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The Hereditary Statistics of Hugo de Vries

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INTRODUCTION

Today, Hugo de Vries is chiefly remembered as the first of three botanists who, in 1900, publicly announced that they had discovered what we now call the laws of Mendel. All three maintained that they had found the laws on their own and that, at the moment they did their discovery, they had been completely unaware of the fact that the Austrian amateur botanist Gregor Mendel (1822–1884) had published similar conclusions already in 1866. Whereas his contributions to the development of evolutionary thought are generally unappreciated or simply unknown, De Vries is credited in many surveys on the history of genetics for his rediscovery of Mendel's laws. It is generally accepted that, together with his two fellow-rediscoverers, Carl Correns from Tübingen and Erich von Tschermak-Seysenegg from Vienna, De Vries made these basic rules of genetics widely known to the scientific world. The year 1900 can be considered as the year of birth of modern genetics, and Hugo de Vries as one of the founders of the discipline.

Among historians of biology the fame of De Vries as a rediscoverer is mingled with a good deal of notoriety. That he was indeed the first who published the rediscovered laws nobody can deny. But his claim that he was also an independent rediscoverer is widely doubted. Over the past 40 years many attempts have been made to reconstruct the way De Vries has arrived at his rediscovery.[1] Some researchers have found evidence that supports De Vries' claim, but they form a minority. The more recent studies, in particular, have argued that De Vries' views on the nature of the material carriers of hereditary characters prior to his 'rediscovery' was so non-Mendelian in several respects that it is virtually impossible that he found the famous laws on his own. It must have been only after the incidental reading of the original paper of Mendel, presumably sent to him in early 1900 by his colleague and friend Martinus Beijerinck, that De Vries formulated them. Frustrated and irritated, it is said, De Vries first silently changed his original views quite substantially to bring them into line with those of Mendel, and subsequently completely absorbed Mendel's findings in his much cherished theory of speciation through genetic mutation, giving them eventually only a minor position in his elaborate theoretical framework.

Although different in approach and conclusion, there is one point all researchers agree on: there is a vexing lack of sources to rely on. And those that are present are for a good part vague, contradictory, hard to verify or difficult to interpret. It is, for instance, a great difficulty that notes of the experiments De Vries carried out in the years prior to the announcement of the rediscovery are almost completely lacking. De Vries kept his notes in exercise books that he called 'Journalen' (Journals), keeping one Journaal each year. He probably started this practice in 1889 and certainly continued it until his death in 1935.[2] Each right-hand page of the Journalen was devoted to one experiment and, when needed, De Vries continued his notes on the opposite page or somewhere else in the book. The next stage in an experiment was recorded in a new Journaal. Cross-references kept the several stages together. The only copies of the Journalen that are present are those covering the years 1928–35, when De Vries had since long drifted away from the scientific *avant garde* and had more or less lost his way in the labyrinth of *Oenothera* deviations.[3] Of the other Journalen, only some odd pages are present. From those of the years 1889–1900, a mere 34 pages and the cover of the Journaal of 1899 have survived.[4] From these scanty remnants we can conclude that De Vries cut out the pages from the Journalen, possibly to reconstruct the lines of his experiments and to facilitate the writing of his opus magnum *Die Mutationstheorie* in 1900–03. The cover of the Journaal of 1899 still has the outer rims of the pages attached to its back. I troubled myself to count these strips of only a few millimetres width and concluded that the book once contained 284 pages. If we assume that each Journaal was of the same size as this one (the Journalen from 1928 to 1935 indeed are), the total number of Journaal-pages for the period 1889–1900 must have been 3408. The sad conclusion is that the pages that remain make up only 1% of the original amount. Next to his Journalen, De Vries kept notes in other books and probably on loose sheets. A number of these types of notes are also present, but it is impossible even to guess how much has been preserved and how much has been lost as we have no indication of the original extent. Apparently, De Vries did not attach much value to his research notes after he had used them for his publications. The notes that are present all seem to owe their survival to the fact that De Vries could reuse them. Of some, the back had remained clear so they could serve the economical De Vries as scribbling paper. Other sheets he gave a second life as a separator in a bunch of photographs.[5]

In this paper, I shall discuss some of the surviving notes.[6] I hope to show that they hold new, unexpected and valuable information for a more detailed picture of the rediscovery story. A more detailed picture, but unfortunately not a clearer picture. The information the notes give on De Vries' reasoning and thinking is unique, compared with other notes and his publications. It is impossible to say how representative the notes are and to draw firm conclusions from them. Besides, the puzzling, often contradictory, elements in De Vries' thinking that earlier researchers have demonstrated are not refuted by the new information. They remain as puzzling as before, and combined with the facts presented here the confusion only seems to increase. One thing is clear: the door is not closed yet. And I am afraid it never will be.

THE THEORY OF PANGENESIS

The principal source for De Vries' views on heredity in the years prior to 1900 is his book *Intracellulare Pangenesis*, written in the summer and autumn of 1888 and published in one of the early months of the following year.[7] In the intermediate decade De Vries published many papers on several topics related to heredity, but in none of them is he as explicit on his ideas about the nature and behaviour of the material carriers of the hereditary information as he is in this book. It is only in the last part of the second volume of *Die Mutationstheorie* of 1903 that De Vries discussed his views again in a rather elaborate way. From occasional remarks in papers from the 1890s, the discussion in *Die Mutationstheorie,* and letters to his friend and colleague Jan Willem Moll, Professor of Botany at the University of Groningen, it is clear that his reasoning was always firmly rooted in the ideas he had laid down in *Intracellulare Pangenesis.* His belief in their great value remained just as strong in later years. Both Mendel's laws and the mutation theory were derived from them, and the correctness of the laws and the theory was in turn a splendid confirmation of the original views. *Intracellulare Pangenesis* was translated into English in 1910, and as late as 1918 a translation into Dutch was published of the first and the last part of the book.[8] And when in February 1923 De Vries read a 1922 paper by Thomas Hunt Morgan on 'The mechanism of heredity' in which the chromosome theory is discussed, he simply noted in one of his exercise books: 'Dit mechanisme is nog precies hetzelfde als in *Intracellulare Pangenesis*' (This mechanism is still exactly the same as in *Intracellulare Pangenesis*).[9]

Intracellulare Pangenesis was De Vries' comment on the hereditary ideas of Charles Darwin. In the second part of his *On the Variation of Animals and Plants under Domestication* (1868) Darwin had described his 'provisional hypothesis of pangenesis'. All characters of an organism, Darwin had stated, are the visible expressions of information that is carried by invisible particles that reside in the cells. He depicted these particles, that he called 'gemmules', as representatives of the cells. They were 'thrown off' by each cell during all parts of its life, that is, during all the successive stages in its development, carrying all the characteristics the cells had on the moment the gemmules were produced. Gemmules moved freely through the body, from cell to cell. New cells, originating from old cells, were blank; they received the instruction how to function and how to develop in the form of an influx of gemmules coming from the cells that had produced them. In addition, gemmules from all cells moved to the reproductive organs where they amassed in the germ cells. All hereditary information from an individual was in this way passed on to its offspring.[10]

Even as a student, Hugo de Vries opposed Darwin's hypothesis of pangenesis. In one of the theses that accompanied his dissertation (1870) he stated that 'de hypothese der pangenesis ... de veranderlijkheid der soort niet (kan) verklaren' (the hypothesis of pangenesis cannot explain the variation of a species).[11] In the next 15 years, while pursuing a fairly successful career as a researcher in plant physiology, De Vries further shaped his ideas on heredity that he eventually presented in *Intracellulare Pangenesis.* From letters that he sent to his friend Moll during the writing of the book, it appears that De Vries had great difficulties in expressing his views in a clear and consistent way. De Vries had a profound knowledge of cell physiology and was well aware of the latest developments. But he knew much less about heredity. The subject was hardly studied by scientists. The real experts on the subject were nurserymen. They fairly mastered the transmission of characters from one generation to another at hybridization, but their ability was the outcome of centuries of practical work. The underlying mechanism was a mystery to them and they felt no need to unravel it. As a consequence, De Vries was quite speculative in his hereditary views. Moll played an important role in the completion of *Intracellulare Pangenesis*: he kept an eye on De Vries' reasoning and in this way saved him from several errors.[12]

De Vries made some considerable changes to Darwin's hypothesis of pangenesis. The most important change was the elimination of the transport of particles, both from one cell to another and from all cells to the reproductive organs. The assumption of this transport, De Vries argued, was not supported by the facts that Darwin had presented and that had became known since his publication. On the basis of new facts and insights he even concluded that the transport could be regarded as completely unnecessary. It was generally accepted that new cells emerge from the splitting of already existing cells. When it is assumed that all hereditary information is present in each and every cell, then at cell division all the information is simply transferred to the daughter cells. Physiological research had shown that this principle did not only hold for somatic cells but also for germ cells. There was not much difference between the two, De Vries argued. The only point was that the latter type contributes to the propagation of the species and the former does not.

De Vries had at least one strong motive for abandoning the idea of transport of gemmules. The idea that successive phases in the life of a cell were 'recorded' in the gemmules and that these gemmules moved to the germ cells implied that new characters acquired during lifetime could be passed on to the offspring. This was the old Lamarckian idea of the heredity of acquired characters, an idea that was strongly opposed by De Vries. The recent work of the German physiologist August Weismann (1834–1914) had to his mind clearly demonstrated that the whole idea was completely untenable. Pangenesis itself was not at all weakened when the transport hypothesis was eliminated, De Vries stated. Darwin had introduced it only as an auxiliary hypothesis to explain some exceptions that the great master thought could not be sufficiently understood without it.

Instead of an intercellular transport of hereditary particles, De Vries proposed an intracellular transport from the cell nuclei to the cytoplasm to explain cell differentiation. He imagined the nucleus to be a kind of storehouse where all types of hereditary carriers were present. Some of them wandered from the nucleus into the cytoplasm to fulfil their specific duties; that is, only those types of particles that gave the cell its specific traits. In the terminology of De Vries, these carriers became 'active'. All the other particles, that had no function in that particular cell, just stayed in the nucleus; they were in a 'latent' state. Changes from activity to latency and vice versa could occur. They were the source of the sudden disappearance and appearance of characters. Each character De Vries pictured as an independent unit. This is a very important point to him; he stresses it time and again.[13] It is the core of pangenesis: the appearance of a species is made up of many different hereditary units. The same sort of units can be found in different species. They are like the chemical elements: all species in nature can be considered as 'das Ergebniss unzähliger verschiedener Kombinationen und Permutationen von relativ wenigen Faktoren'. Hybridization in particular demonstrates very clearly that the units can be mixed in every possible way.[14]

De Vries' hereditary particles were of a completely different nature to those of Darwin. That is why De Vries thought it appropriate to give them another name. He chose to call them 'pangenes', to express their close relation to Darwin's hypothesis of pangenesis. De Vries could only speculate on the structure of the pangenes. He thought that they certainly could not be identical to the chemical molecules. They had to be 'morphologische, jede aus zahlreichen Molekülen aufgebaute Gebilde'.[15] Pangenes had to be living things that fed, grew and multiplied by splitting themselves in two. An ever-continuing multiplication was essential. It ensured that the pangenes were present in sufficient quantities for a more or less equal distribution over the two daughter cells at cell division. Furthermore, each particular kind of pangene had to be present in a sufficient number of copies to be able to show the character it was carrying and to perform its job properly in the cytoplasm. But sometimes, De Vries argued, things went differently. The distribution of the pangenes over the two daughter cells was not always equal, and multiplication was sometimes less than normal and sometimes greater than normal. An increase or decrease in the number of pangenes was the result. Besides, the splitting of a pangene did not always result in two identical pangenes. It could happen that a new pangene would arise, having a new structure and, as a consequence, carrying a new character. Changes in the normal process of multiplication was hence the source of the two kinds of variation Darwin had already distinguished.

> Nach der Pangenesis kann es zwei Arten von Variabilität geben. Diese werden von Darwin in folgender Weise unterschieden. Erstens können die vorhandenen Pangene in ihrer relativen Zahl abwechseln, einige können zunehmen, andere können abnehmen oder gar fast verschwinden, lange Zeit unthätig gebliebene können wieder aktiv werden, und schliesslich kann die Verbindung der einzelnen Pangene zu Gruppen möglicherweise eine andere werden. Alle diese Vorgänge werden eine stark fluktuierende Variabilität reichlich erklären. Zweitens aber können einige oder mehrere Pangene, bei ihren successiven Theilungen, ihre Natur mehr oder weniger ändern, oder, mit anderen Worten, es können neue Arten von Pangenen aus den bereits vorhandenen entstehen. Und wenn die neuen Pangene sich, vielleicht im Laufe mehrerer Generationen, allmählig so stark vermehren, dass sie aktiv werden können, müssen neue Eigenschaften an dem Organizmus zur Ausbildung gelangen.

The first type of variation had to be responsible for 'die zahllosen kleinen, fast alltäglichen Variationen und Monstrositäten', the second type for the variations 'auf welche die almählig steigende Differenzirung des ganzen Thier-und Pflanzenreiche beruht'.[16] It was to be this species-forming variation, under the new name 'mutability' given to it by De Vries, that formed the principal subject of *Die Mutationstheorie* a decade later.

De Vries was not very successful with *Intracellulare Pangenesis*. The book did not sell very well (the publisher still had copies in stock as late as 1910[17]) and De Vries' ideas were accepted by only a small number of his colleagues. His views were highly speculative and his arguments apparently unconvincing. Besides, De Vries was no exception with his pangenesis. There were more theories on heredity circulating at the end of the 19th century, some proposed by scientists that had a much greater reputation in the field than De Vries, such as Oscar Hertwig, Carl von Nägeli and August Weismann.[18] It was possibly this lack of success that made De Vries remain silent, not discussing or promoting his theory too openly in the decade following its publication.

THE USE OF STATISTICS

De Vries has stated several times that *Intracellulare Pangenesis* was the starting point for his research that eventually led him to the formulation of his mutation theory.[19]

However, this is a simplification. *Intracellulare Pangenesis* was rather an interlude. In the 1870s De Vries was collecting deviating, monstrous specimens, looking for variations that might be of evolutionary interest. His first breeding experiments also date from this period. On 15 October 1881, De Vries wrote to Darwin 'for some time I have been studying the causes of the variations of animals and plants, as described in your treatise on the variations of animals and plants under domestication, and have endeavoured to collect some more facts on this theme'.[20] The basic tenets of his pangenesis theory had already been described in a paper that he wrote in the summer of 1886,[21] and the basic tenets of the mutation theory can already be discerned in *Intracellulare Pangenesis.* There is undeniably a good deal of consistency in De Vries' reasoning from at least the mid 1880s up to the early 1900s. New and original elements were brought in, however, in the course of the 1890s, resulting from the enormous amount of experimental work De Vries did to elaborate his theoretical ideas. One of these new elements was the use of statistics. This new way of working eventually became very important to De Vries. It gave him new evidence against Darwin's theory of the origin of new species by minute changes over a long period, and hence evidence in favour of his own theory of the sudden appearance of new species by pangenetic change. Moreover, it led him to theorize on the splitting and combination of hereditary characters.

