Vast in het spoor van Darwin : biografie van Hugo de Vries

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Summary

Firm and fixed in Darwin's footsteps. Biography of Hugo de Vries.

When Hugo de Vries was buried on the cemetery of the village of Lunteren on 25 May 1935, his eldest son Otto pointed out to the gathered crowd that his father had served science for almost eighty years. He was slightly exaggerating, because during the first twenty years of his life he had not contributed anything to science yet. But it is a fact that De Vries was involved in botany for almost eighty years. And as he died at the age of 87, this involvement lasted for nearly his entire life. Probably because of the botanical diversity of the surroundings of Haarlem, the city De Vries was born in on 16 February 1848, he had taken an interest in plants already as a child. While at secondary school (initially in Haarlem, from 1862 onwards in The Hague), this interest had evolved into a serious hobby. Through graduating in botany at the university in Leyden, De Vries had turned his hobby into his profession, as one of the very few in The Netherlands. After his retirement in 1918 he had continued to work in his own experimental garden. Hugo de Vries had died on the battlefield.

De Vries' demise was news both in The Netherlands and abroad. Before 1900, he had already earned wide recognition as a scientist and as a writer for a non-specialist audience. After this year he had become a world celebrity. The number of tributes that had fallen to him, consisting of honourary doctorates, honourary memberships and gold and silver medals, was truly impressive. But after his death his fame did not last very long. While his achievements have once been equally valued as those of Charles Darwin, in present-day text books his name is only mentioned in passing as one of the rediscoverers of Mendel's laws and as the one that has made the word 'mutation' popular in genetics. A century of research in genetics and evolution, the two fields of science De Vries was mainly involved in, has erased virtually all his tracks.

In this biography, De Vries' scientific work is not viewed or judged from the standpoint of present-day knowledge, as has been the case in many earlier descriptions of his work. Instead, it tells what his sources of inspiration were, what the questions were he asked, how he tried to find answers, what problems he encountered while doing so, what solutions he found when his results were conflicting with his expectations, and which new questions these problems raised. It is a historical account, showing how a natural scientist from over a century ago reasoned and acted, from childhood until his death.

As a younster De Vries devoted most of his spare time to collecting trips to complete his collection of dried plants. In this respect he did not differ from the average amateur and professional botanist in The Netherlands during that period of time. Botany was nearly equal to plant systematics. While at the university, De Vries got acquainted with two fields of botany which were virtually unknown then in this country, plant physiology and the study of evolution. Although he retained his love for wild plants for the rest of his life, it was on these two subjects that he would concentrate. Until about 1885 De Vries was engaged in physiological research, after this year in genetical and evolutionary work, sometimes separate but very often in combination. Two major authorities were his main inspirators. For his physiological research it was Julius Sachs, professor of botany at the university in Würzburg, for his genetical and evolutionary work it was the British naturalist Charles Darwin. In both periods of his scientific career De Vries tried to give a theory of each of them a strong scientific basis through experimentation. First, it was Sachs' mechanical theory of growth, then, it was Darwin's 'provisional hypothesis of pangenesis', his theory of heredity.

During 1871-1876, De Vries spent several times in Sachs' laboratory in Würzburg. Under his guidance he investigated the curvations of leaves, stems and ribs (1871), the curvations of tendrils and the stems of twining plants (1872), the growth of tree rings (1872-1874), and the elongation of internodes (1873-1876). Time after time the observation could be explained with Sachs' theory that cells attract water, causing a tension ('turgor'), resulting in a stretching of the cell wall, which enables new molecules to fit into the wall. In 1877, De Vries was appointment as a lecturer of experimental physiology at the University of Amsterdam, a position that was soon turned into a full professorship. Being on his own now, De Vries quickly broke away from Sachs. He concentrated on the attraction of water and this brought him from Sachs's mechanical physiology to chemical physiology. In 1881-1883 he discovered which substances dissolved in the cell sap are responsible for the attraction of water. He was able to express their relative force of attraction in a series of numbers, which he called 'isotonic coefficients'. In 1884 he established which cell organ is responsible for the formation of these substances and how these are transported to the vacuole, stating that the actual 'turgor maker' is the wall of the vacuole, which he named 'tonoplast'. This research had led him from chemical physiology to physiological anatomy. Finally, he established (in 1885) that the tonoplast depends for its functioning on the circular movement of the protoplasm. By taking these successive steps, De Vries forged a 'causal chain', penetrating deeper and deeper into the causes of plant growth:

growth (irreversible change of form) is caused by
intusception, which is caused by
turgor, which is caused by
endosmosis by water-attracting substances, which are produced by
the tonoplast, which receives the necessary material for these substances through
the movements of the protoplasm

