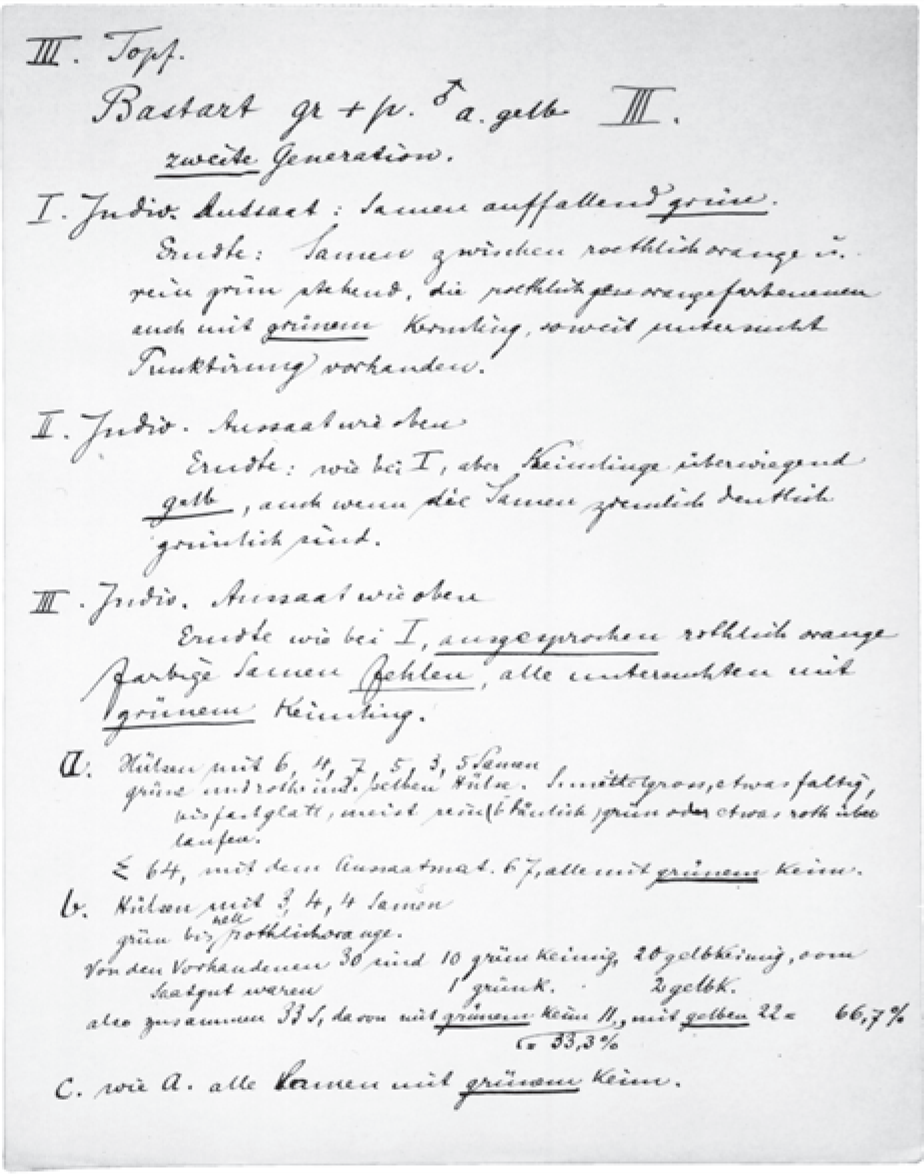
In 1898, Correns obtained a second generation of the hybrid $P_{gr♀ + p♂}$. He took nine seeds from plant III (A1) of the previous year's hybrid generation and sowed them in three pots. Six of these seeds were yellowish-orange, while the other three had a strong green tinge. Correns also sowed three seeds from plant IV (A1) (two yellow seeds and a green one), three from plant II (B1) (again, two yellow seeds and a green one), and three from plant I (B1) (all yellow) in another three pots.[48] When, later, he reconstructed the number of yellow and green germs that he had obtained from the harvest of the preceding year, 1897, the numbers exactly matched. There is, however, one interesting discrepancy. Correns had sown three green seeds from plant III of A1—in the 1898 protocols, we find the words "seeds conspicuously *green*."[49] Yet when he reconstructed the number of yellow and green germs in the margin of the 1897 protocol, he describes only two of the germs as "green." The reason is that in 1898 only two individuals of the second-generation hybrid plants produced germs all of which were green; one produced both green and yellow germs. Correns therefore concluded retrospectively that this greenish seed must have contained a yellow germ, and therefore counted it as yellow. This too implies that his supplementary marginalia must date from fall 1898 at the earliest.

Correns raised another set of second-generation hybrids from the reciprocal cross, that is, $P_{p♀ + gr♂}$. He observed that germs from the seeds of these plants were "sometimes green, sometimes yellow" and that most of the individuals represented "the normal hybrid." Two individual plants, however, were "pure p"; Correns therefore paid no further attention to them.[50]

Let me here emphasize once again that Correns was at all times thanks to the exactness of his protocols in a position to trace every single seed and the plant raised from it to a particular plant and seed of the preceding generation. He kept a virtually complete physical collection of *individual* seeds, which he also catalogued and annotated. This fact, too, bears out the hypothesis that the aim of the series of *Pisum* experiments was not to corroborate a statistical regularity that he might have noticed on his first, spring 1896 reading of Mendel's paper, and set out to test. He was looking rather for unknown seed characters that would only appear in the course of these hybridizations. The protocols were thus not merely passive data storehouses.[51] Although their design and structure were exactly tailored to the particular interest that Correns took in his object, they could also bring other, diverging aspects of that object into the light. And they contained an excess of information, allowing for a reorientation of the experimental gaze later on.

