

Hugo De Vries: from the theory of intracellular pangenesis to the rediscovery of Mendel

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Abstract – On the basis of the article by the Dutch botanist Hugo De Vries 'On the law of separation of hybrids' published in the Reports of the Académie des Sciences in 1900, and the beginning of the controversy about priority with Carl Correns and Erich von Tschermak, I consider the question of the posthumous influence of the Mendel paper. I examine the construction of the new theoretical framework which enabled its reading in 1900 as a clear and acceptable presentation of the rules of the transmission of hereditary characters. In particular, I analyse the introduction of the idea of determinants of organic characters, understood as separable material elements which can be distributed randomly in descendants. Starting from the question of heredity, such as it was defined by Darwin in 1868, and after its critical developments by August Weismann, Hugo De Vries was able to suggest such an idea in his *Intracellular Pangenesis*. He then laid out a programme of research which helps us to understand the 'rediscovery' published in 1900. © 2000 Académie des sciences/Éditions scientifiques et médicales Elsevier SAS

Mendel / Hugo De Vries / Weismann / intracellular pangenesis / germinal plasm / Correns / Delage

Résumé – Hugo De Vries : de la théorie de la pangenèse intracellulaire à la redécouverte de Mendel. À partir de la lecture de la note de Hugo De Vries « Sur la loi de disjonction des hybrides » des *Comptes rendus de l'Académie des sciences* en 1900, et de l'analyse du début de controverse de priorité avec Carl Correns et Erich von Tschermak, je pose le problème de l'influence posthume du mémoire de Mendel. Pour cela il faut comprendre comment fut construit le cadre théorique nouveau qui permettait sa lecture, en 1900, comme une présentation claire et acceptable des règles de la transmission des caractères héréditaires. En particulier, j'analyse la mise en place de l'idée de déterminants des caractères organiques, entendus comme des éléments matériels séparables qui peuvent se distribuer aléatoirement dans la descendance. C'est à partir de la question de l'hérédité telle qu'elle fut définie par Darwin en 1868, et après ses développements critiques par August Weismann, que Hugo de Vries put proposer une telle conception en 1889 dans sa *Pangenèse intracellulaire*. Il définissait alors un programme de recherche qui permet de mieux comprendre la « redécouverte » publiée en 1900. © 2000 Académie des sciences/Éditions scientifiques et médicales Elsevier SAS

Mendel / Hugo De Vries / Weismann / Pangenèse Intracellulaire / Plasma germinatif / Correns / Delage

On the 26 March 1900 there appeared in the *Comptes rendus de l'Académie des sciences de Paris* a note by Hugo De Vries (1848–1935) entitled: *Sur la loi de disjonc-*

tion des hybrides (On the law of separation of hybrids) [1]. In it he introduced what would later be called the 'Laws of Mendel', but does not quote this author. On the contrary

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his paper starts thus: "According to the principles that I described elsewhere (*Intracellular Pangenesis*, 1889), the specific characters of organisms are composed of fully distinct units".

And, what was going to be considered as the basis of a new science of heredity was introduced as the confirmation of the 'Theory of Intracellular Pangenesis' that Hugo De Vries had developed in a short book 11 years before [2]. Carl Correns (1864–1933) in Germany, like Erich Tschermak von Seysenegg (1871–1962) in Austria, was working on the same questions and had arrived at the same results. Correns received a special edition of the note of Hugo De Vries on the 21 April, and in 1 day finished the writing of an article for the *Berichte der Deutschen Botanischen Gesellschaft* which was going to be published at the end of May [3]. Equally, Tschermak who had just finished his thesis rapidly sent an article to the *Berichte* [4]. They had both read the memorandum that Gregor Johann Mendel (1822–1884) had published well before in 1866. For Correns the influence of Mendel on the work of Hugo De Vries was clear, if only because of the use of the vocabulary ('dominant' or 'recessive' characters). He decided to call his article: *G. Mendel's Regel über das Verhalten der Nachkommenschaft der Rassenbastarde* (G. Mendel's law with regard to the behaviour of the descendants of hybrid varieties). In attributing in this way the discovery to this unknown cleric, native of Moravia, he forestalled any claim to priority that Hugo De Vries might have made. However, the latter had already sent an article to this same magazine in which he quoted Mendel and which was published at the end of April [5]. This reference was perhaps added at the last minute [6], but it indicates in any case that Hugo De Vries accepted the idea that he had been preceded by Mendel. Moreover, he did not seem to attach any great importance to this discovery and preferred to concentrate his subsequent research on questions regarding the evolution of species. Even in 1900 one can mention among an impressive collection other articles of Hugo De Vries about variation and evolution [7–10]. The memorandum of Mendel was quickly republished, translated into English, and would have an immense and rapid posthumous success. Through the works of William Bateson and Wilhelm Johannsen it would serve as the foundation of Mendelism and then of genetics.