Following Sachs, De Vries initially considered plant growth, just as any other biological process, as an effect of the cooperation of chemical and physical laws. However, De Vries developed a different stand from Sachs again after his appointment in Amsterdam. In the early 1880s his strictly mechanistic view of life gave way for a more biological view, influenced by a new philosophy gaining popularity under German biologists. The new idea was that in organisms specific biological forces are acting, directed by molecules that are only found in living beings. So, simultaneously to his deepening into the causes of plant growth, De Vries successively approached the subject from a physical, chemical, anatomical, and a biological point of view.

Soon after his arrival in Amsterdam, De Vries started to engage in the other subject that had fascinated him during his study at the university, namely the work of Charles Darwin. He set out to collect evidence for Darwin's theory of heredity, his 'provisional hypothesis of pangenesis', published in 1868 and highly critized ever since. During the 1880s De Vries developed his 'theory of panmeristic division of cells', which state that each cell organelle arises from another cell organele. He applied the theory to the origin of the vacuole and the tonoplast, two cell organelles to which he had attributed a prominent role in plant growth. In doing so, he linked his earlier and new studies, merging them into each other.

According to the theory of pangenesis, hereditary characters are independent entities and, as a consequence, they can be mixed. To prove this De Vries applied two methods. First, fixing deviating characters, and second, crossing varieties. For the first line of experiments De Vries collected a large number of so-called 'monstrosities', e.g., flattened stems, petioles, and flowers, twisting stems, cup-shaped leaves, and petales, doubled leaves, and changed numbers of petales, anthers and stamens. Through the selection of the best developed specimens and optimizing manuring and other growth conditions, De Vries managed to grow several monstrous races. However, these monstrosities never went to fixation. Some normal copies were always popping up among the progeny. In his hybridization experiments De Vries tried to swap monstrous characters and characteristics like a deviating flower colour or the lack of pubescence between varieties. He also tried to make new combinations. He succeeded in both.

And so it was that at the end of the 1890s, after more than a decade of experimental research, De Vries was convinced he had collected sufficient proof for the theory of pangenesis. This was, by the way, not Darwin's pangenesis but an adapted version that De Vries had developed during the 1880s and that he had published in 1889, in his book *Intracellulare Pangenesis*. From Darwin's pangenesis he had retained the idea that hereditary characters are independent entities, that these characters are carried by sub-microscopic particles, and that the intensity of a character is determined by the number of particles. In contrast to Darwin, he had not considered the particles as representatives of organs or tissues but as molecules that increade in number by division (the 'living molecules' from the protoplasm); he had the idea that the particles move from the cell nucleus to the protoplasm where they would contribute to physiological processes and that they do not wander through the whole organism and come together in the germ cells; and he was convinced that new characteristics arise as a consequence of a change in the molecular structure of existing particles and not, as Darwin had claimed, are transmitted by the representative particles of organs and tissues that have been changed by external circumstances. Darwin had named the particles 'gemmules', considering them to be the starting point of larger structures. De Vries gave them a new name: pangenes.

To judge the success of his selection experiments De Vries handled his data statistically. It enabled him to establish quite easily whether a shift of the average of a value was taking place in successive generations. Moreover, his graphs showed that a character could not vary infinitely but that variation was limited between fixed boundaries. Only in rare cases one of the boundaries was passed over. This crossing did not happen gradually but with a small yet clearly visible leap. De Vries also interpreted the results of his hybridization experiments in a statistical way. He concluded that two antagonistic forms of the same character in a hybrid combine in its offspring according to the laws of chance, resulting in the ratio 1 : 2 : 1. In 1900 he discovered that the Austrian teacher of natural sciences and amateur botanist Gregor Mendel had stated the same conclusion already thirty years earlier. It seems that it was no problem for De Vries not having the priority of this discovery. Of prime importance to him was that this rule confirmed pangenesis in a convincing way.