At the top of the page in the 1898 protocols is a short, summary description of the material sown and the form and coloration of the harvested seeds. Like the protocols of the preceding year, the 1898 protocols contain supplementary notes that could only have been added later. Located in the left margin of the page in 1897, these notes appear in 1898 at the bottom of the page. Here Correns noted the total number of seeds obtained from each plant, the number of green and yellow embryos, and the ratio of the embryos, expressed as a percentage. As before, he added to the actual number of seeds left in his boxes the number of those he had sown to obtain the next generation. For instance, we read on the protocol for pot three, under point b, about individual plant number two (fig. 8): "Pods with 3, 4, 4 seeds, green to light reddish-orange. Of the 30 extant, 10 have green germs, 20, yellow germs; of the seeds sown, 1 had a green germ, 2, yellow germs, making a total of 33 seeds, of which 11 = 33.3% had a *green* germ, 22 = 66.7%, a *yellow* germ."[52] Another remark on the protocol for pot 6, about individual plant number 2, reads: "Σ now: 7 green 20 yellow. Sown: 1 green 2 yellow. ΣΣ 30, of which 8 green = 26.7%, 22 yellow 73.3%."[53] In light of these calculations again including the seeds sown out, we can conclude that Correns made his supplementary annotations—and, therefore most probably those found in the 1897 protocols as well—only after he had sown the next generation of plants in spring 1899.

Let us now turn to another series of experiments that Correns carried out in 1898. In two more pots, he raised six more individuals of the first



III. Topf.

Bastart gr + p. ♂ a. gelb III.

zweite Generation.

I. Indiv. Aussaat: Samen auffallend grün.

Ernte: Samen zwischen röthlichorange u. rein grün stehend, die röthlich orangefarbenen auch mit grünem Keimling, soweit untersucht Punktirung vorhanden.

II. Indiv. Aussaat wie oben

Ernte: wie bei I, aber Keimlinge überwiegend gelb, auch wenn die Samen grünlich deutlich grünlich sind.

III. Indiv. Aussaat wie oben

Ernte wie bei I, ausgesprochen röthlich orange farbige Samen fehlen, alle untersuchten mit grünem Keimling.

a. Hülsen mit 6, 4, 7, 5, 3, 5 Samen
grüne und röthl. u. gelben Hülse. Samen mittelgross, etwas faltig, bis fast glatt, meist rein (bläulich) grün oder etwas roth überlaufen.

Σ 64, mit dem Aussaatmat. 67, alle mit grünem Keim.

b. Hülsen mit 3, 4, 4 Samen
grün bis hell röthlichorange.

Von den Vorhandenen 30 sind 10 grün keimig, 20 gelbkeimig, vom Saatgut waren 1 grünk. 2 gelbk.

also zusammen 33 S., davon mit grünem Keim 11, mit gelben 22 = 66,7%
(= 33,3%)

c. wie a. alle Samen mit grünem Keim.

8. Page of Correns's research protocol entitled "III. Topf [pot]. Bastart [Hybrid] gr + p ♂ A. gelb III." MPG Archive, Section 3, Folder 17, No. 115, File "Pisum Resultate 1898."

generation of hybrids, obviously using seeds obtained from the fertilization of P_{gr} with pollen from P_p in 1897. Again he included a short description of the resulting seeds in his protocol. About one plant, he noted that he had made a backcross with pollen from P_p: "1 ovary pollinated with p (wool red) (the other pollinations produced no results)." This pollination produced five seeds, all with yellow embryos.[54] The protocols for these experiments do not reveal which individual plant of 1897 provided the seeds in question. Correns does, however, state that the resulting plants yielded "yellow or green germs," but he omits any more precise counts.[55] Here too we find addenda on the bottom of the page about the number and percentage of green and yellow germs; manifestly, they were written only after some of the seeds from this crop were sown the following year (1899).

