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Hugo de Vries: life and work

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LIFE

Hugo de Vries was born in Haarlem on 16 February, 1848. He came from a wealthy academic family and grew up in a cultural and scientific environment. Among his ancestors and relatives we find several that acquired a place in Dutch history by their activities in the realms of art and sciences. Hugo's father, Gerrit de Vries, had settled in Haarlem as an attorney in 1840. In 1850 Gerrit became a member of the Provinciale Staten (Provincial Council) of North-Holland, some years later of the Gedeputeerde Staten (Deputive Council) of that province. In 1862 he was appointed as a member of the Raad van State (State Advisory Council) in The Hague, a position he held untill his retirement. From 1872 to 1874, moreover, he was Minister of Justice. Hugo's mother was a daughter of the Leyden professor of archaeology Caspar Reuvens.

As a child, De Vries became interested in nature. After school hours and during holidays he made long walks through the dunes and meadows, collecting plants and trying to find their names. In 1860, at the age of 12, he brought in a herbarium of 100 plants for an exhibition organized by the Hollandsche Maatschappij van Landbouw (Dutch Agricultural Society). When he reached the age of 15 De Vries also began to make microscopic observations. In 1866 he entered the University of Leyden to read *philosophia naturalis* (natural philosophy), with botany as his principal subject. His parents were not pleased with their son's choice, in view of the limited prospects the discipline offered. At that time, the only job that was open to a professional botanist was a teacher of natural history at secondary school. Reluctantly they conceded, but when they saw how eagerly and dilligently young Hugo studied, they understood that their son had made the right decision.

De Vries retained his former enthusiasm for collecting plants and floristic studies during his student's life. He eagerly attended the lectures in botany given by W.F.R. Suringar and enthusiastically participated in his excursions. However, for the young and aspiring student, traditional systematics soon had to give way for the new, upcoming branches of the biological sciences that gave a completely new insight into the secrets of nature. It was particularly plant physiology that took De Vries' interest. He became fascinated by experimental botany after the reading of Julius Sachs' *Lehrbuch der Botanik*, published in 1868. Soon afterwards he began his own experimental research. For the formulation of an answer to the question 'What can be said about the influence of high temperatures on plant roots', issued as a contest by the University of Groningen, De Vries carried out an appreciable number of experiments. His answer was awarded the first prize and it served as the basis for a study from which he was awarded his doctor's degree in 1870: *De invloed der temperatuur op de levensverschijnselen der planten [The influence of temperature on the phenomena of life in plants])*. Also during his university study, De Vries became deeply impressed by Darwin's theory of evolution. Suringar rejected the new ideas but his students were fascinated by it. Among the theses

Fig. 2. Title page of a book containing the autographs of students and former students of Hugo de Vries who presented a tablet in memory of the opening of the new botanical laboratory of the University of Amsterdam, 1915. A new laboratory was one of De Vries' conditions to decline the professorship offered to him by Columbia University in New York and to stay in Amsterdam (Library of the Biological Centre, University of Amsterdam: Archive Hugo de Vries).

that accompanied his dissertation De Vries included several about evolution, no doubt as provocation to his conservative professor.

De Vries wished to continue his studies in experimental botany and after having earned his degree he moved to Heidelberg where he entered the university. He followed the lectures in chemistry and physics and by following practical courses he became well acquainted with plant anatomy and physiology. In the laboratory he studied the effect of high temperatures on the plant cell and the semipermeability of the protoplasm. During the first half of 1871 De Vries entered the university of Würzburg, where he worked in the laboratory of Julius Sachs whom he so greatly admired. Here, he investigated growth and growth curvatures in plants.

After this year of additional studies De Vries went into secondary school education, just as his parents had feared. In September 1871 he became a teacher of botany, zoology and geology at the HBS and the Openbare Handelschool in Amsterdam, but when possible, he spent his summer holidays in the laboratory in Würzburg where he continued his previous investigations on plant growth.

In 1875 De Vries was offered a professorship in plant physiology at the future Landwirtschaftliche Hochschule in Berlin. Upon a recommendation from Sachs the Prussian Ministry of Agriculture ordered him to study several agricultural crops in anticipation of that appointment. De Vries accepted the offer, left the Amsterdam schools with relief and moved to Würzburg, where he studied red clover, potato and sugar beet, in the meantime continuing his work with Sachs.