Such an event in the history of science posits a whole collection of questions which are more or less important according to the kind of enquiry that one is pursuing.

Either one accepts the perspective suggested by Correns and which was taken up again by the founders of genetics. In this case, the research as to the origin of this discipline will have to be concentrated on Mendel's work. The isolation and absence of the diffusion of his famous memorandum of 1866 will lead one naturally to identify individual genius as an incomprehensible element of scientific discovery, possibly against the thinking of his time. Likewise, the quasi-simultaneous publications of 1900 will essentially have to be explained by the common reading of the foundation text of Mendel. But if one admits that the

future laws of heredity were contained in black and white in "This memorandum, too fine for its age" [11] one will have difficulty in explaining why it was not understood in 1866 as it was in 1900. Neither will it be understood why it was in fact read independently and in the same period by Correns, Tschermak and De Vries.

From another point of view, one can concentrate on the simultaneous rediscovery of these three authors, which leads rather to the search for external, shared factors explaining the similarity of their research. One seeks then to understand the movement of the history of biology, beyond the noting of individual genius, in order to show various forms of rationality, whether scientific or sociological, technical or conceptual. In this case one takes the memorandum of Mendel as a text whose meaning cannot be determined independently from the context. And one has to analyse what was new in the conception of life in 1900 and absent in 1865 so that it is so widely and suddenly understood like a clear and convincing demonstration of the law of the distribution of characters in the descendants of hybrids, which the modern reader understands as an introduction to the 'Mendelian laws' of heredity. In particular, it must be understood how, in 1900, an equal and strictly random distribution of characters in sexual cells can be admitted. And in the same way it will be necessary to study what the memorandum of Mendel meant for him and his contemporaries, which is perhaps very different from what we assume today [12–14].

One often wonders whether Hugo De Vries rediscovered the Mendelian laws alone, or whether he had used the Mendel paper to interpret his results. He wrote, on several occasions, that he alone had discovered the laws of the independent segregation of characters. In his *Mutationstheorie* [15], he points out the case of the hybridisation of *Silene alba* and of *Silene alba* var. *glabra* that he had carried out from 1892 onwards, and which gave him in 1894, 392 hairy descendants (pubescent) against 144 hairless. In the letter that he wrote to H.F. Roberts in 1924 to describe the conditions of his discovery, he quotes one of the hybridisations that he carried out in 1893 on the primrose, between *Oenothera Lamarckiana* and *Oenothera Lamarckiana brevistylis*. In 1894, the descendants were perfectly uniform and he caused them to fertilise themselves. In 1895, he was able to observe the segregation of particular characters of *O. L. brevistylis* according to the Mendelian system. In the autobiographical article that he wrote in 1917, Hugo De Vries quotes rather the case of his hybridisation of the poppy between *Papaver somniferum Mephisto* and *Papaver somniferum Danebrog*. The third generation gave him in fact, in 1896, Mendelian proportions.

But, the opinions of historians are divided. Some admit that this discovery could have been made in the course of the first theories of Hugo De Vries and by inference as a result of his experiments [16–19]. Others point out that such an analysis is incapable of explaining either the experimental programme that Hugo De Vries was following just before 1900, or the theoretical articles that he was

then writing [20–23]. However, if one recognises that every scientific text, in order to be accepted and used by the community of researchers, has to be retranslated in the context of their theories and experimental practices, it is practically equivalent to showing either one or the other. The conditions for understanding Mendel's article as it was in 1900 are practically the same as making the discovery without it. One will not seek then so much to evaluate the influence of the memorandum of Mendel on botany just before 1900, as to understand the influence of the discoveries and speculations of this period on the reading of this memorandum. By so doing one will escape the risk of short-circuiting 35 years of the history of biology when the difficult genesis of modern conceptions of heredity took place [24].