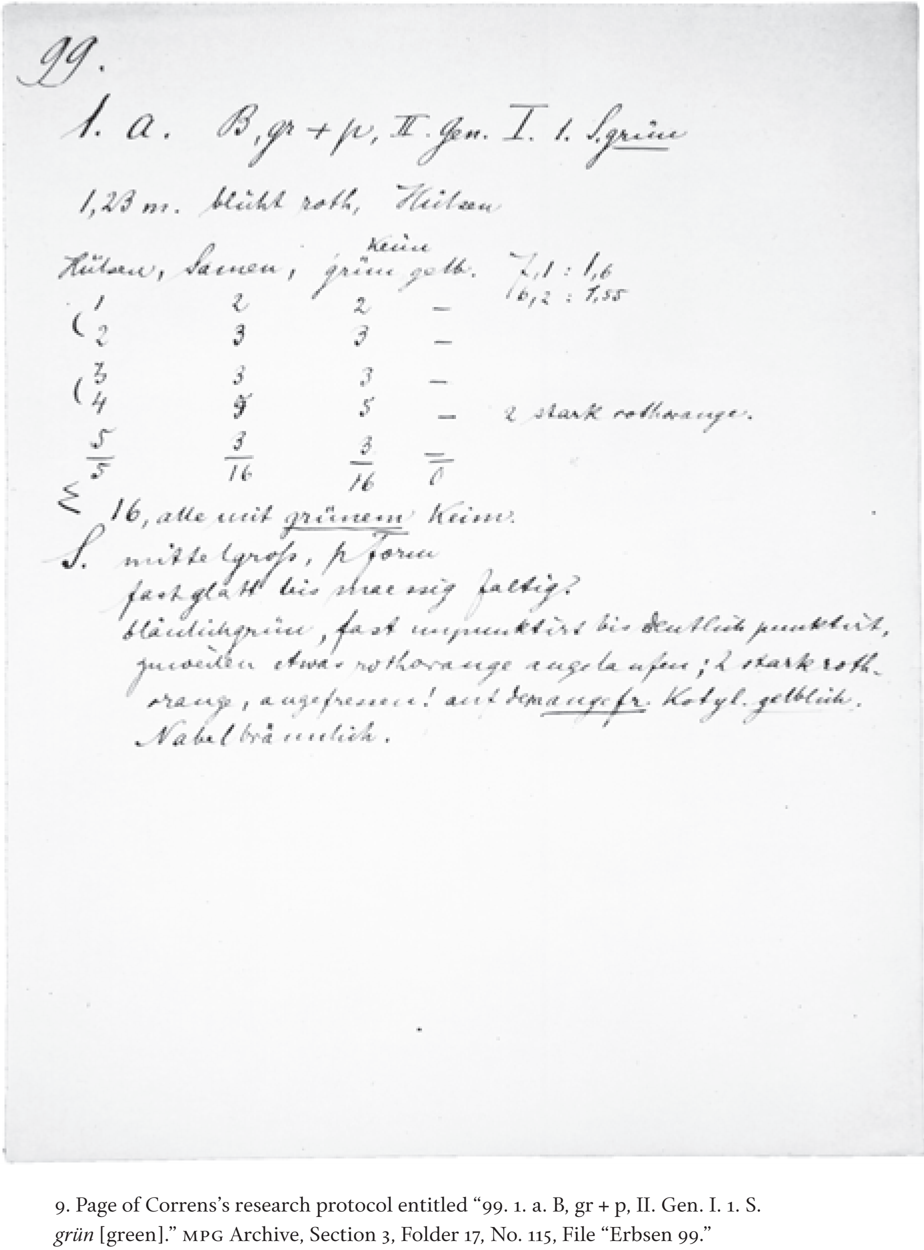
Correns does not say why he cultivated these additional hybrids. We cannot exclude that he wanted to produce more seeds for a statistical evaluation—but if so why did he not raise many more plants? At this point, he could easily have carried out a large-scale screening to test the 3:1 ratio among the descendants, concentrating on a few select hybrids. But the protocols speak a different language: Correns cultivated together with the appropriate control plants more different first-generation hybrids, namely, BE + gr (pots 8 and 9), BE + p (pot 10), gr + BE (pots 14 and 15), gr + π (pots 18 and 19), gr + WH (pots 20 and 21), p + WH (pot 26), π + gr (pot 28), and π + WH (pot 29).

The 1899 Protocols

In the protocols of the last year in which Correns experimented with peas, we see a fairly systematic extension of the experiments of 1898. Correns performed a first series of experiments with seeds from the second-generation hybrid gr + p. The result was a third generation of hybrids and the fourth generation of seeds overall. Correns sowed fifty-four seeds, of which forty-nine developed into seed-bearing plants. It appears that he took three seeds from each of the plants that he had obtained the previous year, a total of eighteen in all. Twenty-four green germs (ten of them from a plant which, by the second generation, already produced only green germs, and fourteen from a plant with only green germs in the first generation) and twenty-five yellow germs (seven of them from a plant with only yellow germs in the first generation) developed into plants, bringing forth a considerable number of seeds. In contrast to the 1897 and 1898 protocols, those for 1899 show no sign of having been revised; formally, they all look alike. They also differ from the previous protocols in that Correns records, immediately below the identifying description of the plant (for example, "1.a. B, gr + p, II. Gen. I. 1. seed *green*"), the number of seeds contained in the pods, distinguishing them according to whether they have green or yellow germs. Only then does he provide further information about the form, size and additional characteristics of the seeds, rather than proceeding the other way around, as he had earlier (fig. 9).[56]

A second group of similarly designed protocols (pots 46 to 48) describes a second generation of gr + p hybrids derived from the first-generation hybrids of 1898; a third group of protocols (pots 55 to 58) contains the results from a second generation of reciprocal p + gr hybrids. These plants yielded an impressive number of seeds, all of them classified according to whether their cotyledons were yellow or green. The question of the xenia makes itself heard one last time, in connection with two hybrids raised in 1899 and labeled "BE + gr ('xenia')." This was in all probability an ambiguous case, since the term "xenia" now appears in inverted commas and inspires no comment other than Correns's remark on the results: "Obviously gr + BE!"[57] In the paper to which the *Pisum* experiments ultimately gave rise, Correns laconically says: "my experiments on the formation of xenia here [yielded] only negative results."[58]

As usual, the individual pages of the protocol bear no dates, but there can be no doubt that they were written in the fall of 1899. As has already been said, it can be safely assumed that the addenda to the 1897 and 1898 protocols also date from this period: Correns was now fully aware of the segregation pattern with its pure lines on the one hand and the 3:1 segregation ratio for hybrids on the other hand. The set of *Pisum* protocols offers no straightforward indication as to whether Correns began to move toward a solution after thinking about the results of his 1898 harvest, or even earlier. In theory, he could have understood after observing the second generation of hybrids that all the germs resulting from his green peas remained green, whereas only some of those resulting from his yellow ones remained yellow, the others dividing up into yellows and greens. But the addenda to the 1898 protocols clearly suggest that the numbers and percentages were inserted only after the 1899 crop had been sown. Yet the tremendous energy that Correns expended on raising the hybrids of the second and third generations with gr + p and p + gr combinations as well as a number of others also suggests that he must have had good reasons for engaging in such an extensive, demanding experimental program in spring and summer 1899—at the same time as he was completing his book on mosses.