The founding of the Hochschule was much delayed and for that reason in 1877 De Vries became an unsalaried reader in the physiology of cultivated plants at the University of Halle-Wittenberg. The atmosphere did not suit De Vries at all and, moreover, his lectures were poorly attended. When the newly established University of Amsterdam, in that same year (1877), offered him a readership in experimental plant physiology, he returned to The Netherlands. On 29 October 1877, De Vries accepted his appointment officially with an inaugural address. Soon after (27 June, 1878) followed his appointment as extraordinary professor of anatomy and physiology. In 1880 the Landwirtschaftliche Hochschule in Berlin was opened at last and De Vries was invited to take up the position offered to him previously, but the University of Amsterdam managed to keep him by appointing him ordinary professor on 16 February, 1881. In Amsterdam, De Vries came to work in the Botanic Garden, or Hortus Botanicus, that had existed since the 17th century and had now become a part of the universities' organization. The laboratory facilities were very modest; De Vries' predecessors had carried out hardly any work in the field of experimental research. On his initiative the laboratory rooms in the building of the Hortus were considerably expanded.

De Vries was to stay in Amsterdam until his retirement in 1918. He was offered professorships in The Netherlands and abroad but he always declined them. Only once did he accept an offer, presented by the Columbia University in New York in 1910. He immediately withdraw his acceptance when the municipal council of Amsterdam appeared to be ready to fulfil his wishes: a greater and more modern laboratory and the appointment of a lecturer who would partly take over his lectural duties.

After the retirement of his colleague, Prof. C.A.J.A. Oudemans, in 1896 De Vries also became director of the Hortus Botanicus and the associated laboratories. He retained his position until his retirement in 1918. His concern with the garden was strongest in the years immediately after his appointment to the directorship. After 1900, when he became well-known all over the world and was much engaged with his scientific studies, he left most of the daily running to the curator of the garden.

As a professor De Vries lectured especially to students in medicine and pharmacy; the number of students in botany and zoology always was relatively small. He was a well-liked and popular lecturer, but also feared for his sometimes sharp tongue and unkind behaviour. He tended to treat colleagues and students in an inconsistent manner:

some of them could do no good, while others could not do evil. Between 1885 and 1911 De Vries was proposer of doctor's theses 14 times.

On 16 February, 1918, De Vries reached the age of 70 and became emeritus. He retired to the estate of De Boeckhorst in Lunteren, where he had laid out a large experimental garden. There he continued his scientific studies until his death on 21 May, 1935.

WORK

The scientific studies of De Vries can be divided into two categories: plant physiology and (evolutionary) genetics. With the first he occupied himself from the attainment of his doctor's degree until about 1890, and the second from about 1885 until his death. For De Vries the two disciplines were closely connected. In both he attempted to find out what chemical and physical laws rule natural life. Genetics he referred initially to as 'the physiology of heredity'.

De Vries' physiological studies were centred around the phenomenon of growth in plants. He investigated, for instance, the growth of leaves, growth in length, the growth of tendrils of scandent plants and the relation between growth and the pressure of the vacuole liquid on the cell wall (turgor). Sachs had already surmised the role of the turgor in longitudinal growth. De Vries proved this supposition to hold true. In his experiments he managed to lower or even eliminate the turgor. By using the semipermeability of the cell wall he managed to extract water from the cell by submersion in concentrated salt solutions, thus eliminating the tension. Using this procedure the cell contents became loosened from the cell wall, a phenomenon De Vries dubbed 'plasmolysis'. The rate of shortening of a cell or of a plant organ through plasmolysis indicates to what extent the turgor contributes towards elongation. By using solutions of other salts De Vries could determine the 'osmotic pressure' of different salts. Solutions with the same power he called 'isotonic'. The degree of affinity to water he expressed in a number he called the 'isotonic coefficient'. By means of this coefficient De Vries could calculate to what extent the various substances in a cell each contribute to the turgor. When the dehydrating force of a substance is known, the molecular weight of that substance could be determined. The turgor experiments induced De Vries to study the nature of the membrane between vacuole and protoplast (the tonoplast) and the translocation of solutes within the cell. The chemist J.H. van 't Hoff, like De Vries professor at the University of Amsterdam, made good use of the studies of the isotonic coefficient in his theory of diluted solutions.