A clutch of elements of the scientific, technical, epistemological and social context ought to be taken into consideration. We will give here only a few indications about one of these elements, crucial, although not sufficient by itself alone: the idea of a material determinant of character, that is to say of independent, separable units, representing the different qualities of an organism. This quite new idea, disseminated in 1900 though contested, was absent in Mendel's time. It made a non-idealistic interpretation of the organisation of living beings compatible with their study as entities composed of distinct characters, capable of separating and being redistributed in a probabilistic way in their descendants. In the developed organism, all the characters are linked. Colours, biochemical activities, the textures of surfaces, the dimensions and dispositions of the parts, are not separable in the matter of the living being. But if one admits that they have been determined by distinct particles, one could conceive that they combine in diverse ways in their descendants; the independence of the characters is only foreseeable at the level of the determinants and not of what is determined.

One finds a first systematic introduction of this idea in the short book that Hugo De Vries had published in 1889 when he had no knowledge of Mendel [25]. This work, which was read by Correns and Tschermak, shows in what context and with what difficulties this idea was constructed. The purpose was to justify theoretically the ancient know-how of the botanists, and this by adopting the 'Darwin's method' that he had followed in his work of 1868: "We will not try to explain the morphological details of this process; our knowledge is too limited for that. But, following Darwin's method, to find in each special case the material substratum of the physiological processes, such is our problem" ([2], page 6).

Taxonomy defines species by different combinations of simple characters and for De Vries, phylogenesis shows that the differences between neighbouring species must only be due to the presence or absence of some independent characters. Evolution would consist only in the appearance (or disappearance) of these discrete characters. And above all, the practice of hybridisation, of crosses and of selection permits the isolation and combining of these different characters: "The preceding considerations

are verified in a striking manner by the experiments in hybridisation and crosses. In no other case is the concept of the species as a unit formed by autonomous factors demonstrated more clearly" ([2], page 27).

However, following 'Darwin's method', it was necessary to define these 'autonomous factors' as units having a specific material substratum (*stofflichen Trägern*): "The hereditary factors, whose hereditary characters are the visible signs, are independent units which can be apparent separately in time, and can also be lost independently by each other." (*Die erblichen Anlagen, von denen die erblichen Eigenschaften die für unser Auge sichtbaren Merkmale sind, sind selbstständige Einheiten...*) ([2], page 33).

But, the fact that the horticulturists take in their practice the characters of plants as independent units does not permit one to construct directly the idea of distinct corresponding material units. It is very difficult, in a frame of thought which refuses all idealistic explanation, to treat qualitative characters as independent, manipulatable and distributable material units. A theoretical construction has to be made. The difficulty here is better understood if one adopts the contemporary but critical appraisal of a French neo-Lamarckian like Yves Delage [26, 27]. For him, "It is perfectly possible that they [the characters] are linked to each other and to a same material particle and that their dissociation is operated by our intelligence in the form of an abstraction" ([28], page 662).

For his theoretical work, De Vries claims to lean essentially on the works of Darwin [29]. The theory of natural selection laid out a programme of research on the mechanisms of hereditary transmission of individual variation [30]. Darwin had then made a synthesis of the known observations and put forward a theory which could account for it without departing from the framework of a materialist explanation: 'the hypothesis of pangenesis' that he published in 1868 [31]. He had thus described at length phenomena of variability independent of observable characteristics. But he drew from them a very different conclusion from that which De Vries attributed to him: "All the characters which can vary independently of each other must, according to him [referring to Darwin], be dependent on a specific material support" [2]. But for Darwin, these facts serve to justify a divisibility of the organism into elementary constituted units that he called 'gemmules'. The separability is not that of properties or qualities, but that of constituent parts of the organism (especially cells). The gemmules are understood as germs of cells. It is in developing that, according to their nature, they form the different cells. There is a cycle of transformation from gemmules to cells which, in their turn, produce new gemmules which for example will serve to constitute the matter of sexual cells. Note that in this framework, the hereditary variations are acquired during the individual life, either at the level of cells, or at the level of gemmules. This hereditary transmission of acquired variations did not aim in the first place to rehabilitate Lamarckism (which assumes immediately adaptable variations), but simply to form a sufficient quantity of variations to supply material