De Vries derived his statistical method initially from the book *Anthropométrie, ou mesure des différentes facultés de l'homme*, written by the Belgian mathematician, astronomer and sociologist Adolphe Quetelet (1796–1874) and published in 1870. In the introduction, Quetelet stated that the aim of his book was 'de faire connaître les parties les plus importants du corps humain, ainsi que le développement des lois qui concernent l'homme'. The main point Quetelet tried to make was that the physical and mental characters of man are subjected to mathematical laws. When measuring traits such as height, weight and strength in a group of comparable persons (i.e. persons of the same age, from the same region, etc.) it appeared that the majority had more or less the same size. Deviations from this mean type follow a simple rule, Quetelet stated: the greater the deviation is, the rarer it occurs. When the measurements of the mean type and the deviations are graphically expressed, with the measured values on the x-axis and the number of the observed values on the y-axis, the result is a Gaussian, bell-shaped curve. The majority of the group forms the top of the curve, those that deviate in a negative way form the left side of the curve and those that deviate in a positive way form the right side. Quetelet noted that this curve was very much akin to a curve showing the normal distribution. This curve is the graphical representation of the expansion of the formula $(a+b)^n$, the so-called binomium of Newton. The form is prompted by the laws of probability. Quetelet's conclusion was that the appearance of man's outer and inner characters are governed by the same laws.[22]

Hugo de Vries probably first heard of Quetelet's statistical work in the late 1880s through Julius MacLeod (1857–1919), Professor of Botany at the University of Gent (Belgium). The two men met for the first time in 1885 and kept in contact ever since. On 30 September and 1 October 1887, MacLeod was in Amsterdam to attend the first Nederlandsch Natuur- en Geneeskundig Congres. De Vries was vice-president of the section Natuurlijke Historie en Biologie, which held its own meeting during these 2 days. On the first and the second day of the meeting of this section, MacLeod read a paper on 'De bevruchting der bloemen door de insecten (statistische beschouwingen)' (The fertilization of flowers by insects (statistical considerations)). De Vries lectured on the second day.[23] MacLeod's father, Aimé MacLeod, had been one of the correspondents of Quetelet and was well informed about his work. Julius himself came to value the statistical method only in the early 1880s, then used it with great enthusiasm for several years but abandoned it after highly critical remarks from two men he reckoned to be experts on the subject. When after some years other researchers appeared to use the method, MacLeod picked it up again.[24] It is not clear what De Vries' opinion was of the use of statistics in biology when he became acquainted with MacLeod.[25] From his publications it is clear that De Vries carried out statistical measurements as early as 1886. Around that same time, De Vries had already developed his own image to represent continuous variation within a group of specimens from the same species, which differed from that of Quetelet only in appearance. His image had the form of a target, with the individuals of the most frequently occurring form in the centre and the deviating forms in circles around it; the greater the deviation, the farther it stood from the centre.[26]

Quetelet had restricted himself to measurements of man, but he was convinced that the principles he had discovered were valid 'pour tous les êtres vivants, soit animaux, soit plantes'. For De Vries, who was every inch a botanist, this was an important point. Immediately after reading Quetelet he tried to check it. In a paper, written in the first half of 1890, De Vries expresses his appreciation for Quetelet's discovery of the presence of the normal distribution in nature. He illustrates the phenomenon by giving data for the number of rows on cobs of corn. This is, as far as I know, both the first time he mentions Quetelet and his first symmetrical curve.[27] In November 1891, De Vries again applied the statistical method and obtained symmetrical curves. He measured the length of fruits of 75 specimens of *Helianthus annuus* and the length of 99 fruits from a single specimen of *Oenothera lamarckiana*. The results of the second experiment De Vries depicted on a lecture plate, combining a curve which shows the normal distribution with the curve of the numbers he had actually found. Besides the bell curve he wrote: 'Wet van Quetelet (Law of Quetelet) $(a+b)^n$'.[28]

In the spring of 1892, De Vries continued his experiments. He now tried to influence a given variation and, as a consequence, the form of the corresponding curve. In the years 1892–94, he managed to shift the top of a curve to the right or to the left through manuring and selection.[29] He also succeeded in changing a half-curve to a symmetrical curve,[30] and eventually to a new half-curve, which was skewed in the opposite direction.[31] Further, De Vries managed to separate two varieties that were mixed and whose combined presence was indicated by a curve with two peaks.[32] And finally, he isolated a variety that initially had not shown itself in the curve.[32]

De Vries' interest in statistics was probably stimulated further through the cooperation with Edward Verschaffelt (1868–1923), a pupil and assistant of MacLeod from Gent. Verschaffelt worked in De Vries' laboratory from late 1891 until early January 1892, mainly to become acquainted with experimental physiology. In May 1893, after he had set up courses in physiology at the university in Gent using his Amsterdam experience, Verschaffelt again came to Amsterdam where he was appointed as an assistant of De Vries. In the years 1894–99 he published several papers in which continuous variation is analysed statistically.[33]

It was probably in the autumn of 1893 that De Vries read the paper of W.F.R. Weldon 'The variations occurring in certain decapod Crustacea – I, *Crangon vulgaris*', published in the *Proceedings of the Royal Society of London* of 1890.[34] Weldon (1860–1906), lecturer on invertebrate morphology at the University of Cambridge, describes in this publication that he had collected measurements of a particular kind of shrimp and had worked these data out in curves. In doing this, Weldon admitted, he had been greatly helped by the mathematician Francis Galton (1822–1911). 'My ignorance of statistical matters was so great that, without Mr Galton's constant help ... this paper would never have been written.' The object of the investigation was first to determine 'the average length of three or four organs ... and secondly the frequency with which the average length and every deviation from it occurred in one or two local races'. Weldon describes how, 'following [the] way, which is that adopted by Mr Galton', he expressed his data in so-called 'curves of error': 'At equal distances along a given base, ordinates are erected equal in number to the observations, one ordinate being proportional to each observed value of the organ. By joining the tops of these ordinates, a curve is obtained'. Weldon then goes on to describe how he established the values of the Median (the ordinate that is erected in the middle of the base and separates the number of observations into two equal parts) and the two Quartiles (the ordinates that form the boundaries of the first and third quarters of the base, separating the curve in four equal parts and making check points at 25%, 50% and 75% of the observations). Finally, he compared the curves produced from the data with a curve showing the normal distribution in which the Median is taken as 0 and the two Quartiles as $+1$ and -1 (the 'possible error'), respectively.

De Vries applied Galton's method, as described in Weldon's paper, to the data of the length of 568 fruits of *Oenothera lamarckiana* he had collected in October 1893. On a page of one of his notebooks he drew a curve of error, established the Median and the Quartiles and compared the empirical curve with the normal curve, just as Weldon had done (Fig. 9. A transcription of the original Dutch text and an English translation are given in Appendix 1).[35] But some difficulties arose. De Vries had drawn an x-axis representing the number of measurements with a unit of 2 mm and a y-axis representing the deviation from the Median with a unit of 1 cm. The result was a histogram and to obtain a curve De Vries had drawn a smooth line through the centres of the tops of the bars. These points did not correspond with the ordinates of the theoretical curve of error for which Weldon had given the values of the deviation from the Median (for 5%, 10%, 20%, 30% and 40% of the measurements, deviating both positively and negatively). For a proper comparison of the empirical curve with the theoretical one it was necessary that the deviation belonging to any given ordinate could be calculated, De Vries wrote in his notebook. But De Vries did not know how Weldon had calculated the values; he had not given the formula for that. For the same reason De Vries could not establish the values of the two Quartiles, the two main reference points of the deviation from the Median, in an accurate way. De Vries was not very enthusiastic about Galton's 'curve of error' and he preferred the type of curve Quetelet had used with the observed values on the x-axis and the number of observations for every value on the y-axis. 'De curven $(a+b)^x$ zijn voor mijn werk beter' (The curves $(a+b)^x$ are better for my work), he concluded.

Despite this conclusion (or perhaps just because of it), his interest in Galton's work was raised and he started looking for the mathematician's publications. In a letter dated 17 November 1893, he asked his friend and colleague Jan Willem Moll whether he had any books by Galton because he would like to read them.[36] Moll's answer is not known, but somehow De Vries managed to get hold of Galton's *Hereditary Genius* (1869) and *Natural Inheritance* (1889) during the following months. After a careful study he came to value Galton's work at least as much as Quetelet's. The 'law of Quetelet' now became 'the law of Galton–Quetelet', the curves he drew he now called

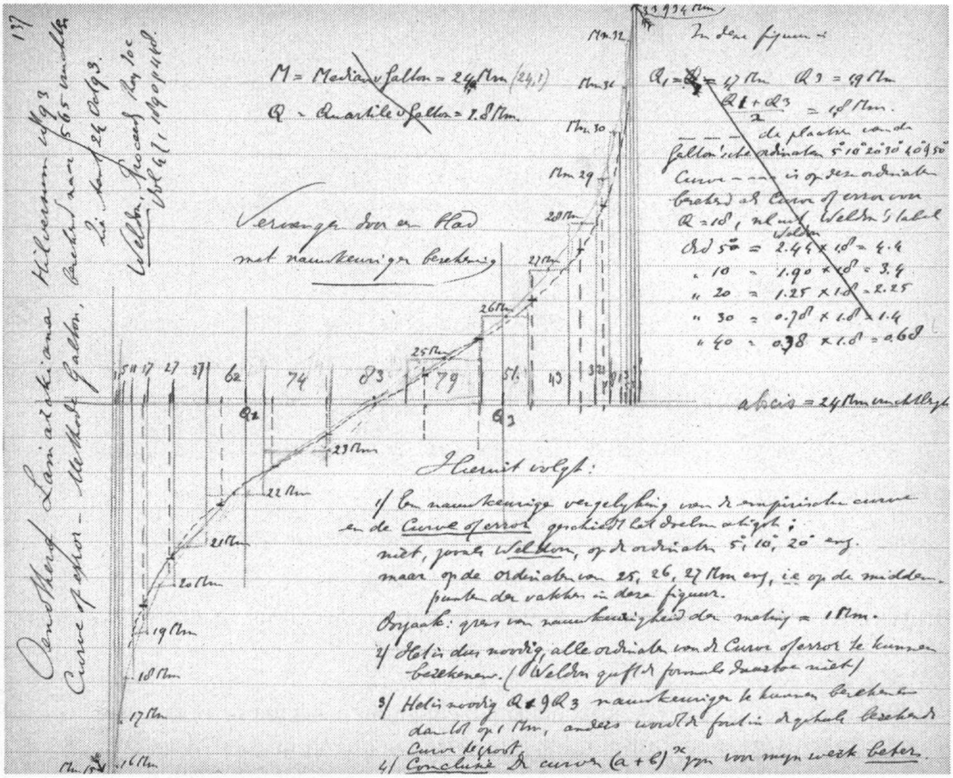

Fig. 9. A curve showing continuous variation in 568 fruits of *Oenothera lamarckiana*, drawn by De Vries according to the method Francis Galton had discussed in his book *Natural Inheritance* (1889) (Library of the Biological Centre, University of Amsterdam: Archive Hugo de Vries).

'Galton curves' and the calculation of the Median and the Quartiles became a standard operation after drawing a curve. He did, however, still prefer the bell-curve that Quetelet had used. The name 'Galton curve' he used henceforward was thus quite inappropriate.

THE LAWS OF CHANCE

Whether it was through the reading of Galton or not, in the early months of 1894 De Vries was at last totally convinced of the great value of the statistical approach for the study of the laws of continuous variation (or 'fluctuating variability', as he preferred to call it). He now wrote his first paper on the subject, which was received for publication by the *Berichte der Deutschen Botanischen Gesellschaft* on 20 July 1894.[37] In that same year he prepared a revised, third edition of his *Leerboek der Plantenphysiologie* (*Textbook of Plant Physiology*). To the paragraph on 'Heredity and variability' he added a new passage in which he discussed the law of Galton–Quetelet.[38] Other papers on continuous variation in which statistics were used appeared in 1895, 1896, 1898, 1899 and 1900.[39] In most of his publications, De Vries restricted himself to the presentation of his experiments, the data they yielded and the conclusions that could be drawn from them. Only seldom did he discuss the theoretical side of the matter. The 1894 paper in the *Berichte* and the *Leerboek* are the most informative in this respect.

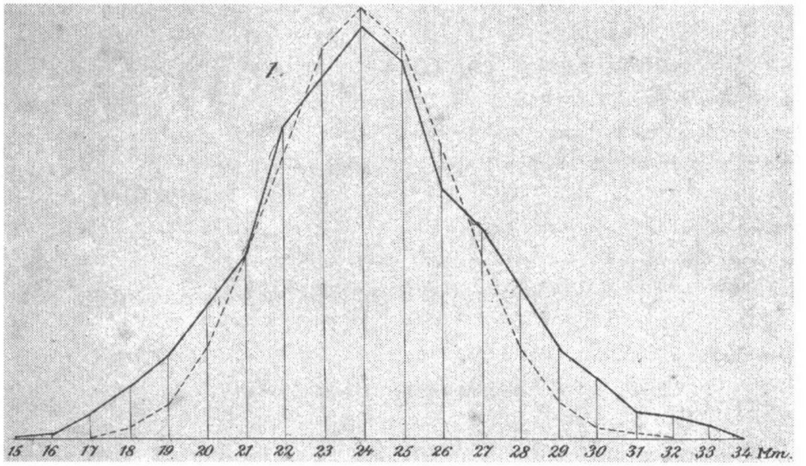

Fig. 10. A curve showing continuous variation in 568 fruits of *Oenothera lamarckiana*, compared with a curve of a normal distribution (from Hugo de Vries (1894): Über halbe Galton-Curven als Zeichen discontinuirlicher Variation. *Berichte der deutschen botanischen Gesellschaft* 12: 197–207).

In the *Leerboek*, De Vries states that continuous variation is ruled by two separate laws.

> De eerste wet is, dat elke afzonderlijke eigenschap slechts in twee richtingen varieeren kan, n.l. toe- en afnemend. Overal, waar het den schijn heeft, alsof eene eigenschap in meerdere richtingen varieeren kan, overtuigt men zich bij nader onderzoek, dat men met eene vereeniging van twee of meer eigenschappen te doen heeft (The first law is that each distinctive character can vary in only two directions, namely increasing and decreasing. Everywhere when it looks as if a character can vary in more directions, one should convince oneself by a closer look that one is dealing with a combination of two or more characters).

To illustrate this 'law', De Vries gives the curve of the length of 568 fruits of *Oenothera lamarckiana*, mentioned above. The example was very appropriate indeed: length can only increase and decrease. The second law is that:

> de afwijkingen van eenig orgaan of eigenschap ... zich (groepeeren) om de gemiddelde waarde daarvan, als om een centrum van grootste dichtheid, volgens de leer der waarschijnlijkheidsrekening (the deviations of any organ or character group around the mean value, like a centre with the greatest density, according to the theory of probabilities).

De Vries concludes with:

> De reden, waarom de variabiliteit deze eenvoudige mathematische wet volgt, is daarin gelegen, dat de grootte van een eigenschap in elk gegeven geval door een zeer groot aantal omstandigheden bepaald wordt, en dat deze omstandigheden door het toeval beheerscht worden (The reason why

> the variation follows this simple mathematical law is, that the size of a character is determined in every possible case by a very great number of circumstances, and that these circumstances are governed by chance).

Earlier in his discussion, De Vries had explained that when the binomium $(a+b)^n$ is expanded to a high value for n, the result is a symmetrical curve that has the same shape as a curve that results from an experiment as discussed. What De Vries means here is stated more clearly by his assistant Edward Verschaffelt in a paper on asymmetrical Galton curves from 1895. When explaining the meaning of the binomium, Verschaffelt says:

> Concret ausgedrückt hat dieser Satz die folgende Bedeutung: die Vertheilung der Abweichungen von verschiedener Grösse um den Mittelwerth einer gegebenen Eigenschaft herum lässt sich am besten erklären durch die Annahme der Einwirkung einer grossen Anzahl von unabhängigen Variationsfactoren, welche ebenso stark im Sinne einer Vergrösserung, wie einer Herabsetzung des Werthes der betreffenden Eigenschaft wirken.

