Mendel's Two Genetics Papers Viewed from the Standpoint of Evolution*

Yosito SINOTÔ**

Mendel published only two genetics papers, in 1866 and in 1870 respectively. One is concerned with *Pisum* and the other with *Hieracium*. The first paper is well-known and is the source of the so-called Mendel's laws of heredity on which the modern genetics is based and developed. The second is a short interim report and seems to have been regarded as a less important work.

Now, I would like to talk about my views on the characteristics of these two papers and also on Mendel's idea inherent in or attitude taken in these studies.

Of the various fields of the highly progressed genetics in recent years, the relation of heredity and evolution is one. I would like to consider how Mendel thought of this theme, how he performed his experiments, how he evaluated his own studies, and what was his intention in writing and publishing his papers, etc.

The paper on peas is written in German and is 45 pages long without any illustrations. It is divided into 11 chapters beginning with "Introductory remarks" and ending with "Concluding remarks" (Table 1).

Table 1. Contents of Mendel's paper on peas

* A part of the memorial lecture given in Japanese at the centennial anniversary of the discovery of Mendel's laws, held in Japan in 1965.

** Department of Biology, International Christian University, Mitaka, Tokyo, Japan

If I may give a number to each chapter, chapters 4-9 are the portion dealing with pea experiments, and chapter 10 is concerned with the generalization test to see whether or not the laws obtained from the study of peas can be applied to other plant groups, for instance, beans, as used here. The final chapter for "Concluding remarks", is rather long compared with the usual way of papers published nowadays, because here Mendel discussed possible interpretations of various problems presented by his predecessors, with his planned experiments, on the basis of the laws from the study of peas.

The whole paper on the study of peas can be separated into two parts. The first part occupying about two thirds of the paper relates experiments on peas, and the other part, one third of the paper, contains the chapter dealing with experiments on other plants (chapter 10) and the chapter for "Concluding remarks".

The first two thirds are the portion which form the foundation of today's genetics, giving us an impression that the paper had no other part. Of course this

part alone is so important that it deserves the highest evaluation. At the beginning of the remaining one third, application of the laws obtained from the study of peas to other plants is discussed. Here, Mendel succeeded in attaining useful results of experiments, thought the data were not sufficient, for the interpretation of the diversity of color changes of bean flowers, adding explicit explanations to them which were developed later by his successors.

In the following chapter (11), "Concluding remarks", roughly three problems were taken up for discussion based on the renewed experiments. The first problem was that living things vary both inwardly and outwardly. In the second place, explanation was attempted about the distinction between a hybrid, such as peas, whose offspring are changeable and one such as willows whose offspring are unchangeable. Here we may be able to see that Mendel introduced a concept of gene and its nature and action. The third problem was about the transformation of species. These problems all can be said to be those of organic evolution. I surmise that Mendel attempted to solve these problems by means of the laws gained from his genetics study of peas. Altogether, it may be said further that the paper on peas is, especially in the latter part, in conjunction with the first part, entirely dealing with the problems of evolution.

When Mendel published this paper, "Origin of species" by Charles Darwin, which had been published six years before, was gaining the attention of the world and Mendel might have known the reputation. It is guessed from some passages of Mendel's paper that he was not always agreeing with Darwinism, though not denying it entirely.

Mendel's second paper dealing with *Hieracium*, is a short work written in German of only 6 pages without any figures. This was a kind of an interim report. Mendel thought he would have enough time for study if he were appointed abbot of the monastery. But, contrary to his expectation, this duty kept him busy with various responsibilities both in and out of the monastery, which almost prevented him from studying of *Hieracium*. He continued, however, to work on this chrysanthemum with his native perseverance. After all, he wrote in his last letter to Nägeli, his esteemed teacher and friend (November 18, 1873): "The hieracia have withered again without my having been able to give them more than a few

hurried visits. I am really unhappy about having to neglect my plants and my bees so completely."* Mendel is said to have called peas and hieracia "my dear children". The flowers of hieracia are very small and are open at the time between 7 and 9 o'clock in the morning when the tips of their pistils come out. In order to pollinate, he never failed to come to that flowers every morning at the right time. He even had eye trouble as a result. Concerning the publication of the short report of hieracia, he stated in his paper as follows:

"It will be clearly understood from the littleness of what I can report here that this study has progressed not a step from the starting point. I should have hesitated to report on an experiment which is just started. I believe it will take several more years to complete the schedule of experiments, moreover, I am not sure whether or not I can continue to work to the end. That's why I decided to make this report."**

Mendel gave in his paper a number of reasons for his taking up hieracia as an experimental material to substitute for peas.

1) Genus *Hieracium* has an abundance of independent varieties.

2) Among them, while there are fundamental types, in other words, species, there are intermediate types or transitive types with which fundamental types are bound to each other.

3) Therefore, the classification of the genus *Hieracium* is so difficult that it drew the attention of specialists and many papers had been published, but no definite conclusion was obtained. To solve the problem, Mendel thought, the value and meaning in classification of intermediate types or transitive types must be found.

4) There were different opinions on the relationship between polymorphism and crossability of this genus.

5) A problem of sterlity of hybrids exists.

6) A problem was raised as to the origin of constant (stable) intermediate

---

* Cited from an English translation of this letter included in "The birth of genetics", Supplement to Genetics, 1950.