99.

1. a. B, gr + p, II. Gen. I. 1. S. grün

1,23 m. blüht roth, Hülsen

Hülsen,	Samen,	Keim grün	gelb.
1	2	2	—
2	3	3	—
3	3	3	—
4	5	5	—
5	3	3	—
5	16	16	0

7,1 : 1,6
6,2 : 1,55

2 stark rothorange.

Σ 16, alle mit grünem Keim.

S. mittelgroß, p Form
fast glatt bis schwach faltig?
bläulichgrün, fast unpunktirt bis deutlich punktirt,
zuweilen etwas rothorange angelaufen; 2 stark roth-
orange, angefressen! auf dem angefr. Kotyl. gelblich.
Nabel bräunlich.

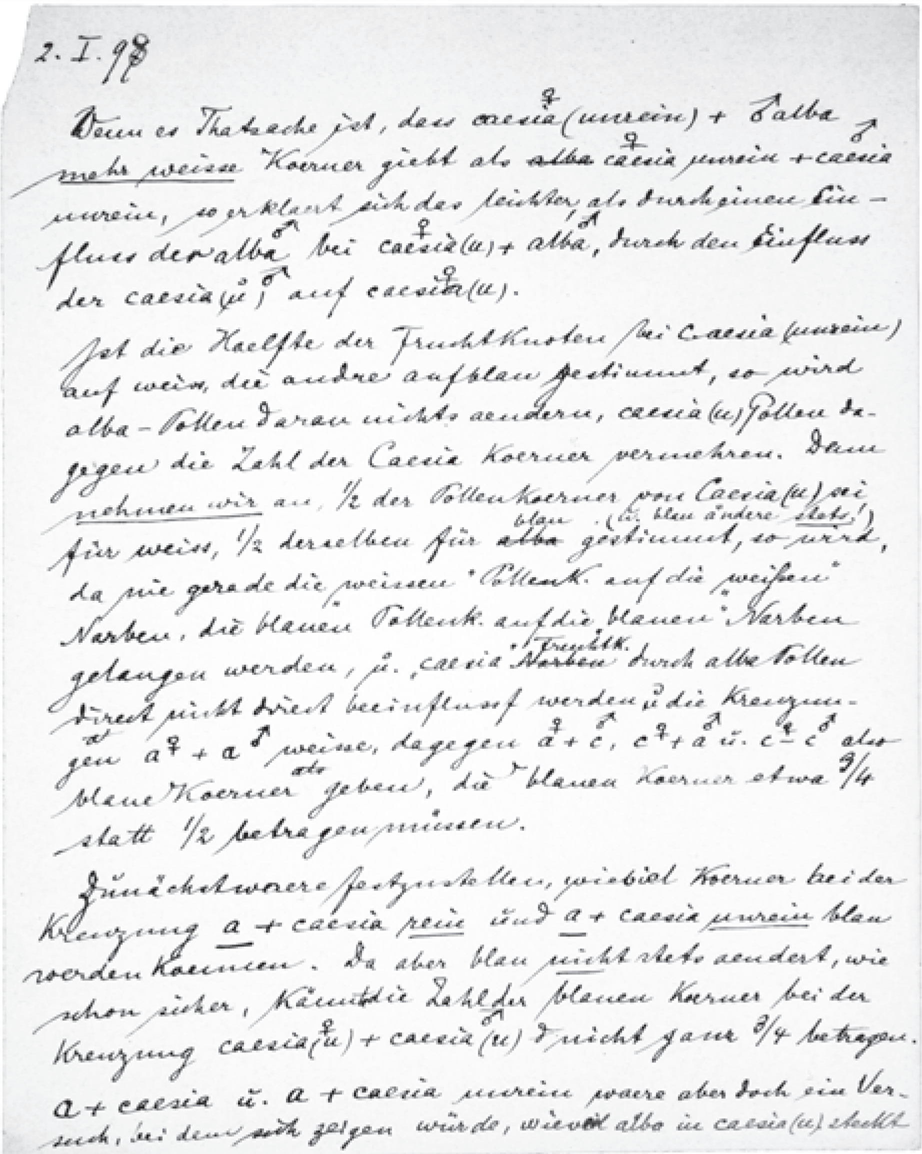
9. Page of Correns's research protocol entitled "99. 1. a. B, gr + p, II. Gen. I. 1. S. *grün* [green]." MPG Archive, Section 3, Folder 17, No. 115, File "Erbsen 99."