for the process of natural selection. At the time of ontogenesis, the gemmules come together according to precise affinities in ordered aggregates which, progressively, give the new organism. One cannot conceive here a distribution of the hereditary organic qualities in the process of reproduction which would occur independently from their nature. The causes that determine them, that is to say collections of gemmules, are linked among themselves in the sexual cells and in the egg as they will be in the developed organism. There is a communal relationship between gemmule and cell and no asymmetric determination. The origin of such an idea is rather to be found in the works of Karl von Nageli (1817–1891) and particularly in the works of the German biologist, August Weismann (1834–1914) whom De Vries studied at length in his book.

At the beginning of the 1880s, following a theoretical remark on natural selection which resulted in a systematic rejection of the transmission of acquired characters, Weismann had suggested explaining heredity by means of the durability of a substance, the germ plasm, which would be preserved unchanged from generation to generation. In a first phase, he distinguished two types of cellular lineage: the immortal germinal lineage whose cells, indefinitely capable of division, form the sexual cells, and the somatic lineage whose cells form the organism but which can only undergo a limited and defined number of divisions [32, 33]. There is no possibility of heredity of acquired characters in so far as the variations undergone by the somatic lineage do not affect the substance of the germinal cells. There is an asymmetric relationship of determination of the somatic characters starting from the germinal cells. In effect, the germinal cells would be capable of effecting two kinds of division. On the one hand homogenous divisions where the daughter cells conserve all the properties of their mother, and in particular the property of dividing indefinitely in a homogeneous fashion. On the other hand a heterogeneous division which would occur at the very beginning of embryogenesis and which would produce, on the one hand, a germinal cell preserving all its properties, and on the other, a somatic cell. In the somatic lineage the divisions would be counted and would determine precisely a series of cellular differentiations.

To face up to many criticisms and to integrate the results of the cytology of cellular division and of fertilisation which was then making rapid progress, Weismann had quickly transformed his theory. The separation between two types of cellular lineage became an internal distinction in each cell between the germ plasm contained in the nucleus and the somatic plasm of the cytoplasm. There again, the germinal plasm would be both capable of homogeneous division preserving the whole of its properties, and of a determining action of the cellular characters. But how can the germ plasm act so as to determine the characters of the cytoplasm. Here is how Weismann described later, in 1892, this difficulty:

"In order to exercise a determining influence on the minute structures of the cellular body and on the chemical composition of its different components, it [the nucleus]

must either be capable of exercising an influence by emission, or material particles must pass out of the nucleus into the cellular body." [34].

Before 1889, Weismann only seemed to envisage the first hypothesis. In so far as it determines the characters of the organism without being for all that altered itself, the germ plasm cannot then be understood as a collection of initial material conditions which, following the laws of physical chemistry, would give the developed organism in its final state.

Here, the cause is not transformed into its effect. It acts rather as an 'influence by emission', that is to say a cause which controls its effect without being exhausted therein.

De Vries developed his own theory starting from a dense critique of Weismann. In particular, he refused the idea of a too strict directing relationship of the nucleus with regard to the cytoplasm: "He [Weismann] posits that the nucleus dominates and determines the nature of its cell..." [2]. His first studies of plant physiology in the 1870s had taught him that the cytoplasm was an active and fully alive part of the cell. It contains in particular organic elements such as vacuoles which seem capable of growth and division [35]. The solution that he proposes consists then in a transfer from the nucleus towards the cytoplasm of living units that he named the 'pangenes' in honour of Darwin. All the organic characters are determined by these living particles contained in the nucleus of the fertilised ovule. The pangenes can be in two different states, either active or inactive. In the nucleus the pangenes are all in an inactive state, which does not prevent them from multiplying while conserving their type. In the course of development, at each stage of the cellular differentiation, the appropriate pangenes migrate from the nucleus towards the cytoplasm where they pass into the active state and express the particular characters of which they are carriers. The resemblance between a mother cell and her two daughter cells is thus explained by supposing that each type of pangen is reproduced at the time of division. Several regroupings of pangenes can give various combinations of cellular characters. However, the initial stock of pangenes is preserved in the nucleus and will serve in the formation of sexual cells. At the time of fertilisation the stocks of pangenes of the two parents mix, which explains the occurrence of separation and recombining of the characters in the descendants, which was already well known. Moreover, certain pangenes that have remained in an inactive state during all the development of the organism are nevertheless transmitted, which explains the phenomena of atavism and reversion, that is to say the reappearance in the descendants of characters of the ancestors that were not visible in the parents.