In other words: the exponent of the binomium can be compared with the 'Variationsfactoren' in nature. Because these can work 'in allen denkbaren Stufen der Intensität', it must have a high value to arrive at a curve that is similar to an empirical curve. The two terms a and b can be compared with the 'Vergrösserung' and the 'Herabsetzung des Werthes der betreffenden Eigenschaft', respectively. Normally, a and b are equal. When this is not the case, it simply means 'dass die negativen Abänderungsursachen einen grösseren Einfluss haben als die positiven, oder umgekehrt'. In his paper Verschaffelt gives several examples of skewed curves and argues that they are special cases of binomial curves.[40]

To illustrate the laws of chance and the normal distribution for his readers and listeners, De Vries sometimes made use of the so-called 'Russian billiard'. It was a device that Francis Galton had constructed and he had featured in his *Natural Inheritance*. Galton had described it as 'a frame glazed in front, leaving a depth of about a quarter of an inch behind the glass. Strips are placed in the upper part to act as a funnel. Below the outlet of the funnel stands a succession of rows of pins stuck into the backboard, and below these again are a series of vertical compartments'. When a quantity of shot is put inside the apparatus, 'the cascade issuing from the funnel broadens as it descends, and, at length, every shot finds itself caught in a compartment immediately after freeing itself from the last row of pins. The outline of the columns of shot that accumulates in the successive compartments approximates to the curve of frequency'. The reason why the shot took this shape was, according to Galton, 'that a number of small and independent accidents befall each shot in its career. In rare cases, a long run of luck continues to favour the course of a particular shot towards either outside place, but in the large majority of instances the number of accidents that cause deviation to the right, balance in a greater or less degree those that cause deviation to the left.'[41]

In a lecture on variation he held for the Maatschappij Diligentia in The Hague on 18 March 1899, De Vries supplemented the example of the Russian billiard with Pascal's triangle. The triangle is a system of numbers, triangularly arranged in rows consisting of the coefficients in the expansion of the binomium $(a+b)^n$, with $a=b=1$ and n ascending from 0 to infinite. If one counts the amount of shot that falls into the compartments of the billiard, De Vries told his audience, it appears that the shot falls according to the numbers of Pascal's triangle. 'De val van die knikkers wordt dus beheerscht door dezelfde wet als de gewone kansberekening, die opklimt van $(a+b)$ en $(a+b)^2$ tot $(a+b)^n$, waarbij dan $a^2+2ab+b^2$ gelijk is aan $1+2+1$ enz.' (So the fall of the shot is governed by the same law as the ordinary theory of probabilities, that ascends from $(a+b)$ and $(a+b)^2$ till $(a+b)^n$, with $a^2+2ab+b^2$ being similar to $1+2+1$, etc.). De Vries had lecture plates of both the Russian billiard and Pascal's triangle and it is likely that he used them in this lecture. To make his point more clear, De Vries actually wrote the figures of Pascal's triangle next to the pins of the billiard on the lecture plate. Thus, if there were only three rows of pins, the shot would be distributed in three compartments in the ratio 1:2:1.[42]

In his 1894 *Berichte* paper, De Vries discusses the phenomenon of continuous variation in relation to his theory of pangenesis. He quotes the passage from *Intracellulare Pangenesis* where he distinguishes 'fluctuirende Variabilität' and 'artenbildende Variabilität', the first being caused by 'dem wechselnden numerische Verhältnis der einzelnen Arten von Pangenen, welches Verhältnis ja durch deren Vermehrung und unter dem Einflusse der äusseren Umstände ... verändert werden kann', the second being caused by the fact that 'die Pangene bei ihre Theilung zwar in der Regel zwei, dem ursprünglichen gleiche neue Pangene hervorbringen, dass aber ausnahmsweise diese neuen Pangene ungleich ausfallen können'. The subject of this 1894 paper is to show that in a half curve another type of the same species can be hidden. In this particular case, a type of *Ranunculus bulbosus* with (more or less) 10 petals appears to be hidden in a population of *Ranunculus* with five (and more, but not fewer) petals. The seemingly continuous variation of the five petaled *Ranunculus* was, to De Vries' mind, the sudden appearance of a previously latent character. It is not always easy to establish if such a new type is present, De Vries says in the introduction of the paper. 'Die Pangene des neuen Merkmales können ... offenbar selbst zu einer fluctuirenden Variation Veranlassung geben, welche sich mit der des Artcharakters oft vermischen wird.' What De Vries is probably saying here is that continuous variation is in fact a variation in the number of pangenes. The laws of chance bring about that most individuals of a population have about the same number of pangenes, that some individuals have more and some have less.

To be clear: the shot in the Russian billiard is of course not the same as the pangenes in a population that shows continuous variation. The curve from the billiard shows the distribution of shot that was pushed in two different directions, whereas an empirical curve is the graphical representation of the distribution of individuals with, from the left to the right, an increasing number of pangenes. Although they yield the same curve, the two are entirely different phenomena. I think De Vries was well aware of that. In his 1899 Diligentia lecture he compared the curve of the billiard with a curve representing the size of a sample of ordinary beans. His conclusion was: 'de grootte van de boonen ... hangen af van precies dezelfde wet die het vallen van de knikkers in het Russisch biljard beheerscht' (the size of the beans depends on exactly the same law which governs the fall of the shot in the Russian billiard). The purpose of the billiard was only to demonstrate the validity of the laws of chance, not what actually was happening in terms of pangenes.

THE *VERONICA* NOTE: THE 5/16 LAW

It is now time to turn to the surviving pages from De Vries' notebooks that form the actual subject of this paper. Before doing that, I want to summarize the main points of De Vries' views on heredity and statistics so far.

1. All characters of an individual are connected to material carriers called pangenes, which reside in the cell nuclei.
2. The pangenes, and hence the characters, can act as independent units.
3. Pangenes are present in either the active or the latent state.
4. The intensity of a character is expressed by the number of pangenes present.
5. As a rule, the number of pangenes and hence the intensity of a character within a group of individuals from the same species is distributed according to the normal distribution.
6. An infinite number of influences, acting together according to the laws of chance, determines the distribution of the number of pangenes and hence the intensity of a character.
7. The intensity of a character can vary in only two directions: it can increase or decrease.

The first of the two notes I will discuss is the most revealing for De Vries' thinking, but it is at the same time the most difficult to interpret (Fig. 11). (A transcription of the original Dutch text and an English translation are given in Appendix 2.)[43] The quintessence of the matter is clear, however: De Vries tries to mould a set of data from an experiment in such a way that it harmonizes with a general law. The plant that he is concerned with is a specimen of *Veronica longifolia* (long-leaved speedwell); it is a perennial plant that normally has blue flowers. In *Die Mutationstheorie* De Vries tells us that he received a *Veronica* plant from his friend Moll in 1889. This specimen later appeared to be a hybrid between a blue-flowering plant and a specimen from the white flowering variety. From seeds collected in 1892, De Vries yielded 214 plants in 1893, of which 48 (22%) were white and the others blue.[44] The data mentioned in the note come from 'de kinderen van Moll's plant' (the children of Moll's plant). We are most probably dealing with the same plant, but with another experiment than that described in *Die Mutationstheorie*. The percentage of 22 cannot be reconstructed from the data which, moreover, seem to have been collected in 1896.[45]

The percentages in the note are described by De Vries as 'erfcijfers' (hereditary numbers). It is not directly clear what is expressed by them. From the second part of the note it must be concluded that they denote percentages of white flowering individuals in an otherwise blue population. In *Die Mutationstheorie*, De Vries discusses 'hereditary number' in the description of his 'Methode der Erbzahlen' (method of hereditary numbers). For 'hereditary number' he gives a clear definition: 'Die procentische Zusammensetzung einer reinen Samenprobe werden wir die Erbzahl ihrer Eltern nennen'. The percentage of a certain visible character in the offspring of a plant is a reflection of the invisible inner structure of the hybrid parents of this same offspring. In modern terms: the 'Methode der Erbzahlen' is a way to establish the genotype of a F1 by using the phenotype of the F2.[46]

When we apply this definition to the *Veronica* note, we must conclude that each percentage denotes a group of plants stemming from a single mother plant. De Vries had 15 (and after a closer look at his data 2 months later 17) percentages or groups with 1–33% white flowering plants and an unspecified number of percentages or groups

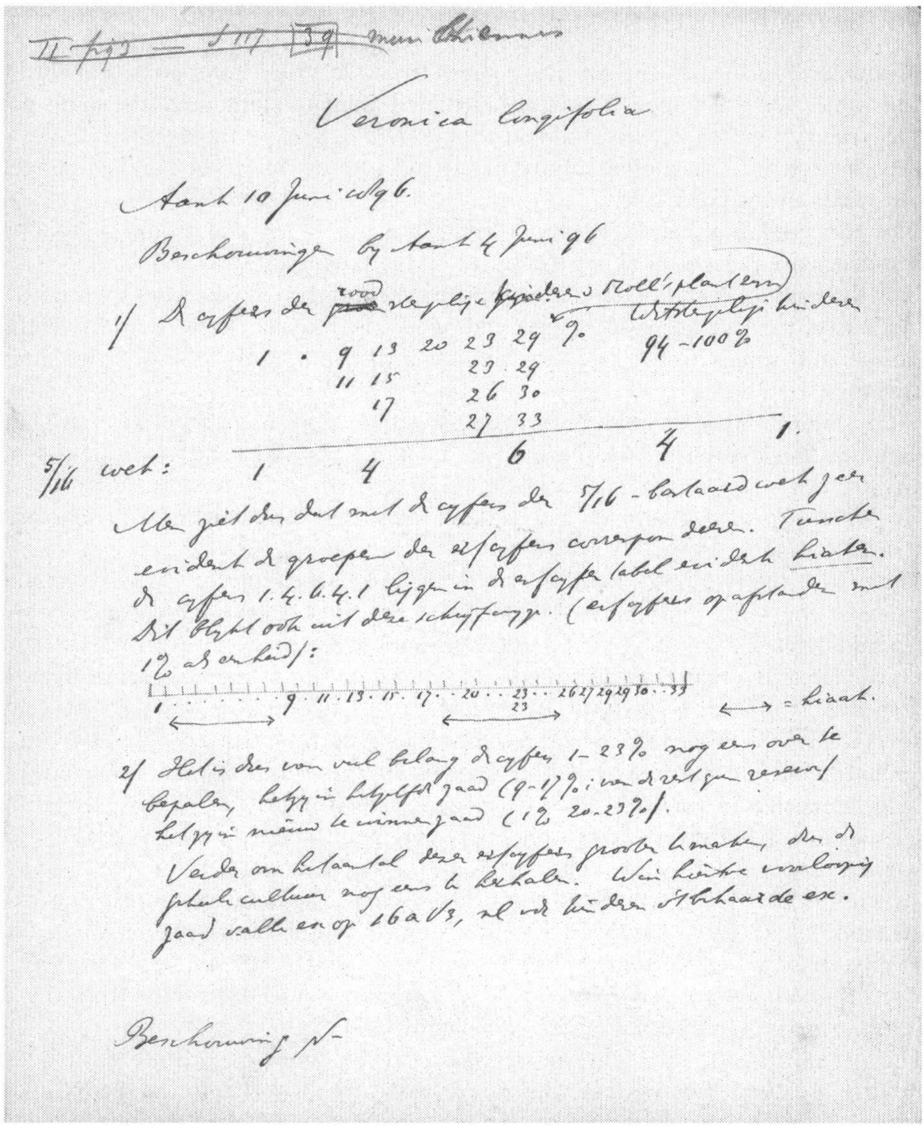

Fig. 11. (a) Note from Hugo de Vries in which he analyses the results of an experiment with *Veronica longifolia*, summer 1896 (Library of the Biological Centre, University of Amsterdam: Archive Hugo de Vries).

with 94–100% white flowering plants. My interpretation is that these 17-plus groups together form a F2-generation, that the 17-plus parent plants make up the F1-generation and that the plant from Moll forms the P-generation. There is further evidence that supports this interpretation, but I will give it later in this paper to avoid complicating the discussion any further. At the same time, I will demonstrate that De Vries is using his Erbzahlen method in this *Veronica* experiment.[47]

De Vries groups the percentages into two categories: percentages 1–33 are plants coming from parents with a red stem; percentages 94–100 are plants coming from

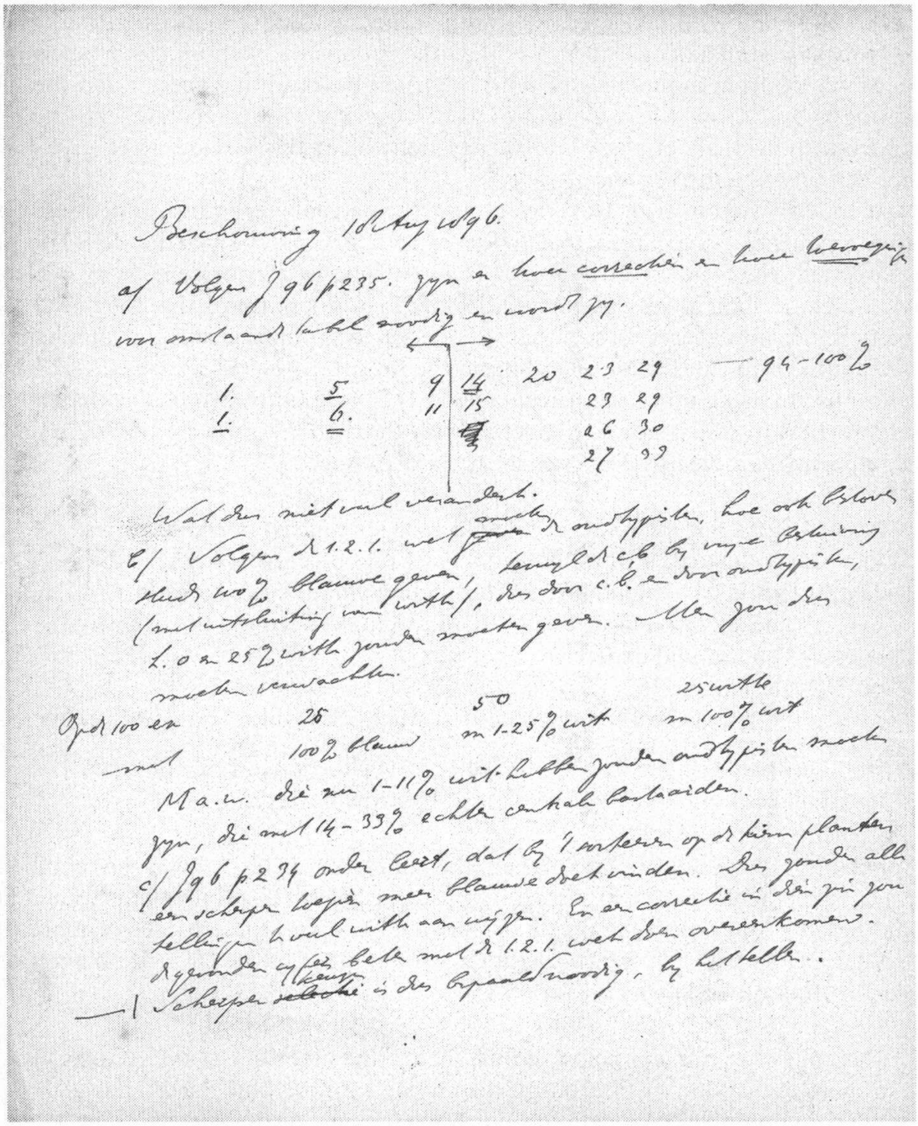

Fig. 11. (b) Reverse of the note on *Veronica longifolia.*

parents with a white stem. The percentages of the first category seem to be the most important: De Vries gives them all, whereas those of the second category are simply lumped together. The colour of the stem of *Veronica* is closely connected with that of the flower. In his paper 'Bastaardering en bevruchting' (1903), De Vries says that the blue-flowering species (the 'wild type', in present day terminology) and the hybrid have a foliage of 'blauwachtig groen, naar het roodbruine overgaande' (bluish green, shading into reddish brown). The white flowering variety, on the other hand, has 'helder groene stengels en zuiver donkergroene bladeren' (bright green stems and pure dark green leaves).[48] If we allow 'bright green' to be the same as 'white', than the remark in the note is explained. The consequence is that the groups of offspring with percentages 1–33 can come from individuals of both the true blue-flowering species and the blue-flowering hybrid form, whereas the groups of offspring with percentages 94–100 must come from individuals of the white variety only. That this is indeed the case I will, again, demonstrate further on.