The Impact of the Zea mays Series

The other notes accompanying the set of *Pisum* protocols likewise fail to close this gap in our information. There is, however, a crucial note in Correns's protocols on the experiments he was simultaneously conducting with maize, contained in a folder labeled "Theoretical Matters etc." (fig. 10).[59] The note is dated January 2, 1897; an eight has been written on top of the seven. It is possible that early in the new year Correns first wrote the date of the old year by force of habit; the accompanying notes, insofar as they are dated at all, all bear dates from late 1897 or early 1898. In the note that I shall cite at length here, Correns made the following observation about one of his maize crosses: "If it is a fact that caesia ♀ (impure) + alba ♂ produces *more white* kernels than caesia ♀ (impure) + caesia ♂ (impure), this is more easily explained by the influence of caesia ♂ impure on caesia ♀ impure than by the influence of alba ♂ on caesia ♀ (impure)." The quote indicates that he was inclined to exclude xenia effects of *alba* pollen. But he had not yet made up his mind about the ratio of white to blue kernels in the two cases. "Caesia impure" is a hybrid between the two varieties *caesia* and *alba* that yields somewhat impure blue grains. Correns was comparing the result of self-fertilization of "caesia impure" and a backcross of the hybrid with the *alba* parent. He followed his observation up with a hypothetical alternative explanation:

> If half the ovaries in caesia (impure) are disposed to white and the other half to blue, alba pollen will change nothing here, whereas caesia (impure) pollen will increase the number of caesia grains. *Let us therefore assume* that half the pollen grains of caesia (impure) are disposed to white, and half to blue (and that blue *always* alters!); then, because "white" pollen grains will never only meet "white" stigmas and blue pollen grains will never only meet "blue" stigmas, and because "caesia" ovaries are directly [*sic*] not directly influenced by alba pollen and the crosses a ♀ + a ♂ yield white grains, where a ♀ + c ♂, c ♀ + a ♂ and c ♀ + c ♂ yield blue grains, the blue grains must amount to approximately ¾ rather than ½.
>
> One would first have to find out how many grains can turn out blue when *a* + caesia *pure* is crossed with *a* + caesia *impure*. But because it is already certain that blue does *not* always alter, the number of blue grains . . . could come to slightly less than ¾.[60]

Here we have, for the first time, a rather clearly formulated, albeit hypothetical supposition that there is a 3:1 split in the first hybrid generation and concomitantly an underlying disjunction of the factors responsible



10. Note on maize, 2. I. 98. MPG Archive, Section 3, Folder 17, No. 85, File "Theoretisches etc. [theoretical matters etc.]"

for the blue or white color of the corn grains. It is obvious that Correns rules out the influence of xenia in the present case—for he observes that "'caesia' ovaries are . . . not directly influenced by alba pollen"—and, consequently, thinks that something altogether different must be taken into consideration in the case of these maize crosses. He comes back to this in a note of February 24, 1898: "As far as a dissociation of characters *in the pollen* is concerned, experiments would have to be carried out with the hybrid vulgata + dulcis. (Because the grains are *either* smooth *or* wrinkled, whereas intermediate formations occur with alba + caesia)."[61] These intermediate formations showed a less intense blue coloration of the seeds. It appears thus possible that, as Correns prepared the crosses of the 1898 season, he was already on the track of the future explanation for his findings.

As is suggested by these tentative formulations, the first suspicion may have occurred to him thanks to crosses between the maize varieties *caesia* and *alba* in which one of the crossing partners turned out to have been "impure." On closer inspection of the relevant maize protocols, we find a few of the elements that played a role in the above explanation. As early as 1894, Correns had observed that when the variety *alba* was pollinated with *caesia*, "a short, but full cob" resulted, with "*all* grains but one, +/- 'caesia', partially spotted."[62] That is, blue—almost—"always alters," as Correns would later put it in the note we have already cited. In 1896 again he found that the "influence of *caesia*" was "no doubt certain," although he continued to entertain doubts about the "purity of the *alba*"[63] (the mother plant). A self-pollination experiment which he then carried out with another caesia plant led him to the conclusion that "the caesia was *not pure*."[64] The reciprocal cross, in which he fertilized a *caesia* plant with pollen from *alba*, showed him that, with the exception of just one experiment, in which one of the crossing partners of the *caesia* had once more not been pure, "*no influence of the pollen on the ovary is recognizable*."[65] Hence he knew that *alba* pollen did not give rise to xenia and that blue suppressed white more or less completely. In a series of further pollinizations of *alba* plants with *caesia* pollen, however, the expected alteration to blue grains did not occur in all cases. Instead, Correns obtained a mixture of blue and white grains. Yet his previous findings had so thoroughly convinced him by this time that he concluded that the *caesia* he had used "was not pure, but c + a!"[66] The reciprocal cross between a *caesia* mother plant and an *alba* pollen plant likewise yielded "grains approximately ½ *alba*, ½ *caesia*."[67] Inadvertent backcrosses were at issue here—one of the crossing partners happened to be a hybrid itself. Thus we come to the surprising result that unintended backcrosses with varieties of maize together with the impression of a rather well-established dominant character—in a context in which xenia could be ruled out—precipitated the turn in Correns's later experimentation.