Another subject that interested De Vries, because it might elucidate the laws governing life, was the formation of galls. When he noted that the biologist M.W. Beyerinck had advanced much further in the study of galls he abandoned the subject, although he kept lecturing on it inside and outside the University.

It was finally the phenomenon of variability that yielded, in De Vries' opinion, the greatest insight into the manifestations of life. After a 20-year study of several aspects of variation, he developed a theory that explained all kinds of deviations and changes in species, including evolution. At first, De Vries approached the problem in a theoretical and physiological way. His starting-point was Charles Darwin's 'provisional theory of pangenesis', published in *The Variation of Animals and Plants Under Domestication* in 1868. Darwin had speculated that hereditary features are housed in minute, invisible particles that were 'thrown off' by each organ and each cell, during all stages of their

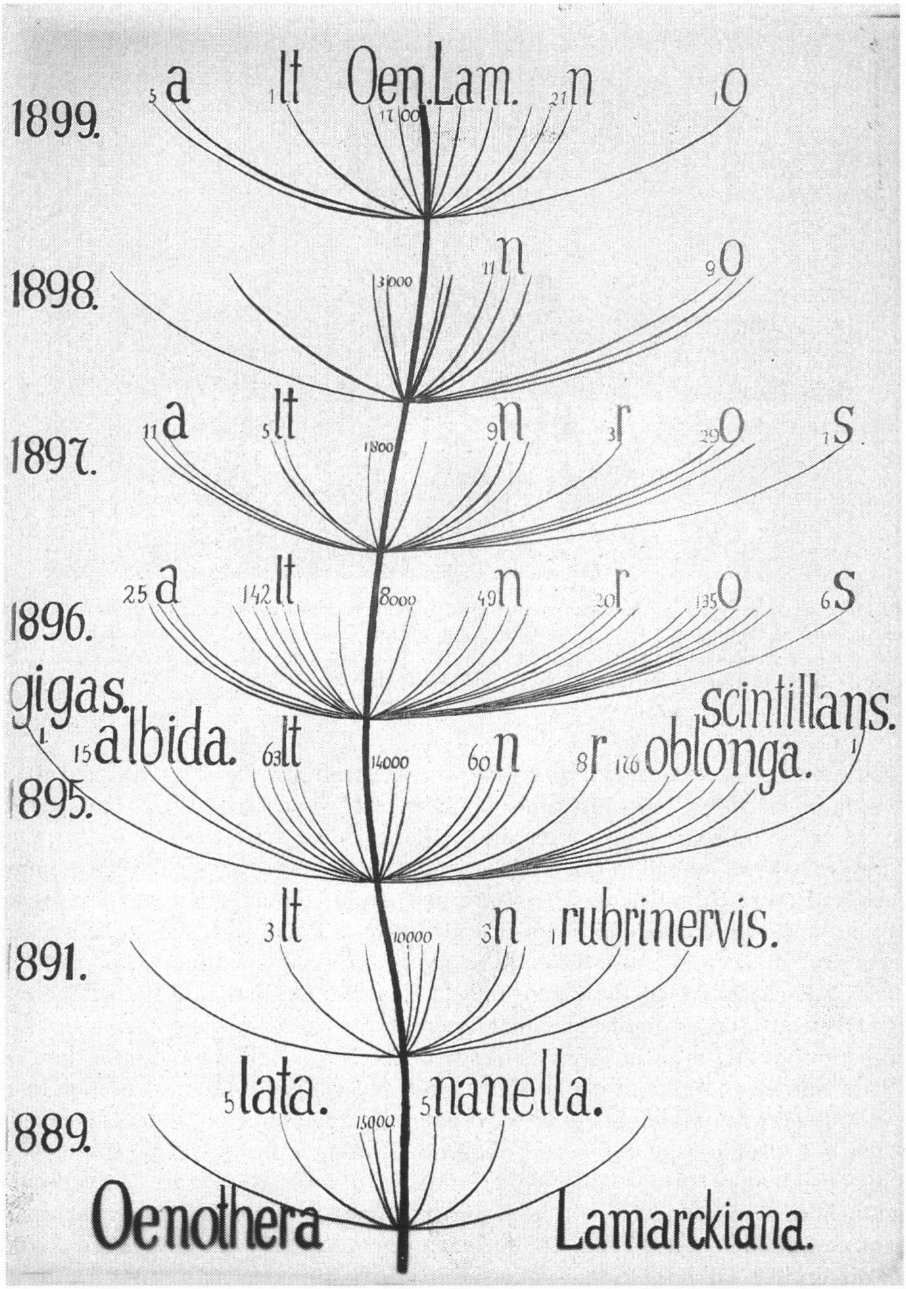

Fig. 3. Lecture plate used by De Vries showing the repeated emergence of mutants from *Oenothera lamarckiana* in seven successive generations (University Museum De Agnietenkapel, University of Amsterdam).

life. These particles ('gemmules', as Darwin called them) wandered from existing cells to new cells and in this way 'instructed' the new cells how to act and how to function. Besides, he supposed that the gemmules amassed in the reproductive organs and through

Fig. 4. Hugo de Vries (standing far right) on a trip in September 1908 to Rockanje with some of his most promising students he had selected to form 'The Club of Ten'. Standing next to De Vries is his daugther Eva, who was a student of botany at that time but who was not a member of the Club (Library of the Biological Centre, University of Amsterdam: Archive Hugo de Vries).

the generative cells were passed on to the next generations. De Vries adopted the idea of hereditary particles, but most other features of Darwin's hypothesis he rejected. In 1889 De Vries published his own hereditary theory in *Intracellulare Pangenesis.* One of the things De Vries argued in this book was that all the hereditary particles are present in each and every cell nucleus. They were of a totally different nature than Darwin's gemmules and as a consequence it was apt to give them another name. In honouring Darwin and to keep as close as possible to the original hypothesis, he called these particles 'pangenes'. What these pangenes looked like De Vries did not know, but he imagined them as macromolecules that were situated on the chromosomes of which the function and nature was largely unknown at that time. The most important point De Vries