Next to a division in two, De Vries groups the percentages in five categories. Their relative frequencies appear to match the ratio 1:4:6:4:1, which he calls 'de 5/16 bastaard wet' (the 5/16-law of hybrids). The matching is 'zeer evident' (very evident).

After a closer look at his data, 2 months later, De Vries notices that they need some correction.[49] It now seems to him that it is better to group the range of numbers not in five but in three categories, according to the ratio 1 :2:1 ('de 1.2.1-wet', 1.2.1-law). The groups are made up of the percentages 1–11, 14–33 and 94–100. The matching of the data with this law is not as perfect as with the 5/16 law, however. What ought to have happened is stated by De Vries in the next passage:

> According to the 1.2.1-law, all the old type specimens, in whatever way they are pollinated, always have to yield 100% blue ones, whereas the central hybrids at free pollination (excluding white ones), so by central hybrids and old type individuals, should yield between 0 and 25% white ones. So one should expect
>
> | | | | |
> |---|---|---|---|
> | on 100 specimens | 25 | 50 | 25 |
> | | with 100% blue | with 1–25% white | with 100% white |
>
> In other words: those that now have 1–11% white should be old type individuals, those with 14–33% central hybrids, however.[50]

Apparently, something is going wrong: the data from the experiment are conflicting with De Vries' theoretical expectations. The presence of 1–11% white plants where there should be only 'old type' blue plants on the one hand and the presence of more than 25% white plants with the 'central hybrids' on the other hand, De Vries blames on a careless sorting of seedlings:

> Journal 1896 page 234 below learns, that at the assorting of the seedlings a more critical look will produce the finding of more blue ones. Thus all the counting would indicate too much white ones. And a correction in that way would better harmonize the numbers that have been found with the 1.2.1-law. Thus a more careful choice is certainly necessary when counting.

This passage suggests that the percentages are actually not of white flowering plants but of seedlings whose white stem indicates that they will flower white. This suggestion becomes more likely when we consider that *Veronica* normally flowers in July and August while the data are collected in June. Apparently, De Vries had difficulty in establishing with certainty whether the stem of a seedling was red or white.

Here, my statement that the percentages are not those from a F1-generation but from a F2-generation is confirmed. De Vries says: old type ones should yield old type ones (but give 1–11% whites), and central hybrids should yield a maximum of 25%

whites (but give more). So, the various groups of individuals showing the percentages 1–11 and 14–33 indeed have different mothers that, moreover, are not even of the same type: these are old type individuals and central hybrids, respectively. Secondly, De Vries' conclusion that 'those that now have 1–11% white should be old type individuals, those with 14–33% central hybrids' affirms my statement that De Vries is using his Erbzahlen method: the nature of the plants in the F2 (expressed in the percentages) is used to deduce that of the plants of the F1.[51] At the same time, this conclusion demonstrates that the percentages 1–33 refer to the offspring of both individuals of the true blue-flowering species and the blue-flowering hybrid form, as I proposed before.

For 'old type individuals' and 'central hybrids' De Vries gives no definition in the note. The descriptions do not occur in his publications. I think we can safely translate them as 'individuals of the original type' (or 'the species') and 'hybrids'. But what about the rest of this cryptic little story? As I said earlier, the quintessence of the note is clear: De Vries first tries to match his data with the range 1: 4: 6: 4: 1, then with the range 1: 2: 1. Apparently, both ranges can be applied to the same set of data and are interchangeable. Indeed, the two have a strong common factor: both are ranges from Pascal's triangle.[52] They are the expansions of $(a+b)^4$ and $(a+\mathrm{b})^2$, respectively (5/16 is only a shorter description of 1:4:6:4:1, namely 5 combinations of all 16 possible permutations). Apparently, De Vries thought that the laws of chance governing the distribution of the intensity of a character in a population (continuous variation) also rules the appearance of a character in the offspring of hybrids.

How should we interpret this thinking? Earlier in this paper I showed that De Vries compared the *a* and *b* in the binomium with the only two possible directions in which the intensity of a character can vary: increase and decrease. Translating this idea for quantitative characters to the qualitative character 'flower colour', we can imagine *a* and *b* to be the two colours blue and white. They are the only two possible directions in which the character 'colour' can go. De Vries compared the exponent in the binomium with the influences that guide the variety in one of two directions. If we apply this definition in this case, the consequence is that De Vries must be assuming that with hybrid offspring there are only four or just two influences. But why such a small number of influences, and what must be their nature?[53]

Recourse to Quetelet can show us what De Vries had in mind when he applied the two ratios mentioned in the note. In *Anthropométrie*, Quetelet gives a clearly illustrated discussion of the laws of chance. 'Un phénomène, quel qu'il soit, dépend de causes favourables ou défavourables à son arrivée. Dans le premier cas, les causes favourables ou défavourables peuvent être égales en nombre; dans le second cas, les causes favourables peuvent être plus ou moins nombreuses que les causes contraires.' This is the same point Galton demonstrated with his Russian billiard. When the influences that direct the shot to the left and the right side of the billiard are working in the same degree, the shot will drop in the middle compartment. When these influences are not equal, the shot will drop somewhere at the left side or the right side of the middle. The more unequal the influences are, or, to put it differently, the more dominating one of the influences is, the greater will be the deviation. As the example to illustrate this law Quetelet gives the drawing from a bowl with an equal number of white and black balls.

> Supposons ... qu'on fasse différents tirages, d'abord de deux boules, puis de trois, puis de quatre, etc.; nous aurons successivement, en désignant par *b* et *n* les boules blanches et noires:

$$(b+n)=b+n$$
$$(b+n)^2=b^2+2bn+n^2$$
$$(b+n)^3=b^3+3b^2n+3bn^2+n^3$$

On p. 281 of his book, Quetelet gives a table with the numbers of the possible combinations of drawings from one to 20 balls. The ratios are those of Pascal's triangle. In the pages that follow, Quetelet discusses the possible combinations of drawings with replacing each ball after drawing. Again, now on p. 284, he gives a table with the numbers of combinations for one to 20 drawings. In the next paragraph, Quetelet discusses the weight of man. Again, he discusses the probabilities, this time using the example of the drawing of 16 balls from a bowl with black and white balls in different proportions. The numbers that result are again listed in a table (pp. 353–354).

From his own copy of *Anthropométrie* we can conclude that De Vries studied these discussions and tables in detail. They may even have been the most important parts of the whole book to him. In the contents, next to the summary of the chapter in which the laws of chance are discussed, De Vries wrote: 'Curventabel p. 281, 284' (table of curves page 281, 284). On the half title of the book, De Vries wrote: 'Tabel p. 281, tabel p. 353' (table page 281, table page 353). These notes must have served him as quick references. Also, next to the right side of the table on page 281, he copied a series of numbers listed at the left side of the table, probably to facilitate its use.[54]

In his 'rediscovery papers' written in 1900, De Vries explains the emergence of three different types in the offspring of a monohybrid cross with the expression $(d+\mathrm{r})(d+\mathrm{r})=d^2+2dr+r^2$, with d representing the dominant character and r the recessive character. Corcos and Monaghan[55] have criticized De Vries for this use of the binomial expansion to demonstrate Mendel's law. It was 'an inappropriate mathematical model', in which germ cells are multiplied rather than united. To them, it is further proof that De Vries did not really understand Mendel's paper, otherwise 'he would not have chosen this as an appropriate model'. Moreover, with his probable substitution of d and r with 0.5 and 0.5 ('their relative frequencies as gametes') in order to arrive at the relative frequencies of 25, 50 and 25%, he introduced 'a second and incompatible use and meaning for the same set of symbols'. When we think of his work in statistics, as discussed earlier, we do not need to wonder why De Vries used the binomial expansion. It was a formula he had been familiar with for a decade and it had served him well in expressing his ideas on the role of chance in nature. I think De Vries understood perfectly well what was going on. I even dare to say that, thanks to his work with statistics, he understood the principles of segregation and fertilization better than Mendel did. To Mendel, there was, in all probability, no segregation of carriers on the formation of germ cells nor a combining of them upon fertilization. A homozygous individual was d or r to Mendel, but to De Vries it was dd or rr.[56] Mendelian segregation to De Vries was exactly the same thing as the drawing of two balls from a bowl.

The question now is whether De Vries was also thinking of combinations and permutations of two different characters when he applied his 5/16 and 1.2.1 laws to the data of his *Veronica* experiment in the summer of 1896. If we take the 5/16 law into account we have to assume (following Quetelet's example) the corresponding expansion to be $(\mathrm{B}+\mathrm{W})^4$, where B = blue and W = white. The following range is the result:

1BBBB: 4BBBW: 6BBWW: 4BWWW: 1WWWW

According to De Vries' description of the Erbzahlen method, the inner structure of parent plants is mirrored in the composition of their offspring. Because he grouped the hereditary numbers (the offspring in the F2) according to the ratio 1: 4: 6: 4: 1, we must assume that De Vries supposed that the individuals of the F1 had an inner structure according to the range given above. But why should there be four factors expressing the colour involved? And are these factors to be viewed as separate pangenes, or groups of similar pangenes? Suppose the combinations are made up of 2 × 2 factors, then the possible germ cells of the P-generation must have been BB, BW, WB and WW and, as a consequence, the P-hybrid must have had the structure BBWW. How did this combination come into being? Was it the merging of BB and WW, a crossing between a pure 'old type individual' and a pure individual of the white variety? But why BB and not simply B?

The interpretation of the F2-generation also raises several questions. It is easy to see that BBBB-plants can only yield blue offspring, whatever model of fertilization is assumed. The placing of the hereditary number 1 here by De Vries is fairly sensible. But what about the BBWW plants? Suppose they produce BB, BW, WB and WW germ cells, then on self fertilization the ratio given above would appear. With blue dominating over white, there would only be 6.25% whites in the offspring. If we assume that a BBWW plant would only produce B and W germ cells, the result of self-fertilization would be 25% BB, 50% BW and 25% WW; when dominance is assumed, this indeed matches De Vries' grouping. But why would BBWW plants of the F1 behave differently from BBWW plants of the P?

Things really become complicated with BBBW plants. They would yield a mere 6.25% of whites with one-factored germ cells, and just 0.4% whites with two-factored germ cells. Both numbers are incompatible with the percentages 9–17 that De Vries gives.

It is not possible to say on the basis of this note what De Vries exactly had in mind with his '5/16 law of hybrids'. I have found only one more reference to it in the Hugo de Vries archive, but this is of little help. The reference is written on a tiny scrap of paper, a fragment of a page from a notebook, with only half sentences.[57] It seems to be a description of some hybridizing experiment taken from a paper or book. There are two remarks in the note that De Vries has put in brackets and to which he has added 'dV', by which he must be indicating that these remarks are additions by himself to the original text. My interpretation is that the note refers to some plant with peloric flowers which is 'absolutely constant', as De Vries says. A crossing with the 'normal type' (the species) only yielded normal type individuals; De Vries has added here that this is similar to what he has observed with *Oenothera*, *Lychnis* and another species of which the name is not clear. Individuals arising from the seeds of these hybrids, again had peloric flowers; here De Vries has added the question whether in this case the 5/16 law holds good. Put this way, there is a strong similarity with the *Veronica* note: when the species form is crossed with a variety (P-generation), uniform hybrids arise (F1). On fertilization, individuals of the variety appear again, possibly in the ratio 1:4:6:4:1. But just as with the *Veronica* note, the underlying mechanism De Vries had in mind remains a mystery.

THE *VERONICA* NOTE: THE 1.2.1 LAW

If we interpret the second part of the *Veronica* note where De Vries uses the 1.2.1 law to explain the results of his experiment, keeping Quetelet's example of drawings in mind, the complications are far fewer. In fact, the only complication is that everything De Vries says perfectly matches a Mendelian interpretation which, as earlier researchers have argued, De Vries was not aware of in 1896. If we use the modern Mendelian terminology, De Vries is simply saying in the quotation given on page 442: if old type individuals (blue-flowering, homozygous *Veronicas*) are pollinated with homozygous and heterozygous (both blue-flowering) plants, the offspring in the F2 will consist of both homo- and heterozygotes. As blue is dominant over white, the offspring will be 100% blue-flowering. If hybrids (blue-flowering, heterozygous *Veronicas*) are pollinated with homozygous and heterozygous plants, the offspring (F2) will consist of homozygous blue-flowering, homozygous white flowering (between 0 and 25%) and heterozygous blue-flowering plants.[58] Homozygous white flowering plants would yield, on self-fertilization, 100% white offspring in the F2 (this De Vries does not say, but it is indicated in the scheme reproduced above). De Vries is using here the 1.2.1 law two times, to predict the composition of the offspring of both old type individuals and hybrids. The distribution of old type individuals, hybrids and individuals of the white variety in the F1 is also according to the 1:2:1 ratio. Nothing special really: general validity is, of course, the essence of a law.

My two assumptions, put forward earlier – firstly, that the percentages 1–33 belong to offspring of red-stemmed, blue-flowering old type individuals (homozygotes) and central hybrids (heterozygotes); and secondly, that De Vries uses his Erbzahlen method – make perfect sense with this Mendelian interpretation. De Vries says that the old type individuals and the hybrids from the F1 underwent free pollination (excluding white-flowering individuals). Because both were red-stemmed and blue-flowering it could not, on the basis of their appearance, be decided which plant was a homozygote and which plant was a heterozygote. And this is the very thing De Vries tries to find out by using his Erbzahlen method. We may wonder here why De Vries had not prevented free pollination by packing the flowers in paper bags, a practice he was already familiar with in 1894.[59] When the plants of the F1 had been fertilized exclusively by their own pollen, there was no question about their inner structure. Now De Vries is led astray by hereditary numbers that can vary from 0 to 25%, and indeed are.

From this second part of the *Veronica* note it becomes clear why the percentages of the offspring of the white variety are not mentioned separately but are lumped together. The nature of the white plants did not have to be analysed by the Erbzahlen method because it was already clear. The percentages are just given for completeness. Why De Vries groups his percentages as he does is now also becoming clear. Because old type ones and hybrids should appear in the F1 in the ratio 1: 2 (according to the 1.2.1 law), the percentages of the offspring (the F2) should be according to this same ratio. De Vries groups them in the two categories 1–11% (6 numbers) and 14–33% (11 numbers); 6:11 is fairly equal to 1:2. Also in the case of the 1:4:6:4:1 ratio, De Vries must have grouped his data in such a way that they match a presupposed ratio: 1% (1 number), 9–17% (5 numbers), 23–33% (8 numbers) give the ratio 1:5:8, which to De Vries was apparently in sufficient accordance to the 1:4:6 ratio. He was quite satisfied with it, but nevertheless he regrouped the numbers after a closer look to make them match another law. Not only were the laws interchangeable, so were the numbers. They were all hereditary numbers from blue-flowering plants which, as mentioned before, could not be identified from their appearance. But the regrouped hereditary numbers did not bring solution of the problem any nearer because they conflicted with what would be expected on the basis of the 1.2.1 law: 'those [individuals of the F1] that now have

1–11% white [individuals in their offspring] should be old type individuals, those [individuals of the F1] with 14–33% [white individuals in their offspring] central hybrids however'. De Vries blames himself for having caused the deviations by not establishing the colour of the seedlings with sufficient accuracy. He kept true to his law. But the fact that the hereditary number 0 never occurred suggests that all 17 mother plants of the F1 were in fact hybrids and that there had been no homozygotes at all!