This theory did nothing more than reproduce the fundamental schema of Weismann, and moreover the latter rapidly took up Hugo De Vries solution [34]. To some extent, it is a return to Weismann's first solution – the separation between germinal and somatic cells through heterogeneous division – except that it takes place now inside the cell and that the units reproduced are pangenes.

The continuity of the pangenes replaces that of germ plasm. The maintenance of the stock of pangenes of the species in the nucleus from generation to generation explains the transmission of hereditary characters. In the same way as Weismann with the germ plasm, the pangenes can, by division in the inactive state, give at the same time a stock of identical pangenes that remain there and a stock of pangenes that rejoin the cytoplasm in order to produce characters in it. The pangenes are the determinants of the characters in so far as they are preserved unchanged while directing the formation of these characters. "The visible characters [*sichtbaren Merkmal*] of the organisms are determined [*bestimmt*] by the invisible characters [*unsichtbaren Einheiten*] of the living matter." [2].

In order to explain the mechanism of this determining process, De Vries relied on biochemical examples. For example, the appearance of a coloured pigment was explained simply by division, then the migration towards the cytoplasm of a precise type of pangene which, in passing over to the active state, would produce this substance by an enzymatic action. However, once this line of reasoning had been established for cellular characters, De Vries passed without transition to all the other characters whose independent variations the botanist was able to observe. In so doing, he used in a formal fashion the idea of the particle as a carrier of characters. For example, he did not hesitate to consider pangenes of purely morphological pluricellular characters as the twisting of the stem or the arrangement of the leaves. "These pangenes do not each represent a member of the organism, a cell or a part of a cell, but each one a special hereditary characteristic. These ones can be recognised by their ability to vary independently from each other." [2].

From the moment that one admits the existence of a determining relationship of a substance that is a carrier of heredity towards the organism, nothing prevents one from dividing up this determining principle into different and independent instructions. From the strictly reductionist point of view of a neo-Lamarckian like Yves Delage, one cannot accept the idea of hereditary factors distinct from the morphological characters that they would determine: "...there cannot be material factors of abstract characters" ([28], page 711). Either a cause participates in the effect that it produces, or it is isolated and produces no change. "I understand that an organised aggregate has a tendency to increase in a certain direction, but I do not understand that there can exist an independent material factor to determine this tendency in a neighbouring aggregate which is not it, which itself has no tendency of this order and which derives from the other its tendency in this respect." ([28], page 638.) So, although the theory of De Vries claimed to refer to material particles, for Delage as for many French physiologists, it was not at all a reduction of the phenomena of heredity and development to a purely physico-chemical causality.

However, the theory of De Vries, which had the merit of accounting for practices successfully mastered by horticulturists, had the added value of defining a programme of

experimental research in order to isolate these pangenes, to understand their material nature, and to determine the mechanism of their variations. In particular, the study of the distribution of characters in the descendants of hybrids was to allow one to decipher the questions of sexual heredity. It is within the framework of such research that one discovers the famous Mendelian proportions in 1900. But it must be recognised that some of the hypotheses of De Vries also constituted obstacles to this discovery. For example, the idea that each characteristic was to be determined by a great number of pangenes led him to statistical analyses of continuous variations on the model of the work of Francis Galton (1822–1911) which was far removed from research into the distribution of discrete characters controlled by pairs of determinants [36–40].