Of all the species De Vries grew during the 1880s and 1890s there was one that behaved differently than all others. It was *Oenothera lamarckiana*, the evening primrose. Each generation there was a small percentage among the offsping that did not deviate in one or a few characters but in their appearance as a whole. There was, for instance, a form that was in every respect larger and more powerful, one that had red stripes on the capsules and ribs, a stronger pubesence, narrow leaves and a brittle stem, a form with narrow leaves and hardly any branches, and a form with gleaming, flat, narrow and dark green leaves and small flowers. They all were true-breeding when self pollinated. These forms were clearly very different from monstrosities and varieties. Besides, their appearance did not follow any statistical rule. De Vries concluded that he had stumbled upon a rare example of the saltatory origin of species, an evolutionary mechanism Darwin had already envisaged (besides a gradual origin) and had been defended by several others since then. Considering the peculiar behaviour of the evening primrose, the limits of variation, and the occasional crossing of the boundaries he had observed, De Vries grew more and more convinced that evolution does not proceed gradually but exclusively in small steps. With the evening primrose he had caught evolution red-handed in his own experimental garden!

In the autumn of 1899 De Vries decided to publish his results in a bulky, two-piece work. In the first part he would describe his experiments with varieties and monstrosities, together with the amazing evening primrose. In the second part, he would describe his hybridization experiments. Besides proving Darwin's pangenesis he wanted to show that evolution proceeds in a saltatory way. Close examination of Darwin's books had convinced De Vries that Darwin had set great store by saltatory than by gradual speciation. So the book had to prove Darwin's words in a two respects. His friend and colleague Willem Moll, professor of botany in Groningen, who assisted him while writing, advised him not to mention pangenesis. As a consequence, the emphasis in the book came to lie on evolution rather than heredity. To define a saltatory change of a hereditary character De Vries used, following Darwin, the word 'mutation'. His idea that new types arise in this way he called 'mutation theory'. He choose this expression as the title of his book, which was written in German: *Die Mutationstheorie*.

Although he used pangenesis already for over a decade to interpret his experiments, De Vries had not yet completely worked out the theoretical explanation of his results when he started writing. With the help of Moll he developed a complex but logic and coherent system, while a part of the book had already been printed. Several modifications of pangenesis were necessary. Pangenes were supposed to be not only to be present in different numbers but also in different conditions. De Vries distinguished four conditions: active, latent, semiactive, and semilatent. The last two were introduced to explain the behaviour of monstrosities. A change from one condition into another was called a 'mutation', and so was the origin of a new pangene, expressing a new character. It was only with this last type, called 'progressive mutation', that new species would arise. Whether these are successful in the struggle for life and whether they will be able to propagate is determined by the environment. So De Vries retained Darwin's action of natural selection, but developed a new view on the origin of the material that is subjected to selection.

The first volume of *Die Mutationstheorie* (published in three instalments in 1900-1901) received worldwide attention because of the spectacular discovery of the curious behaviour of the evening primrose. It made Hugo de Vries a world celebrity. The appreciation, however, was not always positive. Some scholars accepted the mutation theory completely, others rejected the theory, and still others combined the theory with other mechanisms of speciation that were going around. Also, the theory was not always interpreted as De Vries had intented. Some recognized the similarities between the new theory and Darwin's theory of natural selection, others considered the theory as inconsistent with Darwin's ideas. Depending on their appreciation of Darwin's views, they either praised or critizied the mutation theory. Also, whether the curious behaviour of the evening primrose indeed supported saltatory evolution was heavily disputed. It was claimed that the deviating forms fell within the normal limits of variation. Moreover, it was assumed that the evening primrose was a hybrid and that the new forms were simply new combinations of existing characters. The second volume of *Die Mutationstheorie* (published in 1902-1903) made only little impression. It added hardly anything to what already was known after the rediscovery of Mendel's laws. There was little doubt that hereditary characters are independent entities. It was however widely debated whether the characters are carried by particles and as a consequence are 'preformed' in each organism, or whether they developed through physiological processes during the growth of an organism (a view called 'epigenesis'). As again De Vries hardly mentioned pangenesis in the second volume, it was not clear to the reader what De Vries' position in this discussion was.