Now, all this nicely matches the modern Mendelian interpretation. But is it also in line with De Vries' thinking about heredity and statistics we discussed earlier? For a Mendelian 1: 2: 1 distribution it is necessary to think of germ cells that contain a character in its pure form, unspoiled by its antagonist. And here we stumble on a problem that has already been noticed by many researchers but was most plainly illustrated by Theunissen.[60] In De Vries' pangenesis, characters were expressed by more than one material bearer (his pangenes). In the perception of De Vries, Theunissen concluded, hybrids must have 'a mixture of active and latent pangenes ... sitting in the cell nucleus like beans in a bag'. At cell division the pangenes were 'split up into presumably more or less equal portions'. Theunissen gives an example of a cross between a parent plant containing pangenes for red with a parent plant containing pangenes for white (latent pangenes for red). He concludes that 'all that can be expected for the F2 generation in our example is some red individuals, a few white, and many shades in between'. An accurate prediction of the ratios of the recombinants in the F2 is not possible. To put it in terms of statistics: the pangenes in the germ cells of a F1-hybrid would be distributed in a normal way. Some germ cells only contain pangenes for red, and some only contain pangenes for white. These are the rare cases which we find at both ends of the curve of the normal distribution. Most germ cells will contain a mixture of both types of pangenes, the most frequently occurring case being a mixture of more or less equal numbers; it will form the peak of the curve. Self-fertilization will be a merging of two normal curves. The most probable result will be the emergence of an individual with more or less equal numbers of both pangenes. Only in very rare cases will equal types of pangenes fuse, leading to an individual that is as pangenetically pure as one of the grandparents. Just as rare is the combination of only unequal pangenes, the result being again a mixture of equal numbers of both types of pangenes. The individuals of the F2 will again form a normal curve, with a mean of ordinary red, and with a rapidly diminishing number of individuals with an increasingly intense red colour on one side, and an equally rapidly diminishing number of individuals with a diminishing red colour, ending in plain white, on the other side.

If we follow De Vries' reasoning a bit further, things must be even more complex. In our discussion of De Vries' ideas on continuous variation we saw that he thought that the number of pangenes of each character fluctuates according to the normal distribution. So, not only the relative number of pangenes for red and white varies, but also the absolute number of pangenes for red and white. An individual could be white because it contained only pangenes for white (latent pangenes for red), but it could just as well be that it contained a very small number of pangenes for red and, due to this scarcity, they were not expressed.

It is a strange thing to see that De Vries stuck to his entirely non-Mendelian idea of more pangenes for one character after 1900. 'Verändertes numerisches Verhalten der Pangene ist somit die Grundlage der fluctuirenden Variabilität', De Vries simply says in *Die Mutationstheorie*, as if nothing had been changed by the rediscovery of Mendel's laws.[61] We can, however, solve the problem if we assume that De Vries was not thinking in independent pangenes, but in independent groups of similar pangenes, or simply in independent characters as he states time and again in *Intracellulare Pangenesis*. Then the germ cells can become as pure as is needed for the probable combinations of the 1.2.1 law. In his German rediscovery paper, De Vries says: 'Die Pollenkörner und Eizellen der Monohybriden sind keine Bastarde, sondern gehören rein dem einen oder dem anderen der beiden elterlichen Typen an. Für Di- und Polyhybride gilt dasselbe in Bezug auf jede Eigenschaft für sich betrachtet'.[62] In *Die Mutationstheorie* similar remarks can be found. At the end of the second volume, for instance, De Vries describes the assumption of Bateson that 'bei der Bildung der Sexualzellen die dominirenden und die recessiven Anlagen sich vielleicht nicht so vollständig trennen, dass nicht, sei es stets, sei es ausnahmeweise, in den Sexualzellen neben den recessiven eine Spur des dominirenden, oder neben den dominirenden eine Spur des recessiven Merkmales vorhanden bleibe'. The data are still scarce, but 'vorläufig spricht die Erfahrung allerdings gegen diese Annahme'. In a footnote he gives an example of the character of *Oenothera lata* (a compact, small-leaved mutant from *O. lamarckiana*), which after 10 consecutive crosses is not weakened nor changed and 'somit wohl eine feste Einheit dar(stellt)'.[63] In *Die Mutationstheorie* we can also see that it was not clear to De Vries how he had to picture this supposed unity: 'Ob diese Anlagen selbst die Pangene des Kernfadens sind, oder ob jede Anlage aus einer Gruppe von gleichnamigen Einheiten aufgebaut ist, ist eine sehr wichtige Frage, welche später sich wohl durch die Erfahrung entscheiden lassen'.[64]

The question whether one or several pangenes were involved in the expression of a character kept haunting De Vries. In 1909, while reading a book of Eduard Strasburger entitled *Ueber Reduktionstheilung, Spindelbildung, Centrosomen und Cilienbilder im Pflanzenreich* (1900), De Vries jotted down some notes in which he argues that when a character is expressed by more than one pangene the existence of meiosis would be unnecessary. Without meiosis, then on fertilization 'zouden de mannelijke en vrouwelijke groepen van gelijknamige pangenen dubbel zoo groot worden. ... Ergo pleit 't bestaan der reductiedeeling ervoor, dat elke eigenschap slechts op 1 pangen berust' (the male and female groups of similar pangenes would double. ... So the existence of meiosis speaks in favour of the fact that each character is determined by only 1 pangene).[65] In 1918, in his farewell speech at his retirement, De Vries expressed himself very vaguely (or should we say diplomatically?): continuous variation is described as 'den wisselenden invloed der voorhandenen pangenen op den groei en de vorming van het individu' (the alternating influence of the pangenes at hand on the growth and development of the individual).[66]

Besides the 'purification' of the germ cells, we also have to assume that De Vries was thinking in terms of dominance and recessivity to make his ideas match further modern Mendelian genetics. In the discussion of his theory of pangenesis we saw that he was thinking in terms of active and latent pangenes. In his rediscovery papers De Vries follows Mendel and uses the words dominant and recessive, but in later publications he preferred to use his own terminology. Sometimes he uses both, apparently regarding them to be synonymous.[67]

Among the notes in the Hugo de Vries archive there are more references to the 1.2.1 law, but they are all from an unknown date or from after the rediscovery. On surviving pages from an index to the Journalen the law is mentioned four times, namely in the cases *Lychnis vespertina* × *L. vespertina glabra* (Journaal 1895); *Oenothera brevistylis* (Journaal 1897); *Lychnis diurna glabra* (Journaal 1898); *Linaria vulgaris peloria* × *L.*

vulgaris (Journaal 1899).[68] The index was probably made for composing *Die Mutationstheorie*, which De Vries kept busy from 1900 up to 1903. It may have been compiled after the rediscovery, and the references can have been added later. The same consideration holds for references in a book in which De Vries kept an index of his dry preparations.[69] From the harvest of 1899 of the cross *Zea mays saccharata* × *Z. mays harlekijn* he had three cobs, 'alle drie bastaardkolven met 25% suikerkorrels ter demonstratie der splitsingswet (1.2.1)' (all three hybrid cobs with 25% sugary kernels for the demonstration of the law of segregation (1.2.1)). On the last page of this book, De Vries made a survey of all the cobs in his collection coming from various experiments; the three specimens 'voor de 1.2.1-wet' (for the 1.2.1 law) are again mentioned. The first recording is not dated; there is no need to assume that it indeed was written down in 1899. The survey of the cobs of corn is dated February 1900. De Vries' German rediscovery paper was received by the *Berichte der Deutschen Botanischen Gesellschaft* on 11 March 1900. Whether De Vries had already read Mendel's paper when he drew up his corn-survey is impossible to tell.[70]

A note on the cross *Oenothera muricata* × *O. hirtella*, also present in the archive of De Vries and dated 11 March 1899, possibly contains an unspoken reference to the 1.2.1 law. In the note, De Vries analyses the amount of tricotyledonous individuals in the offspring of 24 plants from the cross. De Vries jotted down as one of his remarks:

> Het zou zeer goed kunnen zijn dat de gerijpte zaden òf alleen *muricata*, of alleen *hirtella*, of alleen centrale bastaarden waren, en dat de overige mislukt waren. Evenzoo by *O. biennis* × *hirtella* (It might very well be that the ripened seeds were either only *muricata*, or only *hirtella*, or only central hybrids, and that the others have failed. Just as with *O. biennis* × *hirtella*).[71]

After reading Mendel's paper, 1.2.1 became a synonym to De Vries for a Mendelian splitting. He used the phrase in this way as late as 1932.[72]

THE *ASTER* NOTE

Finally, I will discuss the second of the two notes that form the actual subject of this paper (Fig. 12). (A transcription of the original Dutch text and an English translation are given in Appendix 3.) It is a page from the Journaal of 1896.[73] The text is much less obscure than that of the *Veronica* note. Besides, the cross the note is concerned with is clearly discussed in *Die Mutationstheorie*.[74]

The plant that De Vries is dealing with in this note is a white-flowering *Aster tripolium* (sea aster), a rarity because this species normally has blue-purple flowers. Blue dominates over white, so in modern Mendelian terms we would call the white-flowering *Aster* a recessive homozygote. De Vries found it on 20 August 1895, in the village of Huizen among hundreds of ordinary blue-flowering individuals. The flowers had already been pollinated, most likely partly through self-fertilization and partly through the surrounding blue plants. De Vries took the plant with him to his experimental garden in the Amsterdam Hortus Botanicus where the seeds ripened. On 11 April 1896, the seeds were sown and 2 months later De Vries had obtained 72 plants. On the note De Vries described the purpose of this experiment: 'Doel: bloeien allen wit?' (Goal: do all flower white?). Again, 2 months later he wrote down the answer: 'Neen!' (No!). Ten

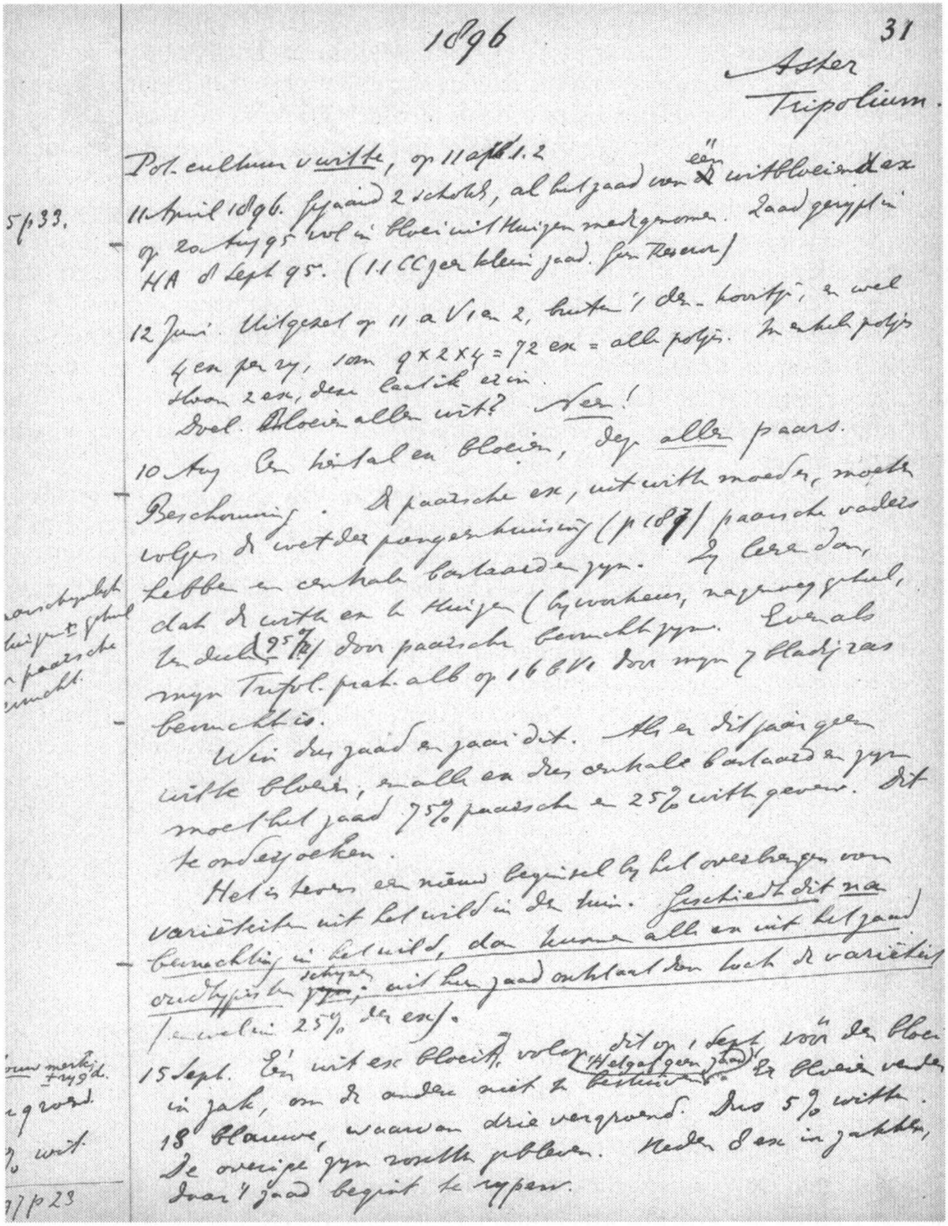

Fig. 12. Note from Hugo de Vries in which he analyses the results of an experiment with *Aster tripolium*, summer 1896 (Library of the Biological Centre, University of Amsterdam: Archive Hugo de Vries).

plants were flowering, all blue. One month later another eight plants were carrying blue flowers, but now there was also one specimen carrying white flowers. In a 'Beschouwing' (consideration) De Vries evaluated the facts and planned the next experiment.

> The purple individuals, from a white mother, must have purple fathers and be central hybrids according to the law of the cross of pangenes (page 187). They learn then that the white individuals in Huizen (by preference, almost totally, partly?) are pollinated by purple individuals. . . .
>
> So, collect seed and sow this. If there are no white flowering individuals this year, and consequently all individuals are central hybrids, then the seed must yield 75% purple and 25% white individuals. This to be investigated.
>
> It is at the same time a new principle in the transportation of varieties from the wild into the garden. When this happens after fertilization in the wild, then all the individuals from the seed can seem to be old type individuals; from their seed the variety will eventually grow (namely in 25% of the individuals).

The new experiment was described in the Journaal of 1897, which unfortunately is not present. In *Die Mutationstheorie*, De Vries reports that the seeds collected from the single white-flowering plant from the F1 yielded only white specimens. Of the blue or purple-flowering plants he collected seeds of seven specimens and in 1897 no less then 682 flowering plants were the result. Of these 169, or 25%, had white flowers, the others only blue flowers.

The whole thing looks like a standard Mendelian cross. A recessive homozygous white-flowering plant is fertilized by pollen with (pan)genes for blue and (pan)genes for white (P-generation). The result is one homozygous white-flowering individual and 18 blue-flowering hybrids (F1). These hybrids give on self-fertilization 25% homozygous white individuals and 75% blue individuals (both homozygous and heterozygous) (F2).