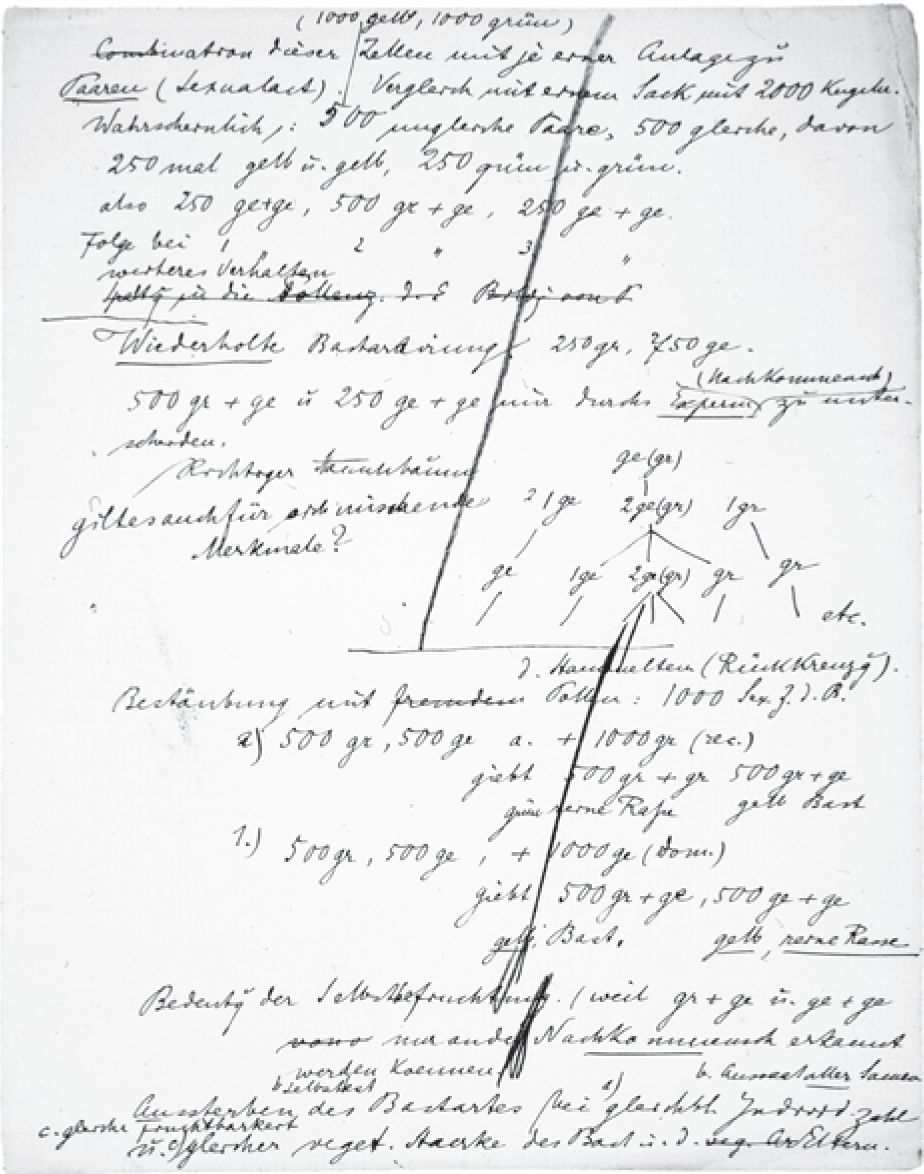
Merging Lines

At this point, maize in which intermediary characters and xenia made it considerably harder to evaluate results yielded the scientific stage to the *Pisum* crosses, which consistently failed to exhibit xenia. In an undated note probably written nearly two years later in winter 1899–1900, Correns finally comes back to the crosses between the maize varieties *alba* and *caesia*—this time, however, with a precise conception of the regularities that had emerged in the *Pisum* crosses of 1898 and 1899. As if he had forgotten the starting point for his thinking, Correns now emphatically asks: "Does the behavior of the hybrids of the races of peas also apply to the hybrids between races of maize??"[68] In another note from the same period, he speaks directly of the possibility of "applying Mendel's theory to the hybrids between races of maize."[69]

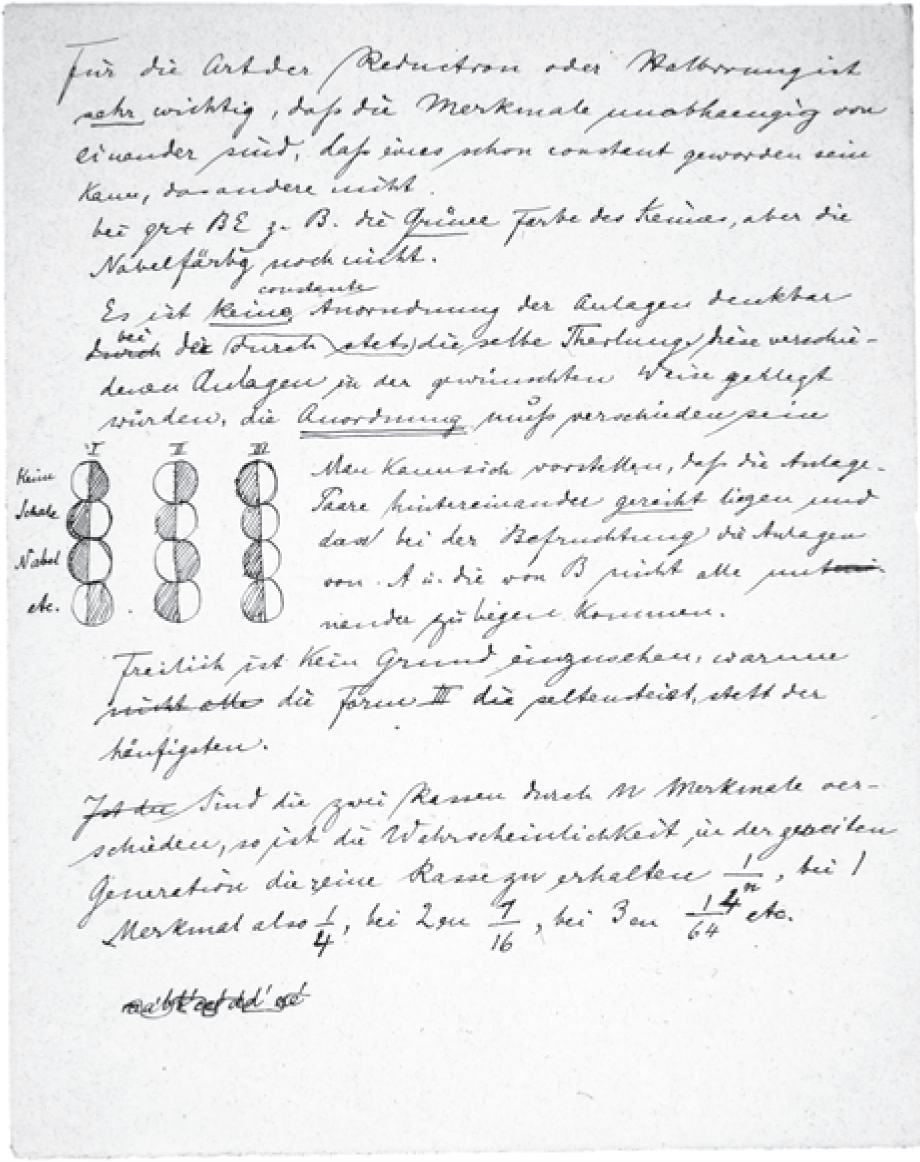
The additional notes on the *Pisum* series, presumably also written in winter 1899–1900, are unfortunately all undated and nothing else allows us to establish their chronology. On one of these pages (fig. 11), Correns engages in statistical speculation about the generative process underlying his results:

> Combination of these cells with one disposition each in *pairs* (sexual act). Comparison with a sack of 2000 balls (1000 yellow, 1000 green). Probable: 500 unequal pairs, 500 equal ones, of which 250 yellow and yellow, 250 green and green. Thus 250 yellow + yellow, 500 green + yellow, 250 yellow + yellow [this should read "green + green," H.-J. R.]. . . . *Repeated* hybridization 250 green, 750 yellow. 500 green + yellow and 250 yellow + yellow only distinguishable through *experiment* (progeny). Veritable genealogical tree. Does this also hold for intermingling characters?[70]

Correns next proceeds to make comparable calculations for backcrosses with the parent plants. These reflections provided the basis for the description in his *Pisum* paper, which he was to submit to *Berichte der Deutschen Botanischen Gesellschaft* on April 24, 1900.[71] On another page we find a drawing (fig. 12) of a hypothetical "sequential order" of "dispositions" in hybrids differing in more than one character pair.[72] This drawing became the basis for the schematic explanation of a chromosome theory of inheritance that Correns published in 1902.[73]


(1000 gelb, 1000 grün)
~~Combination~~ dieser | Zellen mit je einer Anlage zu
Paaren (Sexualact). | Vergleich mit einem Sack mit 2000 Kugeln.
Wahrscheinlich: 500 ungleiche Paare, 500 gleiche, davon
250 mal gelb u. gelb, 250 grün u. grün.
also 250 ge+ge, 500 gr+ge, 250 gr+gr.
Folge bei 1 2 3
weiteres Verhalten
~~[illegible]~~
Wiederholte Bastardirung: 250 gr, 750 ge.
500 gr+ge u. 250 ge+ge nur durch ~~[illegible]~~ (Nachkommen) zu unterscheiden.
[illegible]
gilt es auch für sich mischende Merkmale?
ge(gr)
2 1 ge 2 ge(gr) 1 gr
ge 1 ge 2 ge(gr) gr gr
etc.
d. Hauptzellen (Rückkreuz).
Bestäubung mit fremdem Pollen: 1000 [illegible]
2) 500 gr, 500 ge a. + 1000 gr (rec.)
giebt 500 gr+gr 500 gr+ge
grün reine Rasse gelb Bast.
1.) 500 gr, 500 ge, + 1000 ge (dom.)
giebt 500 gr+ge, 500 ge+ge
gelb Bast. gelb, reine Rasse
Bedeutg der Selbstbefruchtung (weil gr+ge u. ge+ge nur an den Nachkommen erkannt werden koennen.)
Aussterben des Bastardes bei gleichbl. Individ. Zahl
[illegible]

11. Statistical considerations and a genealogical tree.
MPG Archive, Section 3, Folder 17, No. 115.


Für die Art der Reduction oder Halbirung ist sehr wichtig, daß die Merkmale unabhaengig von einander sind, daß eines schon constant geworden sein kann, das andere nicht.

bei gr + BE z. B. die Grüne Farbe des Keimes, aber die Nabelfärbg noch nicht.

Es ist keine constante Anordnung der Anlagen denkbar bei der stets die selbe Theilung, wie verschiedenen Anlagen in der gewünschten Weise getheilt würden, die Anordnung muß verschieden sein.

Man kann sich vorstellen, daß die Anlage-Paare hintereinander gereiht liegen und daß bei der Befruchtung die Anlagen von A u. die von B nicht alle nebeneinander zu liegen kommen.

Freilich ist kein Grund einzusehen, warum die Form III die seltenste ist, statt der häufigsten.