wanted to make in his book was that the pangenes (and, as a consequence, the various hereditary characters of an organism) are completely independent of one another. For instance, the number of pangenes of each and every single character may vary independently. This explains why prominence of a certain feature can vary among individuals of a single species. In addition, De Vries assumed that pangenes may be present in an active and a latent condition. In the latter case the associated character is not discernible. He posited that pangenes may pass from the active into the dormant state, and vice versa. In this way varieties may arise. De Vries further surmised that during the duplication of pangenes at cell division irregularities may occur. A pangene may split into two different pangenes, the deviating pangene on account of its novel molecular structure expressing a new feature. In case this feature appears throughout the whole organism, the new individual may deviate so much from the mother species that one may speak of a new species. Such a change could occur in one leap, in the course of a single generation.

After the presentation of his theory of pangenesis, De Vries settled to elaborate it and to find conclusive evidence for it. At the same time, his research in plant physiology came to a complete standstill. To investigate the independent nature of hereditary characters he made numerous crossings between individuals of closely related species and individuals of the same species that differ in a few characters or in only one. He eventually succeeded in transferring a character from one individual to another individual of a species that had previously lacked this trait. As a result of his hybridization experiments, De Vries concluded that during the formation of the reproductive cells the characters an individual had inherited from his two parents were distributed according to the laws of probability, and that the same laws held good for the new combinations that could occur on fertilization. De Vries published his observations in 1900 after he had noticed that the Bohemian monk Gregor Mendel had already reported the same conclusions in 1865. De Vries hence became one of the 'rediscoverers of Mendel's laws'.

Another line in De Vries' research was selection. After numerous experiments he convinced himself that selection cannot yield new species. A character can be strongly emphasized or rendered almost invisible by selection, but as soon as the tight regime is relaxed there will always be a regression to the previous state. Moreover, the rate of variation of a character appeared to be limited. Deviations from the mean value of a feature can never be so considerably changed that one can speak of a novel character.