There is no mention of the (seemingly Mendelian) 1.2.1 law in the *Aster* note, but perhaps, as with the crossing of *Oenothera muricata* × *O. hirtella* mentioned above, it is simply not reported. However, there is also room for a good deal of non-Mendelian interpretation here. De Vries speaks of his hybrids as children from a 'white mother' and 'purple fathers'. On the basis of De Vries' pangenesis, we can assume that these mothers and fathers contain only one type of pangene: latent blue and active blue, respectively. There is no need to think that the pangenes are arranged in two separate units, the Mendelian character pairs. On the contrary: this would only make things more complicated. The white specimen is now simply a plant in which the pangenes for blue have become latent, not the result of an incidental pairing of two germ cells with latent pangenes produced by hybrids. De Vries' conclusion in the note that the white individual is pollinated for 95% by blue individuals seems to affirm this view. Apparently, he is not taking into account the fact that the white plant can also be pollinated by hybrid blue plants. De Vries' interpretation of the *Aster* experiment seems to be based on what he describes as 'the law of the cross of pangenes'. The 'page 187' De Vries is referring to is probably from *Intracellulare Pangenesis*. On this page there is nothing about the cross of pangenes, but it is the start of a new chapter in the book called 'Die Hypothese der intracellularen Pangenesis'. It is a summary of the assumptions made up to that point. Perhaps De Vries is not explicitly referring to the cross of pangenes, but to pangenes in general. With a 'cross of pangenes', De Vries possibly means that active and latent pangenes are mixed. Only then is a character pair formed, which can subsequently give pangenetic combinations according to the theory of probabilities in its offspring. Thinking again of the 'white mother' and 'purple fathers' we can assume that the pangenes of the homozygous combinations would fuse to one and the character pair would disappear. In this interpretation, De Vries' thoughts would possibly be exactly the same as Mendel's: the result of the self-fertilization of a hybrid is A: 2AB: B, rather than AA: 2AB: BB. Incidentally, note that in this partly non-Mendelian interpretation it must still be assumed that De Vries thinks of separate units of pangenes and of pure germ cells.

CONCLUSION: IN SEARCH OF THE LAWS OF NATURE

It is tempting to conclude on the basis of the *Veronica* and the *Aster* notes that Hugo de Vries knew Mendel's laws in the summer of 1896. All the necessary ingredients are there: the two independent antagonistic characters; the dominance (activity) of one and the recessivity (latency) of the other; the appearance of uniform hybrids in the F1 (with the *Aster* experiment); the splitting in the ratio 1: 2: 1 (with the *Veronica* experiment) in the F1; the predicted splitting in the ratio 3: 1 (with the *Aster* experiment) in the F2; the predicted splitting in the ratio 3: 1 (with the *Veronica* experiment) in the F2. The *Veronica* note, however, clearly demonstrates that there was also a 5/16 law running through De Vries' mind that competed with the 1.2.1 law. The *Aster* note moreover showed that non-Mendelian thinking cannot be excluded.

As to the question of whether De Vries was an independent rediscoverer of Mendel's laws or not, I would like to propose a compromise. Yes, De Vries knew Mendel's laws before 1900 (or, to put it more correctly, he knew the rule that after 1900 would become known as Mendel's first law). But this rule was not the only one he used to interpret the results of his crosses. There were other possibilities he took into account, one of them being the 5/16 law. How much he valued the 1.2.1 law, the 5/16 law, or other models, and how many experiments there were that he could not tie to a general rule at all, we simply do not know because of the lack of material. As I said at the beginning of this paper, the uniqueness of the notes means that we cannot tell how representative is the thinking that appears in them. Nevertheless I like to conclude, on the basis of the notes discussed and the conclusions of earlier researchers, that the reading of Mendel's paper was a watershed in De Vries' thinking: the outcome of the clear and systematically arranged experiments of Mendel must have been a revelation to him, triggering him to make the final choice between the several explanations he had worked out himself in the preceding years.[75] So the story, as told by himself, that he had found the laws before he learned of Mendel's paper would be correct. But it is only a part of the whole story. Whether De Vries should be considered an independent rediscoverer of Mendel becomes, with the compromise I propose, a matter of one's personal definitions. Is it correct to speak of an independent rediscovery when the rediscoverer only becomes aware of what he has found after it has been pointed out to him by the discoverer himself?

More important than providing a possible answer to this 'yes or no' question is that the *Veronica* and *Aster* notes give us an inside view of the way De Vries worked. We caught him in the creative process of trial and error. We saw him wrestling with his data, trying to make them match his presupposed, theoretical views. De Vries was thinking very strongly in terms of laws. In this paper we have seen him using the law of Galton–Quetelet, the laws of chance, the 5/16 law, the 1.2.1 law, the law of the cross of pangenes, and the laws of Mendel. How convinced he was of the general validity of laws seems to be represented in his application of statistics, initially to continuous variation of quantitative characters, then to the discontinuous variation of qualitative characters. The rather forced attempts to mould his data from the *Veronica* experiment first to the 5/16 law, and then to the 1.2.1 law, show a comparable case of this procedure. What must have happened during the 1890s is that, firstly, Quetelet convinced De Vries that the normal distribution and the theory of probabilities hold for the continuous variation of the characters of man. Secondly, that De Vries convinced himself that the same laws are valid for continuous variation in the plant kingdom. And finally that De Vries tried to establish the validity of the laws also for the discontinuous variation of qualitative characters in the offspring of hybrids. This last step in particular seems to be an imaginative outburst of a creative mind, but in the case of De Vries it was probably more the outcome of his rigid conviction that nature is governed by laws. What else can be expected of a law that it is valid for different but related phenomena?[76]

De Vries' eagerness to reveal and understand the laws of nature can be found in many places in his publications. In his inaugural address at the acceptance of his professorship at the University of Amsterdam in 1878, he told his future students: 'Van de feiten op te klimmen tot een helder inzicht in de algemeene wetten der natuur, om daardoor de feiten zelven beter te leeren begrijpen, – zietdaar het doel der wetenschap, zietdaar het doel van uw studie' (To climb up from the facts to a clear view of the general laws of nature, in order to understand the facts better – that is the goal of science, that is the goal of your study).[77] In his farewell speech at his retirement in 1918, he expressed the same view, now applied to his mutation theory: 'De onderzoeker moet trachten, de praktijk te bevrijden van die afhankelijkheid van het toeval. Hij moet de wetten opsporen die hem in staat stellen het verschijnsel [der mutabiliteit – EZ] te beheerschen, en naar willekeur gewenschte, voordeelige mutatiën in het leven te roepen' (The researcher should try to free practice from the dependence of chance. He must trace the laws that will enable him to master the phenomenon [of mutability – EZ] and to induce wanted, beneficial mutations at will).[78] These are only two quotations from the numerous writings De Vries published in the 60 years that he was active in science. Many, many more can be added and all contain the same message: it is the goal of science to unravel the laws that govern nature and human society, to make them known so that individuals, governments and industry can use them to increase the well-being of mankind.[79] So, if we could ask Hugo de Vries posthumously if he really discovered Mendel's laws he would possibly deny it. He only uncovered them.

ACKNOWLEDGEMENTS

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NOTES AND REFERENCES

1. From the enormous amount of literature dealing with De Vries' rediscovery I mention here in chronological order those titles that, in my opinion, are the most important: Th.J. Stomps, 'On the rediscovery of Mendel's work by Hugo de Vries', *Journal of Heredity* (1954) **45**: 293–294; Ilse Jahn, 'Zur Geschichte der Wiederentdeckung der Mendelschen Gesetze', *Wissenschaftliche Zeitschrift der Friedrich Schiller-Universität Jena* **7**: (1957–58) 215–227; J. Heimans, 'Hugo de Vries and the gene concept', *American Naturalist* **96**: (1962) 93–104; Ilse Jahn, 'W.O. Focke – M.W. Beijerinck und die Geschichte der "Wiederentdeckung" Mendels', *Biologische Rundschau* **3**: (1965) 12–25; C. Zirkle, 'The role of Liberty Hyde Bailey and Hugo de Vries in the rediscovery of Mendelism', *Journal of the History of Biology* **1**: (1968) 205–218; Garland A. Allen, *Life Science in the Twentieth Century* (New York, 1975); P.W. van der Pas, 'Hugo de Vries and Gregor Mendel', *Folia Mendeliana* **11**: (1976) 229–242; Lindley Darden, 'Reasoning in scientific change: Charles Darwin, Hugo de Vries, and the rediscovery of segregation', *Studies in the History and Philosophy of Science* **7**: (1976) 127–169; Malcolm J. Kottler, 'Hugo de Vries and the rediscovery of Mendel's laws', *Annals of Science* **36**: (1979) 517–538; Margaret Campbell, 'Did De Vries discover the law of segregation independently?', *Annals of Science* **37**: (1980) 639–655; Robert Olby, *Origins of Mendelism* (Chicago and London, 1985[2]); Onno G. Meijer, 'Hugo de Vries no Mendelian?', *Annals of Science* **42**: (1985) 189–232; A.F. Corcos and F.V. Monaghan, 'Role of De Vries in the rediscovery of Mendel's work I. Was De Vries really an independent discoverer of Mendel?', *Journal of Heredity* **76**: (1985) 187–190; A.F. Corcos en F.V. Monaghan, 'Role of De Vries in the rediscovery of Mendel's work II. Did De Vries really understand Mendel's paper?', *Journal of Heredity* **78**: (1987) 275–276; Bert Theunissen, 'Closing the door on Hugo de Vries' Mendelism', *Annals of Science* **51**: (1994) 225–248; I.H. Stamhuis, O.G. Meijer and E.J.A. Zevenhuizen, 'Hugo de Vries 1889–1903: the trauma of Intracellular Pangenesis', accepted for publication in *Isis* 1999. Stomps, Jahn, Heimans, Darden, Van der Pas and Stamhuis think De Vries was an independent rediscoverer, all the other authors deny this for various reasons.
2. Notebooks from the years 1886–89 are present and have another structure (Library of the Biological Centre, University of Amsterdam: Archive Hugo de Vries, inv. no. 152–155). Surviving pages from an index to the Journalen start with the Journal of 1889 (Archive Hugo de Vries, inv. no. 527; Library of the Biological Centre, University of Amsterdam: Archive of the director of the Hortus Botanicus Amsterdam (1874) 1878–1969 (1977), folder 'Militaire zaken').
3. Archive Hugo de Vries, inv. no. 179–181.
4. The cover of the Journaal of 1899 is present in Archive Hugo de Vries, inv. no. 177. The pages from the Journalen are present in Archive Hugo de Vries, inv. no. 523 (Journaal 1892), 527 (1895), 533 (1896), 143 (1898) and 144 (probably 1899/1900).
5. The allegation that De Vries destroyed his notes in order to disguise the fact that he had not independently rediscovered Mendel's laws is mere speculation (Meijer (*n.* 1) 'Hugo de Vries', 217). My impression from the De Vries archive is that destroying and reusing paper was just his common practice.
6. These notes were found by the present author in August 1992 during the inventarization of the archive of De Vries. The archive had been searched through earlier, but surprisingly enough, the notes had escaped the attention of earlier researchers.
7. Hugo de Vries, *Intracellulare Pangenesis* (Jena, 1889).
8. Hugo de Vries, *Intracellular Pangenesis* (Chicago, 1910); translated by C. Stuart Gager; Hugo de Vries, *Intracellulaire Pangenesis* (Amsterdam, 1918); translated by F. van Hengelaar. I must confess that I have not compared these translations with the original German text, but judging from the contents, the introductions and (in the English translation) the incidential remarks of De Vries and the translator in footnotes, I assume that they are close translations.
9. Archive Hugo de Vries, inv. no. 146 (page 124).
10. Charles Darwin, *The Variation of Animals and Plants under Domestication* (London, 1868; 2 vols.) II, chapter 27.
11. Hugo de Vries, *De Invloed der Temperatuur op de Levensverschijnselen der Planten* (The Hague, 1870).
12. The origin of *Intracellulare Pangenesis* as it appears from letters of De Vries to Moll is discussed by Stamhuis (*n.* 1) 'Trauma'.
13. For instance in the chapter 'Die gegenseitige Unabhängigkeit der erblichen Eigenschaften' of *Intracellulare Pangenesis* on page 7, 9, 10, 11, 16, 17, 18, 19, 20, 22, 24–25, 26, 27, 29, 31, 32.
14. De Vries (*n.* 7) *Intracellulare Pangenesis*, 9.
15. De Vries (*n.* 7) *Intracellulare Pangenesis*, 69. See also pages 46 and 188.
16. De Vries (*n.* 7) *Intracellulare Pangenesis*, 73.

17. The English edition of 1910 (*n.* 8) has an advertisement for the original German edition. See also the preface in the Dutch translation of 1918 (*n.* 8).
18. For a contemporary survey, see: Yves Delage, *La Structure du Protoplasma et les Théories sur l'Hérédité et les Grands Problèmes de la Biologie Générale* (Paris, 1895).
19. For instance: Hugo de Vries, *Die Mutationstheorie* (2 vols. Leipzig, 1901–03) II, 691–692: 'Für mich ist die Pangenesis immer der Ausgangspunkt meines Suchens gewesen'; De Vries (*n.* 8) *Intracellular Pangenesis*, 74: In a note to the translator, De Vries says: 'That sentence [An altered numerical relation of the pangens already present, and the formation of new kinds of pangens must form the two main factors of variability] has since become the basis of the experiments described in my *Mutationstheorie*'; Hugo de Vries, 'Mutations in heredity', *The Rice Institue Pamphlet* **1**: (1915) 340: 'On the basis of these theoretical considerations [Darwin's provisional hypothesis of pangenesis – EZ] I proposed the mutation theory'; Hugo de Vries, 'The origin of the mutation theory', *The Monist* **27**: (1917) 406, 409: 'My book on the mutation theory is the combination of all these preliminary studies into a regular discussion of the main principle'.
20. P.W. van der Pas, 'The Correspondence of Hugo de Vries and Charles Darwin', *Janus* **57**: (1970) 200.
21. Hugo de Vries, 'Beschouwingen over het verbeteren van de rassen onzer cultuurplanten', part 14, *Maandblad van de Hollandsche Maatschappij van Landbouw* 1886–1889. The papers 1–16 were written in April-Aug. 1886 (see De Vries' own copy in Library of the Biological Centre, University of Amsterdam).
22. Adolphe Quetelet, *Anthropométrie* (Brussels, 1870). On Quetelet's work and the influence of statistics in science, see Ida H. Stamhuis, 'De "probabilistic revolution" in de wetenschappen', *Gewina* **15**: (1992) 141–152.
23. *Handelingen van het Eerste Nederlandsch Natuur- en Geneeskundig Congres* (Haarlem, 1888) 126, 133–138.
24. P. van Oye, *Hugo de Vries, Julius MacLeod en Edward Verschaffelt. Vriendschap en Wederkerige Invloed* (Brussels, 1961) 7–12.
25. According to Van Oye, Hugo de Vries was very sceptical in the late 1880s when MacLeod introduced him to Quetelet's work. His appreciation grew slowly until 1894, when he was at last totally convinced of its value and even became one of its strongest advocates 'as a new convert usually does' (Van Oye (*n.* 24) *Hugo de Vries*, 6–7, 16–17). Van Oye points to the fact that statistics only gradually enter De Vries' publications, that he was older and 'more calm' than MacLeod and besides, 'the character of De Vries prevented him from being convinced easily' (Van Oye (*n.* 24) *Hugo de Vries*, 3).
26. Hugo de Vries, 'Über halbe Galton-Curven als Zeichen discontinuirlicher Variation', *Berichte der Deutschen Botanischen Gesellschaft* **12**: (1894) 201, 203; De Vries (*n.* 21) 'Beschouwingen', part 2 (this paper was written in the spring of 1886, as is stated by De Vries in his own copy, present in Library of the Biological Centre, University of Amsterdam). In 'Über halbe Galton-Curven', 203, De Vries states that he counted the number of petals of *Ranunculus bulbosus* in 1886 and 1887 'um die Curve zu ermitteln'. However, in 'Beschouwingen' there is no mentioning whatsoever of curves or the law of Quetelet when De Vries discusses variation. His picturing of the target-like distribution of variants makes it clear that De Vries did not know the Gaussian curve as a representation of continuous variation and hence the work of Quetelet in the spring of 1886. In De Vries (*n.* 19) 'Origin', 406, he says that after the publication of *Intracellulare Pangenesis* 'I chanced to meet with Quetelet's *Anthropométrie*'.
27. Hugo de Vries, 'Suikerriet zaaien', *Album der Natuur* (1890) 235: 'Elke eigenschap is variabel, maar de grenzen, waarbinnen zij varieert, kunnen nu eens zeer wijd dan weer zeer eng zijn. ... Binnen de bedoelde grenzen vindt het varieeren volgens eene bepaalde wet plaats. Men noemt deze de wet van Quetelet. Hoe algemeen zij geldt, is nog niet onderzocht, maar zij geldt in elk geval voor die eigenschappen, die in cijfers kunnen worden uitgedrukt.... Het uitvoerigst vindt men deze wet behandeld in Wallace's jongste boek over het Darwinisme, waar zij door tal van voorbeelden, aan het dierenrijk ontleend, is toegelicht' (Each character is variable, but the boundaries within it varies can sometimes be very wide, sometimes be very narrow.... Within the boundaries in question the variation takes place according to a certain law. It is called the Law of Quetelet. How general it is has not yet been investigated, but in any case it holds good for all those characters that can be expressed in numbers.... The most elaborate treatment of this law one finds in Wallace's latest book on Darwinism, where it is illustrated by many examples, taken from the animal kingdom). De Vries then goes on to illustrate the law by the number of rows on cobs of corn. Quetelet is not mentioned by Wallace in his book *Darwinism* (London, 1889). The examples given by Wallace are expressed in curves drawn according to a simplified version

of the method of Francis Galton. This gives me the impression that De Vries had not yet studied Wallace's book when he wrote his paper 'Suikerriet zaaien'. In his discussion of Quetelet's work in *Die Mutationstheorie* I, 35 he states that Wallace discussed this law 'nur in unvollständiger Weise'. De Vries' own copy of Wallace's work (second edition, reprinted in August and October 1889) is in the Library of the Biological Centre, University of Amsterdam. In Archive Hugo de Vries, inv. no. 441 is an offprint of 'Suikerriet zaaien' which, in De Vries' handwriting, bears the date '1 juni 1890' (1 June 1890). This probably is the date when the paper was published.