Sind die zwei Rassen durch n Merkmale verschieden, so ist die Wahrscheinlichkeit, in der zweiten Generation die reine Rasse zu erhalten $\frac{1}{4^n}$, bei 1 Merkmal also $\frac{1}{4}$, bei 2 en $\frac{1}{16}$, bei 3 en $\frac{1}{64}$ etc.

12. Sequential ordering of hereditary dispositions.
MPG Archive, Section 3, Folder 17, No. 115.

Correns was thus well prepared to put together his *Pisum* manuscript in the span of two days when on April 21, 1900, he was caught unawares by an offprint of Hugo de Vries's "Sur la loi de disjonction des hybrides."[74] All the relevant parts of Correns's manuscript, including the calculations, had been formulated already. Until this date, he does not seem to have been in any particular hurry to publish his results. We can see from his notes that he was busy making a detailed revision of the voluminous protocols of his experiments with maize varieties between December 1899 and March 1900 with an eye both to the calculation of the segregation ratio wherever it seemed obvious and to xenia as well.[75] It was only when he received de Vries's paper that he suddenly felt the need to publish his results as quickly as possible. This may have been the reason that he did not pursue the additional experiments with peas that he had been planning for spring 1900.[76] For he had now to position himself with respect not only to his predecessor Gregor Mendel, but to his contemporary and competitor Hugo de Vries as well. He proceeded subtly. In the introduction to his *Pisum* paper, we read: "When I discovered the lawful behavior and the explanation for it . . . I reacted the way de Vries is obviously reacting now: I took all this to be something new. But then I was forced to conclude that, in the [18]60s, the abbot Gregor Mendel in Brünn . . . arrived at the same result. . . ."[77] This is a multifaceted formulation. Correns not only dissociates the realization that hybrids behave "lawful[ly]" from the "explanation" for it; he further implies that he had already discovered both before he "was forced to conclude" that Mendel had arrived at the same results several decades earlier—although he of course avoids saying anything precise as to how and when he stumbled upon Mendel. Moreover, he suggests that he discovered the solution before de Vries by affirming that he "reacted the way de Vries is obviously reacting now," thereby implicitly criticizing his competitor for "obviously" considering (and giving out) his findings as something new when they were in fact preceded by Mendel's—something which he implies de Vries may even have known yet passed over in silence. Correns heightened the contrast between his presentation of matters and de Vries's by publishing his own paper under the title "G. Mendel's Law about the Behavior of the Progeny of Hybrids;" he also rushed two more papers on hybridization into print before the year was out.[78] On the other hand, his voluminous monograph on maize, *Hybrids between Races of Maize with Special Attention to Xenia* appeared only in 1901,[79] as the sequel to a preliminary publication on xenia in maize dating from 1899.[80] In the field of xenia too de Vries had been a little quicker on the draw than Correns. He published similar results in a preliminary account in 1899 and in the form of a more extended report in 1900,[81] whereupon Correns sullenly decided to "postpone" his own publication on the subject for another year.[82]

Conclusion

My reconstruction of Correns's experiments has led to the conclusion, contrary to what is suggested by his notes on reading Mendel's paper on hybrids in April 1896, that the meaning of the Moravian abbot's observation and explanation of the segregation behavior of varieties of garden peas did not become immediately clear to him. As a result of an unintended backcross of varieties of maize, however, he must at least have suspected the prospective significance of both sometime around the turn of 1898, and pursued his hunch. At the same time, he began to lose interest in the xenia problem; ultimately, he dropped it altogether as far as *Pisum* was concerned, since all his experiments in this direction had negative results. His protocols do not allow us to exclude the possibility that the puzzle finally fell in place for him only in the fall of 1899. But we should no more lend credence to his declaration that the solution hit him "in a flash" one fine day in autumn of that year than we should credit his assertion that he first read Mendel's paper toward the end of 1899. On the most charitable interpretation, this claim can be taken to mean that he *re*read it late that year, this time with new eyes.

My motive for reconstructing the trajectory of Correns's investigation has not been to "unmask" yet another rediscoverer of Mendel's laws. My main interest in this case study and others like it grows rather out of a desire to trace the way experimental systems develop their own dynamics and to point out the unexpected directions in which they can lead scientists.[83] Correns appears as a particularly interesting example in this respect precisely because he *could* have known "it" in advance. He even had important information to hand when he was first setting up his experimental system. From the standpoint that was his at the time, however, this information made no sense to him. For his original intention was not to discover the rules of hybridization, but to shed light on the process that leads to the formation of xenia.

It can of course be deemed a lucky side-effect of this original intention that Correns had to focus on characters which he expected to become visible in the germs. This turned out to be crucial for the further course of his experiments. Pointing to the paradox, we might say that the xenia first prevented him from recognizing the transmission ratios, but ultimately *enabled* him to do so. The seeds that he collected and set aside to sow the next generation served him as a physical and so to speak natural digital protocol: they had either green or yellow cotyledons. Correns could reopen this "protocol," his boxes of peas, whenever he liked, and so reconsider his findings years after first arriving at them—including findings to which he had at first paid no mind. Of course, if what was involved had not been seeds, then these traces would have vanished long since, together with the plants that produced them. Only after Correns had spent some four years familiarizing himself with the hybridization system of *Zea mays* and *Pisum* did this characteristic of his system become relevant. And it was only then that he realized that one possible interpretation of his results pointed in a new direction. The recursive reorientations and assurances made possible by certain material attributes of experimental systems constitute a basic, generalizable feature of research. Researchers rely on them in their laborious endeavor to assign meaning to the data they obtain in their experimental efforts.