In fact, Galton and the English biometricians developed a probabilistic approach to the phenomena of heredity and selection. To account for the distribution of the frequency of variations in a population describing a bell-shaped curve, Galton had suggested an original theory inspired by Darwin. The variations of the characters observed would result in the random selection of multiple gemmules during the process of development and formation of reproductive cells. For Hugo De Vries, such probabilistic studies were to allow him to distinguish between two possible sources of variation, either by quantitative changes in the number of active pangenes (increased or decreased by selection as by nutrition), or qualitative changes creating new kinds of pangenes. "One can distinguish according to the conception of pangenesis two kinds of variability essentially different. The first is fluctuating variability, most often called individual variability, but more precisely continuous. The second is the variability which creates species." ([36], page 494.)

The observation for a given character of a stable means in the course of generations in spite of continuous selection signalled the presence of a single kind of pangene. On the other hand, the possibility of displacing this means by selection or by nutrition signalled the presence of different pangenes. So, Hugo De Vries undertook a large number of experiments constructed according to the statistical methods that he borrowed from Galton. Although rather disappointing, these experiments convinced him that there was a strong distinction between fluctuating variations having no evolutionary significance and the 'mutations' by discontinuous leap. These latter would result in a new pangene and would be solely at the origin of stable variations being capable of producing new species. These mutations were of special interest to Hugo De Vries, particularly since he thought he had observed them in a primrose *Oenothera Lamarckiana* in 1886 near Amsterdam [41]. One knows now that it was not a question of mutation in the modern sense: some of these variations correspond to rare combinations which maintain themselves at the heterozygotic state by means of genetic balance due to the lethality of the homozygotes. Other variations are provoked by changes in the stock of chromosomes (polyploidy) [42]. He sought to discover the conditions govern-

ing the appearance of these mutations and to show that these variations were definitely hereditary by following their behaviour at the time of hybridisation [18, 19]. It is these studies that he would continue after 1900. Abandoning the idea of writing an 'Experimental Pangenesis', he produced in 1901 and 1903 the two volumes of his *Mutationstheorie*, essentially devoted to those sudden phenomena of mutation of one kind to another which ought to conceal the true explanation of evolution [15].

In addition, just before 1900, the works of Sergius Nawaschin (1857–1930) in Russia [43, 44] and of Jean-Louis-Léon Guignard (1852–1928) in France [45] had renewed the interest for the phenomena of 'xenia', which was described as a form of direct influence of the father on the mother. These authors would show that it was a question in fact of a simultaneous double fertilisation, by two male cells of the pollinic tube, of the oosphere on the one hand and of the embryonic sack on the other. Hugo De Vries, who had been studying these phenomena since 1876, then resumed his work by crossing sugar maize with the normal starchy form. The methods employed were very close to those which led to the rediscovery of Mendel. It was necessary right from the start to isolate lines whose purity was assured by several years of culture. The observation of the results of the hybridisations could already be carried out on the characters of the seeds and they gave practically no intermediary characters. Moreover, one of the characters prevailed over the other systematically (in the description of these experiments Hugo De Vries did not yet employ the vocabulary of 'dominance' and 'recessiveness' that he would shortly borrow from Mendel). The hybrids were all of the starchy form and their descendants were distributed according to the proportions 1/4, 3/4: "About a quarter of the seeds were sugary, the other three quarters were starchy" ([46], page 195). The predominant starchy form being able to recover pure lines or hybrids which can only be detected in the following generations: "It is not enough to have just the culture of one year: it is indispensable to sow the harvest grown, in order to judge its character" ([47], page 134).

However, it is not a question there of a veritable recognition of the Mendelian laws. The proportions are approximate and already often observed, and Hugo De Vries envisaged a mixture of the characters giving rare intermediate seeds, half starchy, half sugary. These observations were not supported by a theoretical edifice on the distribution of characters in the descendants of hybrids and have, moreover, another objective (to confirm the simultaneous fertilisation specific to xenia).

The publications of Hugo De Vries on xenia were like a rehearsal of what was going to occur the following year for the famous Mendelian publication. At the very beginning he presented a note to the Académie des Sciences [46], then an article in the *Revue générale de botanique* directed by Gaston Bonnier [47], an article in which he pointed out that his publication in the *Comptes rendus* preceded by several weeks a publication on the same subject by Carl Correns in the *Berichte der Deutschen Botanischen Gesell-*

schaft [48]. Hugo De Vries had, particularly at this period, a formidable capacity to publish multiple articles and simultaneously in Dutch, French, German and English, but the publication of the notes at the Académie des Sciences seems to have been systematically quicker than the appearance of the articles in the *Berichte*.