28. The *Helianthus* experiment is mentioned in De Vries (*n.* 26) 'Über halbe Galton-Curven', 202. The *Oenothera* experiment appears from Archive Hugo de Vries, inv. no. 146 A and the lecture plate which is in University Museum De Agnietenkapel of the University of Amsterdam, cat. no. 076.577.
29. De Vries (*n.* 19) *Mutationstheorie* I, 377–411.
30. De Vries (*n.* 26) 'Über halbe Galton-Curven'.
31. Hugo de Vries, 'Over het omkeeren van halve Galton-curven', *Botanisch Jaarboek* **10**: (1898) 27–61.
32. Hugo de Vries, 'Eine zweigipflige Variationscurve', *Archiv für Entwicklungsmechanik der Organizmen* **2**: (1895) 52–62; Hugo de Vries, 'Über Curvenselection bei *Chrysanthemum segetum*', *Berichte der Deutschen Botanischen Gesellschaft* **17**: (1899) 84–98.
33. According to Van Oye (*n.* 24) *Hugo de Vries*, 17, the collaboration with Verschaffelt was the decisive factor for De Vries' 'conversion' to the statistical approach. However, Verschaffelt had not published on variation before he became an assistent, so it might just as well be that De Vries stimulated Verschaffelt.
34. W.F.R. Weldon, 'The variations occurring in certain decapod Crustacea – I, *Crangon vulgaris*', *Proceedings of the Royal Society of London* **47**: (1890) 445–453.
35. This note is present in Archive Hugo de Vries, inv. no. 156.
36. Central Library of the State University Groningen: letter of Hugo de Vries to J.W. Moll, Nov. 17, 1893: 'Bezit je ook boeken van Galton, *Hereditary genius* enz. Ik kan ze hier niet vinden en zou ze graag lezen' (Do you happen to possess books by Galton, *Heriditary Genius*, etc. I can not find them here and I would like to read them).
37. De Vries (*n.* 26) 'Über halbe Galton-Curven'.
38. Hugo de Vries, *Leerboek der Plantenphysiologie* (Nijmegen, 1895[3]) 294–296. It is not known when De Vries wrote this new passage. The preface of the book is dated February, 1895. The second edition was published in 1885, the first one in 1880.
39. De Vries (*n.* 32) 'Zweigipflige Variationscurve'; Hugo de Vries, 'Sur les courbes Galtoniennes des monstruosités', *Bulletin Scientifique de France et Belgique* **27**: (1896) 395–413; Hugo de Vries, 'Eenheid in veranderlijkheid', *Album der natuur* (1898) 65–80; De Vries (*n.* 31) 'Over het omkeeren'; De Vries (*n.* 32) 'Über Curvenselection'; Hugo de Vries, 'Alimentation et sélection', *Volume Jubilaire de la Société Biologique de Paris* (Paris, 1899) 17–39; Hugo de Vries, '*Othonna crassifolia*', *Botanisch Jaarboek* **12**: (1900) 20–40.
40. Ed. Verschaffelt, 'Über asymmetrische Variationscurven', *Berichte der Deutschen Botanischen Gesellschaft* **13**: (1895) 349–351.
41. Francis Galton, *Natural Inheritance* (London, 1889) 63–65.
42. 'Botanische voordrachten van Prof. Hugo de Vries', *Dagblad van Zuid-Holland en 's-Gravenhage*, 19 and 20 March 1899. Also in: Veranderlijkheid bij uitzaaien', in: P.A. Haaxman (red.), *Maatschappij Diligentia. Natuurkundige Voordrachten* (The Hague, 1899) 85–89. The lecture plates of the billiard and the triangle are now in the collection of the University Museum De Agnietenkapel of the University of Amsterdam (cat. nrs. 076.249 and 076.196, respectively). The plate of the billiard was made by De Vries in 1899, the plate of the triangle bears no date.
43. This note is present in Archive Hugo de Vries, inv. no. 477.
44. De Vries (*n.* 19) *Mutationstheorie* II, 155.
45. The note is dated 10 June 1896 and is a consideration on a note from 4 June 1896. The second part of the note is dated 18 August 1896. Here, De Vries is referring to his Journaal of 1896. This page is not from a Journaal but from one of the other types of notes described in the introduction of this paper.
46. De Vries (*n.* 19) *Mutationstheorie* II, 111–117, esp. 117. 'Hereditary number' is also mentioned in De Vries (*n.* 31) 'Over het omkeeren', 37, where it is defined as 'het percentage-gehalte aan varianten' (the proportion in terms of percentage of variations) of a seed-plant.
47. *Veronica longifolia* is presented several times by De Vries as an example of 'vegatative disjunction', i.e. a plant that shows its hybrid nature by producing both blue en white flowers during life time (Hugo de Vries, 'Das Spaltungsgesetz der Bastarde', *Berichte der Deutschen Botanischen Gesellschaft* **18**: (1900) 86; De Vries (*n.* 19) *Mutationstheorie* II 172; Hugo de Vries, *Species and Varieties* (Chicago, 1905) 284–285; Hugo de Vries,

'Bastaardering en bevruchting', *De Gids* **21**: (1903) 408. A lecture plate of a specimen of *Veronica longifolia* with vegatative disjunction is in the collection of the University Museum De Agnietenkapel of the University of Amsterdam, cat. no. 076.134). The idea has crossed my mind that the data are in fact percentages of white flowers found on single plants. To assume this interpretation of the data makes the whole note inexplicable, however.

48. De Vries (*n.* 47) 'Bastaardering', 408. I wonder if there is any relation between this remark on the colour of the flowers and the stem with *Veronica longifolia* and the following passage: 'Een der allermoeilijkste vragen is die naar de eenheden der eigenschappen. ... Vele roodbloemige soorten hebben een witte variëteit. En als de soort ook in stengel en bladeren, of ook alleen in de kiemplant, een rooden tint bezit, ontbreekt deze dikwijls, doch niet altijd, in de witte variëteit. Is de roode kleur der geheel plant ééne eigenschap, of zijn de kleuren van blad en bloem en tak afzonderlijke eigenschappen?' (One of the most difficult questions is that to the character-units. ... Many red-flowered species have a white variety. And if the species has a red shade also in stem and leaves, or only in the seedling, it is often lacking, but not always, in the white variety. Is the red colour of the whole plant one character, or are the colours of leaf and flower separate characters?) (Hugo de Vries, 'Proeftuinen voor selectieproeven', *Album der Natuur* (1896) 68). Despite this remark, I think there is no need or a possibility to assume that De Vries is referring to a dihybrid crossing in the *Veronica*-note.
49. According to the text of the second part of the note, the percentages 1 and 5 in the new range are corrections and the percentages 6 and 14 are additions. In reality, however, 1, 5 and 6 are added to the original range, 13 is changed into 14 and 17 is removed from the data.
50. Note that De Vries says 'between 0 and 25% white' in de text and 'with 1–25% white' in the scheme. I have no explanation for this change of 0 into 1.
51. With two types of parents that are mutually crossed it is actually not correct to speak of a F2-generation because this expression is reserved for the progeny coming from the self fertilization of individuals from a F1. I like to maintain this inappropriate use however, in order to make things not too complicated.
52. I am much indebted to my brother André M. Zevenhuizen who pointed this out to me when I asked him whether the ratios 1: 4: 6: 4: 1 and 1: 2: 1 did ring a bell to him, shortly after I had found the notes that were quite puzzling to me at that time.
53. Th.J. Stomps, *Vijfentwintig Jaren Mutatieleer* (The Hague, 1930) 32, actually discusses the possibility 'dat zes factoren van invloed zijn' (that six factors are exerting their influence). He does not specify their supposed nature.
54. De Vries' own copy of *Anthropométrie* is in the Central Library of the University of Amsterdam.
55. Corcos and Monaghan (*n.* 1) 'Role of De Vries II', 275–276.
56. For the discussion whether Mendel discovered the laws named after him, see: Robert Olby, 'Mendel no Mendelian?', *Journal for the History of Science* **17**: (1979) 53–72; Olby (*n.* 1) *Origins*, 234–258; J. Sapp, 'The nine lives of Gregor Mendel', in: H.E. le Grand (ed.), *Experimental Inquiries* (Dordrecht, 1990) 137–166; Vitezslav Orel, *Gregor Mendel* (Oxford, etc., 1996) 172–180.
57. Present in Archive Hugo de Vries, inv. no. 220. The text reads: '... vorm is absoluut constant, geeft bij kruising ... fen echter alleen normale exemplaren (evenzoo *Oenothera*, ... *mia*, *Lychnis*, dV). Het zaad van deze bastaarden ... (5/16? dV) weer pelorische individuen' (... form is absolutely constant, gives at crossing ... however, only normal individuals (just as *Oenothera*, ... *mia*, *Lychnis*, dV). The seeds of these hybrids ... (5/16? dV) again peloric individuals).
58. Theoretically, the percentage of white plants can be 50% when the hybrid is pollinated with only germ cells carrying the white character.
59. De Vries (*n.* 19) *Mutationstheorie* I, 186.
60. Theunissen (*n.* 1) 'Closing', 230–231.
61. De Vries (*n.* 19) *Mutationstheorie* II, 693.
62. De Vries (*n.* 47) 'Spaltungsgesetz', 86. This same sentence is in De Vries (*n.* 19) *Mutationstheorie* II, 173, followed by: 'Wir nehmen dabei nach Mendel's Vorgang einstweilen an, dass die Spaltung eine volständige sei, dass keine ungespaltenen Reste übrig bleiben und dass somit die eine Hälfte der Ei- bezw. Samenzellen dem einen Elter, die andere Hälfte aber dem anderen gleich wird.'
63. De Vries (*n.* 19) *Mutationstheorie* II, 693–694.
64. De Vries (*n.* 19) *Mutationstheorie* II, 693.
65. Archive Hugo de Vries, inv. no. 146 (page 1). The original text reads: 'Als elke eigenschap in de kern door meer dan één pangen vertegenwoordigd was, zou er geen reductiedeling noodig zijn. Bij de bevruchting zouden de mannelijke en vrouwelijke groepen van gelijknamige pangenen dubbel zoo groot worden (door de vereeniging), maar als overigens dit aantal van voeding en prikkels afhangt, zou dit er niet op aankomen. Ergo pleit 't bestaan der reductiedeeling ervoor, dat elke eigenschap slechts

op 1 pangen berust' (When each character in the nucleus is represented by more than one pangene, meiosis would not be necessary. On fertilization the male and female groups of similar pangenes would double (through the union), but when this number is dependent of nourishment and stimuli, this would not matter. So the existence of meiosis speaks in favour of the fact that each character is determined by only one pangene).

66. Hugo de Vries, *Van Amoebe tot Mensch* (Utrecht, 1918) 6.
67. Stamhuis (*n.* 1) 'Trauma', argues that active and latent were in fact not synonyms for dominant and recessive. His habit to view them as such brought De Vries in serious trouble.
68. Archive Hugo de Vries, inv. no. 527.
69. Archive Hugo de Vries, inv. no. 146 A. One of the cobs is pictured in De Vries (*n.* 19) *Die Mutationstheorie* II, 150.
70. Another mentioning of the 1.2.1 law is in Archive Hugo de Vries, inv. no. 243. The date can not be established.
71. Archive Hugo de Vries, inv. no. 182. This experiment is discussed in De Vries (*n.* 19) *Die Mutationstheorie* II, 316–317.
72. Archive Hugo de Vries, inv. no. 228. See also inv. no. 146, pages 99, 102 (both entries from December 1920) and 166.
73. This note is present in Archive Hugo de Vries, inv. no. 533.
74. De Vries (*n.* 19) *Mutationstheorie* II, 153–154.
75. The well-known story that De Vries received an off-print of Mendel's paper from his friend M.W. Beijerinck (Stomps (*n.* 1) 'Rediscovery', 293–294) was already published in 1935 (Th.J. Stomps, 'Hugo de Vries', *Berichte der Deutschen Botanischen Gesellschaft* **53**: (1935) 91) and 1941 (Th.J. Stomps, 'De Amsterdamsche Hortus', in: *Amsterdam Natuurhistorisch Gezien* (Amsterdam, 1941) 121). Stomps quotes Beijerinck in his 1941 paper (presumably a sentence that was written in a letter): 'Jij interesseert je voor bastaarden, dan moet je toch eens het artikel lezen, waarvan ik je bijgaand separaatje kan zenden' (You are interested in hybrids, so you really should read the paper of which I can send you the enclosed off-print). In his 1954 paper (*n.* 1), Stomps quotes Beijerinck as: 'I know that you are studying hybrids, so perhaps the enclosed reprint of the year 1865 by a certain Mendel which I happen to possess, is still of some interest of you'. In his 1935 paper Stomps says that it was through a reference in the bibliography of L.H. Bailey's *Plantbreeding* that De Vries' attention was drawn to Mendel's paper (De Vries wrote this to Bailey himself; the letter is quoted in: L.H. Bailey, *Plantbreeding* (New York, 1904[3]) 155–156) and after this had happened Beijerinck sent it to him. When Ilse Jahn quoted this remark of Stomps (Jahn (*n.* 1) 'Focke', 17) Stomps made the following annotation on his offprint of her paper: 'Op blz. 17 bij het × staat dus een slordigheid van mijzelf! Absoluut zeker is dat de uitlating van Prof. De Vries tegenover Bailey slechts een vriendelijkheid was. Mijn gesprek met Prof. De Vr. hierover staat nog woordelijk in mijn geheugen!' (On page 17 at the *x* is then a slovenliness of myself! Absolutely sure is that the remark of Prof. De Vries to Bailey was merely a kindness. My talk with Prof. De Vries about this is still word for word in my memory!). From a letter of Ilse Jahn to Stomps, dated 20 Feb 1957, it appears that Stomps had searched in vain for the letter by Beijerinck and assumed that De Vries had thrown it away (Library of the Biological Centre, University of Amsterdam: Archive Theo J. Stomps, inv. no. 54). The letter of Beijerinck did not show up during the inventarization of the archive of De Vries.
76. So I do not agree with Darden when she says: 'He [De Vries] was examining the percentages of atavistic characters in progeny through several generations. Once he crossed differing varieties, allowed the hybrids to self-fertilize, and noted the patterns of characters in the second generation hybrids, he would have the statistical results on the basis of which the law could be inferred' (Darden (*n.* 1) 'Reasoning', 153). Neither do I agree with Campbell who, as a reaction on Darden, stated that De Vries' reasoning process had moved 'in the opposite direction': 'The law of segregation is not reasoned from the empirical results: it is invented to account for them' (Campbell (*n.* 1) 'Did De Vries', 652). I do however, agree with Corcos and Monaghan when they say that De Vries, contrary to Mendel, was tied to a theoretical structure he had made up earlier: 'De Vries' ideas are dominated by the influence of his theory of heredity' (Corcos and Monaghan (*n.* 1) 'Role of De Vries II', 276).
77. Hugo de Vries, *De Ademhaling der Planten* (Haarlem, 1878) 24.
78. De Vries (*n.* 66) *Amoebe,* 18.
79. See on this topic B. Theunissen, 'Knowledge is power: Hugo de Vries on science, heredity and social progress', *British Journal for the History of Science* **27**: (1994) 291–311.