De Vries used a great many species for his experiments. He collected the specimens that formed his tools during field excursions and some were presented to him by his colleagues and friends. De Vries was especially interested in abnormalities that seemed to hint at speciation, for instance broadened or twisted stems, singular leaf forms, divergent flowers and three cotyledons instead of two. Eventually he settled for one very curious case: the striking behaviour of the large-flowered evening primrose (*Oenothera lamarckiana*, now *O. erythrosepala*). The progeny of the evening primrose showed not only the variation that was common with other species and the incidentally abnormalities that he also had observed elsewhere, but some individuals were so strongly deviating from the mother plant that it seemed as if a totally new species had arisen. This impression was affirmed by the fact that the deviating specimens proved to be constant on self-fertilization in the consecutive generations. De Vries concluded that the new forms were the visible consequences of changes of pangenes. They were the conclusive proof of his theory of pangenesis that he had sought.

In the autumn of 1900, Hugo de Vries presented his new theory for the origin of new species by pangenetic change to the public. In fact, it was his original pangenesis theory of 1889, but now thoroughly re-worked and supplemented by an impressive quantity of evidence taken from the experiments executed during the foregoing 15 years. The change-over from the active to the latent stage of a pangene, the change from the latent to the active stage and the formation of a new pangene he now dubbed as 'mutations', the new individual arising in this way as 'mutants'. His new theory he called 'the mutation theory'. It was by this last-mentioned type of mutation ('progressive mutation', as opposed to 'retrogeressive' and 'degressive' mutations respectively), that new species arise. Whether a new species would survive or would perish was decided by natural selection. Evolution, according to the mutation theory, does not progress by means of selection of the best adapted variants of a species, but by selection of the best adapted mutants that are, occasionally, produced by a species. In 1901–03 De

Fig. 5. After the third international botanical congress in Brussels, Hugo de Vries took part in a trip to the Peel region near Genk on 23 May 1910. De Vries is in the centre, with bowler hat and walking stick (Library of the Biological Centre, University of Amsterdam: Archive Hugo de Vries).

Vries published his two-volumed magnum opus *Die Mutationstheorie. Versuche und Beobachtungen über die Entstehung von Arten im Pflanzenreich.*

The mutation theory received much attention, as it explained several points in the process of evolution for which Darwin could not find an answer. There also came much criticism, however. Closer studies by other workers soon revealed that the phenomenon observed by De Vries in *Oenothera* had to be explained in quite another way than he had indicated. In reality, there were no such things as mutating pangenes present in the evening primrose. Little by little it became clear that the evening primrose has a very complicated genetic structure that gives rise easily to unexpected appearance. The plant is a constant hybrid, with two chromosome complexes that originate from reciprocal translocations of chromosome arms and that exclude one another due to lethal factors. Due to the translocations, during meiosis the chromosomes are connected end-to-end in circles or chains (chromosome catenation). Moreover, *Oenothera* has a strong tendency to trisomery and new reciprocal translocations and hence to new and unexpected looks. The inevitable conclusion was that De Vries' *Oenothera* mutants were not new species, but nothing more than rare chromosome mutations. Parallel to these discoveries De Vries and his mutation theory fell into disgrace with many workers, although the mutation theory as such was not discarded. De Vries continued to pursue the striking behaviour of the genus *Oenothera* until his death, stubbornly maintaining his view that the different forms of *Oenothera* (of which he found still more) indeed were caused by mutation and that he had indeed caught nature in the very act of speciation.

After 1900, De Vries continued to seek the cause of mutation. Knowing this, he stated, an important tool would fall into man's hands. As soon as one could understand and could mould the laws of mutation, one might be capable of modifying the process of speciation and to create novel and better kinds of agricultural crops and domestic animals. De Vries had very firm ideas concerning the relation between science and society and stated that scientific knowledge must be usefully applied to the advancement of mankind. This conviction he propagated himself by giving many lectures and by publishing in popular scientific periodicals. In his papers he gave practical tips readers could use to their advantage. Furthermore, he thought that scientific knowledge has a refining action, especially knowledge of nature which may, in his opinion, contribute towards a 'purer and happier way of life and a feeling for beauty and mental satisfaction'. However, the making of life forms to his own design remained untenable to him. It is only in the last few decades that his dream slowly became reality through the possibilities of genetic engineering.