Although quite satisfied with *Die Mutationstheorie*, De Vries thought that the mutation theory still lacked the ultimate proof: to show that mutations can be induced artificially. After the publication of the book he therefore directed his attention to the causes of mutation, a subject he had hardly touched upon so far. Since the evening primrose provided the largest number of mutations in the most perfect form, De Vries used the species for the next step in his research. He had already noticed that the behaviour of the evening primrose during hybridization did not correspond to the laws of Mendel. De Vries suspected that this was due to its property to produce mutant forms. On the basis of pangenesis he had distinguished three different types of crosses: mutation crosses (one or both parents have a property in mutabele condition), bisexual crosses (antagonistic characters are in different conditions, active – latent), and unisexual crosses (one parent possesses a character and the other does not, present – absent). Each type could be recognized by the way the offspring of a hybrid would segregate. Whether the plants that were crossed had a character yes or no, whether a mutation had occurred, and whether a plant had a character in mutabele condition could all be judged from the result of a cross. Crosses were, in short, an excellent means to gain insight into the internal composition of a species. During several years De Vries carried out thousands of crosses between all species and mutants of the evening primrose known to him, in all thinkable combinations. The results were published in the book *Gruppenweise Artbildung* (1913). The central topic of the book is the 'labile pangene' which is presented as the most important internal cause for the occurrence of mutations. Labile pangenes are thought to change rather easily into the active or latent condition, causing a visible mutation. This was, again, a modification of Darwin's pangenesis which this time played a prominent role in the book. Evolution is, however, almost absent. De Vries had returned to his earlier field, the heredity of characters.

As the next step in his research De Vries wanted to investigate how internal influences can change pangenes into the labile condition and how they can bring about a change from the labile in one of the stabile conditions. But discoveries by other *Oenothera*-researchers soon forced De Vries to return to the internal composition of the species. American researchers discovered that many of De Vries' mutants had a different number of chromosomes. Great doubt was now thrown upon the claim that the mutants were new species. Many scientists considered this to weaken the mutation theory, the mutation theory was even questioned all together. The critisism that the evening primrose was a hybrid was at the same time supported by the discoveries of the German botanist Otto Renner. He suspected that the species is composed of two fixed chromosome complexes. De Vries had earlier suggested something similar for *Oenothera biennis* en *O. muricata*. Why *Oenothera lamarckiana* bred true when selfed was something Renner could not explain. De Vries scored him off by postulating that different lethal factors were present in the germ cells. Equal combinations would not be viable. He stuck however to his point that the evening primrose was a true species. He also adhered to his view that the new forms were new species. He considered the different number of chromosomes as an accessary phenomenon. However, he abandoned the labile pangene as an explanation. But he still maintained that new species arise by mutation and that this is the only evolutionary mechanism at work, in combination with natural selection. De Vries had acquired his independence from Sachs in his physiological work, but in his genetical and evolutionary work he continued to consider Darwin as his inspiration and never gave up his ideosyncratic interpretations of Darwin's theories.

From the early 1920s onwards, while De Vries was gradually withdrawing from science, not having been able to discover the causes of mutation, new facts and insights provided a clearer view of both the mechanisms of speciation and the internal structure of the evening primrose. Heredity and evolution were united in the 'neo darwinistic synthesis'. After several decades it was generally accepted that nature selects from the enormous genetic variation that is present in populations. This variation is partly caused by mutation. As a rule, mutations have only a limited effect. It is not possible that one single mutation produces a new species. New discoveries on the structure of the chromosomes made that De Vries' triad of mutations was replaced by a new, longer series. Renner's theory of chromosome complexes was confirmed by others. Because reciprocal translocations of the chromosomes have taken place in the evening primrose, chromosomes connect end to end during meiosis so that independent assortment is not possible. It is a rare phenomenon, and combined with lethal factors and the frequent occurrence of an extra chromosome the conclusion was that the evening primrose is an extraordinary species, with a peculiar way of transmission of hereditary characters and a particular evolutionary history. The behaviour of *Oenothera* is, as a consequence, of little value for getting a better insight into the general principles of genetics and speciation. The Dutch botanist P.C. van der Wolk had it right when writing in 1919 that 'Hugo de Vries took a brave jump into the dark'.