APPENDIX 1

Transcription of the concluding part of the Oenothera *note*

Hieruit volgt:

1. Een nauwkeurige vergelijking van de empirische curve en de curve of error geschiedt het doelmatigst: niet, zooals Weldon, op de ordinaten 5°, 10°, 20° enz., maar op de ordinaten van 25, 26, 27 mm enz., i.e. op de middenpunten der vakken in deze figuur. Oorzaak: grens van nauwkeurigheid der meting = 1 mm.
2. Het is dus noodig, alle ordinaten van de curve of error te kunnen berekenen (Weldon geeft de formule daartoe niet).
3. Het is noodig Q1 en Q3 nauwkeuriger te kunnen berekenen dan tot op 1 mm, anders wordt de fout in de geheele berekende curve te groot.
4. Conclusie: de curven $(a+b)^x$ zijn voor mijn werk beter.

Translation

From this follows:

1. A careful comparison of the empirical curve and the curve of error happens most efficient: not, as with Weldon, on the ordinates 5°, 10°, 20°, etc., but on the ordinates of 25, 26, 27 mm, etc., i.e. on the centres of the squares in this figure. Reason: boundary of accuracy of the measurement = 1 mm.
2. So it is needed that all the ordinates of the curve of error could be calculated (Weldon does not give the formula for that).
3. It is needed that Q1 and Q3 can be calculated more accurate than on 1 mm, otherwise the error in the whole calculated curve will become too large.
4. Conclusion: the curves $(a+\mathrm{b})^x$ are better for my work.

APPENDIX 2

Transcription of the Veronica *note*

Veronica longifolia

Aant[ekening] 10 juni 1896

Beschouwingen bij Aant[ekening] 4 juni [18]96

1/De cijfers der ~~groen~~ rood stengelige ~~zijn~~ kinderen van Moll's plant zijn

							Witstengelige kinderen	
	1	9	13	20	23	29%	94–100%	
		11	15		23	29		
			17		26	30		
					27	33		
5/16 wet:	1		4		6		4	1

Men ziet dus dat met de cijfers der 5/16-bastaard wet zeer evident de groepen der erfcijfers corresponderen. Tusschen de cijfers 1.4.6.4.1. liggen in de erfcijfertabel evident hiaten. Dit blijkt ook uit deze schrijfwijze (erfcijfers op afstanden met 1% als eenheid):

1 . . . . 9 . 11 . 13 . 15 . 17 . . 20 . . 23 . . 2627282930 . . 33
23

←——→ ←——→ ←——→ = hiaat

2/Het is dus van veel belang de cijfers 1–23% nog eens over te bepalen, hetzij in hetzelfde zaad (9–17%; van de rest geen reserve) hetzij in nieuw te winnen zaad (1%, 20–23%).

Verder om het aantal dezer erfcijfers grooter te maken, dus de geheele cultuur nog eens te herhalen. Win hiertoe voorlopig zaad v[an] alle ex[emplaren] op 16a V3, nl v[an] de kinderen v[an] 't behaarde ex[emplaar].

Beschouwing V[erso]

Beschouwing 18 aug. 1896

a/Volgens J[ournaal] [18]96 p[agina] 235 zijn twee correctien en twee toevoegingen voor omstaande tabel noodig en wordt zij:

1	5	9	14	20	23	29	94–100%
1	6	11	15		23	29	
			~~17~~		26	30	
					27	33	

Wat dus niet veel verandert.

b/Volgens de 1.2.1. wet ~~geven~~ moeten de oudtypisten, hoe ook bestoven, steeds 100% blauwe geven, terwijl de c[entrale] b[astaarden] bij vrije bestuiving (met uitsluiting van witte), dus door c[entrale] b[astaarden] en door oudtypisten, t[usschen] 0 en 25% witte zouden moeten geven. Men zou dus moeten verwachten:

Op de 100 ex.	25	50	25
met	100% blauw	m[et] 1–25% wit	m[et] 100% wit

M.a.w. die nu 1–11% wit hebben zouden oudtypisten moeten zijn, die met 14–33% echter centrale bastaarden.

c/J[ournaal] [18]96 p[agina] 234 onder leert, dat bij 't sorteren op de kiemplanten een scherper toezien meer blauwe doet vinden. Dus zouden alle tellingen te veel witte aanwijzen. En een correctie in dien zin zou de gevonden cijfers beter met de 1.2.1. wet doen overeenkomen.

Scherper ~~selectie~~ keuzen is dus bepaald noodig bij het tellen.

Translation

Veronica longifolia

Note 10 June 1896

Considerations on note 4 June 1896

1/The numbers of the ~~green~~ red-stemmed ~~are~~ children of Moll's plant are

	White-stemmed children						
	1	9	13	20	23	29%	94–100%
		11	15		23	29	
			17		26	30	
					27	33	
5/16 law:	1	4			6		4 1

So one sees that the groups of the hereditary numbers very evidently correspond with the numbers of the 5/16-hybrid law. Between the numbers 1.4.6.4.1 lie in the table of hereditary numbers evidently gaps. This appears also from this way of writing (hereditary numbers on distances with 1% as unit):

1 . . . . 9 . 11 . 13 . 15 . 17 . . 20 . . 23 . . 2627282930 . . 33
23

←———→ ←————→ ←——→ = gap

2/So it is of great importance to establish the numbers 1–23% once more, either in the same seed (9–17%; of the rest no reserve) or in new collectable seed (1%, 20–23%).

Further to increase the number of these hereditary numbers, so to repeat the whole culture one more time. Collect for this for the time being seed of all specimens on 16a V3, namely of the children of the pubescent specimen.

Consideration Verso

Consideration 18 Aug. 1896

a/According to Journal 1896 page 235 two corrections and two additions are needed for the table on the back and will she become:

1	5	9	14	20	23	29	94–100%
1	6	11	15		23	29	
			~~17~~		26	30	
					27	33	

What changes not very much then.

b/According to the 1.2.1-law, the old type specimens, in whatever way they are pollinated, always have to yield 100% blue ones, whereas the central hybrids at free pollination (excluding white ones), so by central hybrids and old type individuals, should yield between 0 and 25% white ones. So one should expect

on 100 specimens	25	50	25
with	100% blue	with 1–25% white	with 100% white

In other words: those that now have 1–11% white should be old type individuals, those with 14–33% central hybrids however.

c/Journal 1896 page 234 below learns, that at the assorting of the seedlings a more critical look will produce the finding of more blue ones. Thus all the counting would indicate too much white ones. And a correction in that way would better harmonize the numbers that have been found with the 1.2.1-law.

Thus a more careful ~~selection~~ choice is certainly necessary when counting.

APPENDIX 3

Transcription of the Aster *note*

1896

Aster Tripolium

Potcultuur v[an] witte, op 11a V1.2

[in the margin:] [J[[ournaal]] [[18]]9]5 p[agina] 33

11 april 1896. Gezaaid 2 schotels, al het zaad van ~~de~~ één witbloeiend ex[emplaar] op 20 aug. 95 vol in bloei uit Huizen medegenomen. Zaad gerijpt in H[ortus] A[msterdam] 8 sept. 95. (1.1 cc zeer klein zaad. Geen reserve).

12 juni: Uitgezet op 11a V1 en 2, buiten 't Oen[othera] kooitje, en wel 4 ex[emplaren] per rij, som 9 × 2 × 4 = 72 ex[emplaren] = alle potjes. In enkele potjes staan 2 ex[emplaren], deze laat ik erin.

Doel: bloeien allen wit? Neen!

10 aug. Een tiental ex[emplaren] bloeien, deze allen paars.

[in the margin:] [W]aarschijnlijk [in] Huizen ± geheel [do]or paarsche [b]evrucht.

Beschouwing. De paarsche ex[emplaren], uit witte moeder, moeten volgens de wet der pangeenkruising (p. 187) paarsche vaders hebben en centrale bastaarden zijn. Zij leren dan, dat de witte ex[emplaren] te Huizen (bij voorkeur, nagenoeg geheel, fendeele? [inserted: 95%]) door paarsche bevrucht zijn. Evenals mijn Trifol[ium] prat[ense] alb[um] op 16b V1 door mijn 7 bladig ras bevrucht is.

Win dus zaad en zaai dit. Als er dit jaar geen witte bloeien, en alle ex[emplaren] dus centrale bastaarden zijn, moet het zaad 75% paarsche en 25% witte geven. Dit te onderzoeken.

Het is tevens een nieuw beginsel bij het overbrengen van variëteiten uit het wild in den tuin. Geschiedt dit na bevruchting in het veld, dan kunnen alle ex[emplaren] uit het zaad oudtypisten ~~zijn~~ schijnen; uit hun zaad ontstaat dan toch de variëteit (en wel in 25% der ex[emplaren]).

[in the margin:] touw merk ± rij 9d [ver]groend [ ]% wit [J[[ournaal]]] [18]97 p[agina] 23

15 sept. Eén wit ex[emplaar] bloeit volop, dit op 1 sept. vóór den bloei in zak, om de andere niet te bestuiven. [inserted: Het gaf geen zaad.] Er bloeien verder 18 blauwe, waarvan drie vergroend. Dus 5% witten. De overige zijn rosetten gebleven. Heden 8 ex[emplaren] in zakken, daar 't zaad begint te rijpen.

Translation

1896

Aster Tripolium

Pot culture of white, on 11a V1.2

[in the margin:] Journal 1895 page 33

11 April 1896. Sown 2 dishes, all the seed of ~~the~~ one white flowering specimen on 20 Aug. 95 full in bloom taken along from Huizen. Seed ripened in Hortus Amsterdam 8 Sept. 95. (1.1 cc very small seed. No reserve).

12 June: Planted out on 11a V1 and 2, outside the small Oenothera cage, namely 4

specimens a row, sum $9 \times 2 \times 4 = 72$ specimens = all pots. In some pots are 2 specimens, I leave those in there.

Goal: do all flower white? No!

10 Aug. Ten specimens are flowering, these all purple.

[in the margin:] Probably in Huizen ± completely fertilized by purple specimens.

Consideration. The purple individuals, from a white mother, must have purple fathers and be central hybrids according to the law of the cross of pangenes (page 187). They learn then that the white individuals in Huizen (by preference, almost totally, partly? [inserted: 95%]) are pollinated by purple individuals. Just as my Trifolium pratense album on 16b V1 is fertilized by my 7 leaved race.

So, collect seed and sow this. If there are no white flowering individuals this year, and consequently all individuals are central hybrids, then the seed must yield 75% purple and 25% white individuals. This to be investigated.

It is at the same time a new principle in the transportation of varieties from the wild into the garden. When this happens after fertilization in the wild, then all the individuals from the seed can seem to be old type individuals; from their seed the variety will eventually grow (namely in 25% of the individuals).

[in the margin:]? mark ± row 9d greened [ ]% wit Journal 1897 page 23

15 Sept. One white specimen is flowering in abundance, this on 1 Sept. before the flowering in bag, in order not to pollinate the other. [inserted: It gave no seed.] Further there are 18 blue specimens flowering, of which three greened. So 5% whites. The others have stayed rosettes. Today 8 specimens in bag, because the seed starts to ripen.

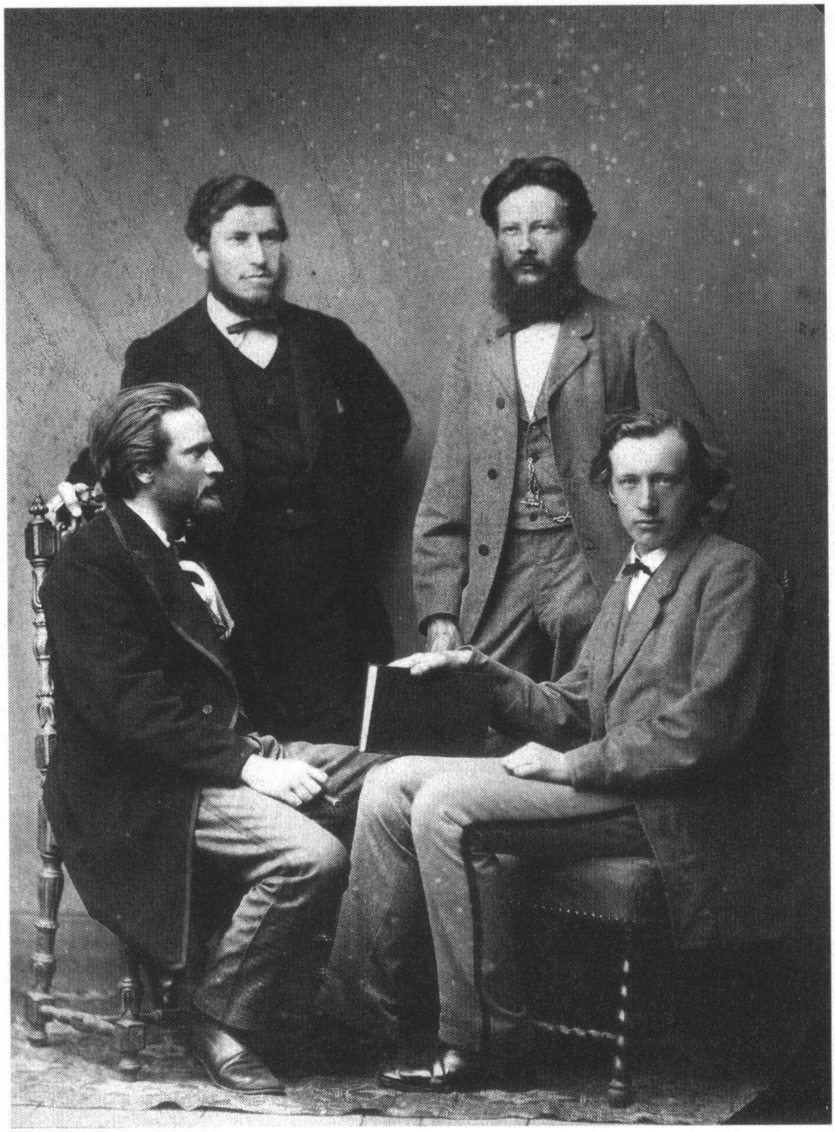

Fig. 13. Portrait of Julius Sachs (seated, left) with three of his co-workers from his laboratory: J. Schuch (standing, left), J. von Baranetzky (standing, right) and Hugo de Vries (seated, right), in Würzburg, August 1871 (Library of the Biological Centre, University of Amsterdam: Archive Hugo de Vries).