Despite its shortcomings, the mutation theory was highly influential. Dozens of workers all over the world were stimulated by it to studies in the fields of both genetics and evolutionism. De Vries was one of the pioneers of evolutionary genetics, applying experimental studies on a large scale and showing that evolution need not only be approached theoretically. He merged evolutionary change with genetic change into one all-comprehensive theory, thus showing the way for further research and hinting at things to come. It is apparent that his basic idea proved to be right: mutations do play a prominent role in speciation. They form partly the raw material from which natural selection occurs. As he once stated himself in a lecture: 'The theory of mutation ... is only one step further in the development of our appreciation of evolutionary phenomena'.

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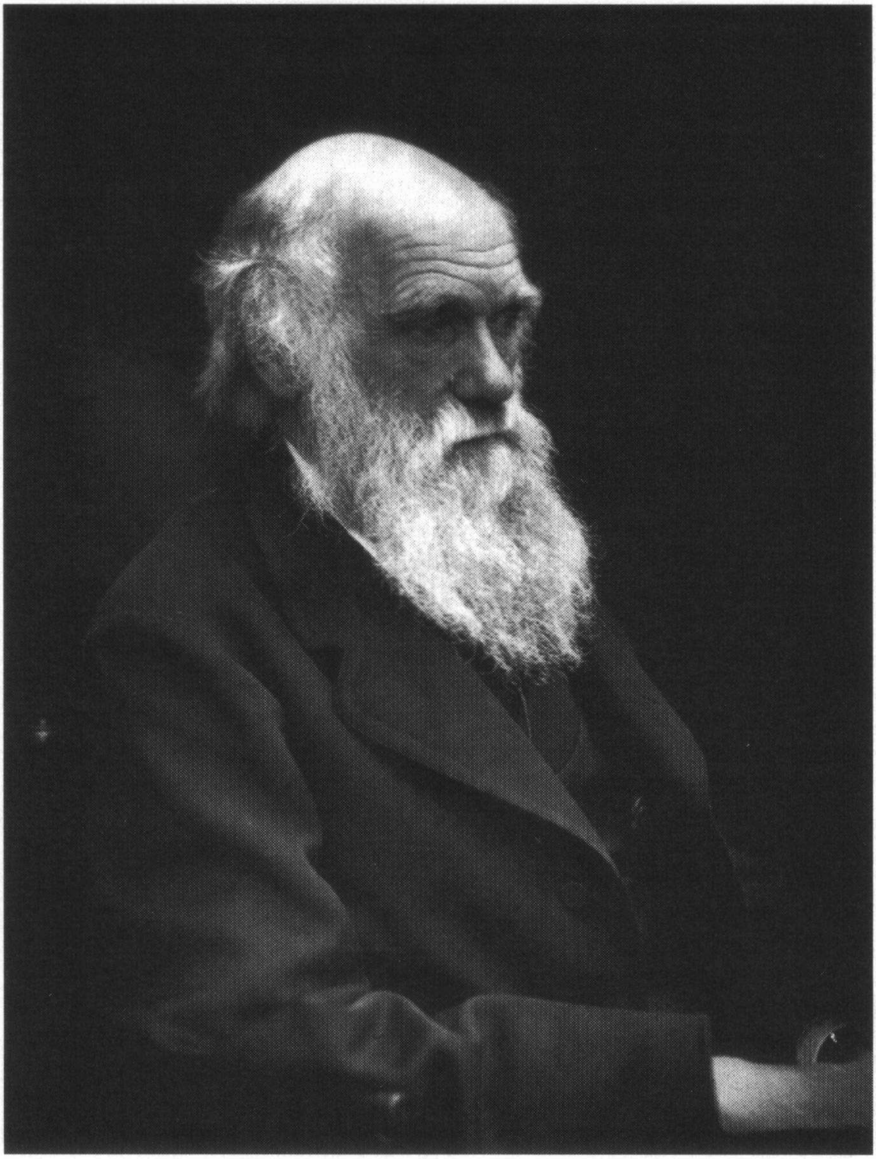

Fig. 6. Portrait of Charles Darwin, around 1875.