One must also point out that Hugo De Vries recalled that the term 'xenia' had been defined in 1881 in an important work by Wilhelm Obers Focke which produced the synthesis of the references necessary for the study of hybridisation [49]. Now, this work also contained numerous references to the work of Gregor Mendel. It is certainly by this path that Hugo De Vries discovered the famous Mendel paper.

From then onwards, if one accepted the idea of separate determinants of the different characters, it was becoming possible to understand the paper of Mendel as a description of their distribution in sexual reproduction. While accepting to consider only a pair of pangenes as determining a difference in the case of a simple character, pangenes which would be found in a single example in each sex cell, one could understand that their transmission in the inactive state could occur independently from the differences of characters that they determine. The existence of the probabilistic laws of heredity became acceptable.

On the contrary, the memorandum of Mendel must have appeared very idealistic to his contemporaries [50]. Its reflections on constant differential characters, which like abstract and unalterable qualities, could be distributed in the descendants without being modified or even interact between each other caught the biologists on the wrong foot, who were looking for mechanisms of continuous transformation, materially comprehensible, of characters of the species. It required the difficult invention of a theory of determinants separable from the different organic characters in order for Mendel's article to assume its modern meaning.

However, the case of Mendelian proportions could only be a very special case of the theory of pangenes. It represented such a distortion of the thought of Hugo De Vries that he rapidly came to relegate it to the periphery of his research. In effect, if there are at the beginning of the development only two pangenes to determine each character of the organism, then, not only the idea of the formation of the characters by multiplication of the corresponding pangenes is accessory, but even the idea of cellular transfer loses all interest. Right from the end of 1900, Hugo De Vries was seeking rather to show that the laws of Mendel were not absolutely universal. The equal probability of the two alternatives of a differential character would only be a special case. "Such an equivalence is, however, by no means essential. The characters may, in other cases, become of unequal value at the separation." ([51], page 249.)

For Hugo De Vries, the ultimate aim was to give an explanation of the origin of species and the case described by Mendel was without importance for evolution. So, he became interested also in the case where hybrids did not

separate, which, following Millardet, he called them 'false crosses', to contrast them with the 'true crosses' in which the equal segregation of the characters took place [52]. This is what led him, as Naegeli had done, to study the case of *Hieracium* which had posed so many problems for Mendel. The perfect segregation of characters must certainly have belonged to the regressive (or retrogressive) variations. The new character was latent, it was probably due to the alteration, or the disappearance, of an old character rather than the acquisition of a new one. When, after 1900, Hugo De Vries used hybridisations, it was to discriminate between a really new elementary species (progressive varieties which were not to undergo segregation) and the regressive varieties (which correspond to latent characters and which must return to their parental types following Mendelian laws). For Hugo De Vries, 1900 was above all the year of the official announcement of his *Mutationstheorie*, and it was the study of the origin and the mechanism of the mutations to which he was to devote the rest of his life.

Initially, just after 1900, Mendelism, which favoured the study of discrete qualitative characters, was opposed to

Darwinism which, in its biometric version of the end of the 19th century, needed, in contrast, quantitative and continuous variations. It came to comfort William Bateson who, like Hugo De Vries, thought that evolution must above all be produced by sudden leaps and not by the continuous selection of small variations [53, 54]. But if one recognises that this idea of determinant had been developed within the framework of a programme of research based on Darwin's work, one can better understand that Mendelism was finally able to agree with the theory of natural selection from the 1930s onwards within the framework of the genetics of population. Over and above their first opposition, Darwinians and Mendelians shared a rejection of acquired characters, a rejection which, with Weismann, gave birth to neo-Darwinism and to the distinction between germ plasm and somatic plasm, between determinant and determined characters. Such an underlying agreement is at the same time underlined by the continuing refusal of the French neo-Lamarckian tradition, from the resistance to neo-Darwinism by Weismann up to the scepticism with regard to Mendelian genetics.

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