** English citations of Mendel's two papers are made from appendix to Bateson, W.1909. Mendel's principles of heredity. 2 ed.

types. This problem aroused interest after a famous specialist (probably Nägeli) stated on the basis of the Darwin's new theory that these intermediate types had been produced by changes of extinct or existing species.

7) For evaluating the effects of hybrid formation on the diversity of intermediate types, it is necessary to know well about hybrids in their types and sterility as well as the behavior of their offspring through many generations.

Mendel stated that, in order to obtain the laws of a hybrid formation in *Hieracium*, an experiment was the only means for approaching the problem solution, and that the purpose of his study on *Hieracium* consisted in the reasons enumerated in the above.

With such knowledge and views about the genus *Hieracium*, Mendel took up this plant group as the material for his experiments and reported some of the results obtained in his letter of 1866 to Nägeli. Nägeli advised Mendel to go ahead with his plan and sent him some kinds of hieracia. It is guessed that, besides the plan of applying the laws found in the study of peas to the case of hieracia, Mendel planned to extend his study from the problem of polymorphism of this plant group to the problem of species. In this series of experiments with hieracia, he succeeded in producing 6 kinds of hybrids which he examined and described from his own point of view. Sometime after discontinuing this study, he wrote the last letter to Nägeli in 1873, sending him 235 hybrid plants of 5 kinds of crossing in *Hieracium*.

The following may be pointed out as the findings Mendel achieved in this study on hieracia:

1) There are combinations of species which produce hybrids and ones which do not.

2) In the progeny of the first generation of hybrids, there are characteristics which follow the laws as found in the case of peas, and ones which do not.

3) There are some plants in the first generation of hybrids, which show polymorphism.

4) Those in the second and later generations showed sterility and homomorphism.

5) Self-pollination is not prevented by the parent's pollen.

6) Even in the case of a wild and fertile species, sterility is observed in its pollen.

7) It is very important that the existence of constant and polymorphic hybrids (*Salix* and *Hieracium*, for instance) has some relationship with the peculiar behavior of hybrids. This problem, however, is not yet solved.

So far I stated outlines of the two papers of Mendel. Now, I would like to tell how Mendel himself thought about these two papers, in other words, what is the reason according to which I may regard these papers as works on evolution.

1) There were many persons who had tried crossing plants before Mendel did. Among them, two eminent hybridists engaged in their work on a large scale. Both of them were Germans, D. J. Koelreuter, whose book was published in 1761, and C. F. Gärtner whose book, including the results obtained by him, was published later in 1848. They examined the problems of pollination, characteristics of hybrids, formation of species and varieties, by means of crossing many plants. In 1830, the Dutch Academy in Haarlem announced an essay contest on the themes of the question of artificial production of species and varieties, and of production and raising of useful or ornamental plants. Gärtner participated in the contest and won a prize. After the death of Koelreuter, E. A. Regel opposed A. Knight of England and J. F. Klotsch of Germany who insisted that a species hybrid was sterile. Similarly, A. Jordan opposed D. A. Godron. With the rise of the controversy, the academy in Paris announced an essay contest on the themes of continuity and self-pollination of hybrids, and atavism of hybrids. Among the participants, C. Naudin won the first prize and D. A. Godron the second. In addition, in 1859, Darwin published his "Origin of species" which drew the world's attention and was also discussed often at the Natural History Society at Brünn. Mendel mentioned in the "Introductory remarks" of his paper on peas the names of researchers on crossing such as Koelreuter, Gärtner, W. Herbert, H. Lecoq and M. E. Wichura. He was familiar with the books of M. T. Schleiden who put forward the "Cell theory", as well as with all books of Darwin in the evolutional cycle. From the above, it is apparent that Mendel was well convinced that the main current theme in the 19th century was the problem of species, in other words, that of evolution.

2) There are many points in Mendel's two papers which are understandable from the viewpoint of 1) above mentioned. If we look at the paper on peas, we will know that Mendel worked from beginning to end along the line of the problem of evolution. Followings are the examples quoted from his paper of 1866.

1. From "Introductory remarks"

a) First, he stated the motive (Veranlassung) of his study saying: "Experience of artificial fertilization, such as is effected with ornamental plants in order to obtain new varieties in color, has led to the experiments which will here be discussed." To obtain plants of new colors is none other than the problem of evolution. To fulfil his purpose, Mendel chose the method of producing hybrids and examining their numbers and behavior from generation to generation. Mendel said that he did this, because proper laws had not yet been found by the patient and careful predecessors such as Koelreuter, Gärtner, and others.

b) To accomplish this task, he said, a large scale "detailed experiment" should be done and at the same time some courage was required. "This appears, however, to be the only right way by which we can finally reach the solution of a question, the importance of which cannot be overestimated in connection with the history of the evolution of organic forms." His course of study is one of the good examples of what is based on the principles of what are called spirit and methods of modern sciences. The characteristic of his studies will not be mentioned here, but it had much originalities never seen before.

2. Secondly, in "Selection of the experimental plants", he said, "If we adopt the strictest definition of a species, according to which only those individuals belong to a species which under precisely the same circumstances display precisely similar characters,..." By this we can see that Mendel had concern with the concept of species and had his own view or difinition of a species.

3. In the chapter 10 of the follow-up test using beans, returning to the problem of diversity of color change of ornamental plants, i.e., the motive of the study, he developed ingenious reasoning in an attempt to explain and analyze the color diversity, using the laws obtained by the study of peas, discussing that there

was no difference in principle between ornamental plants and wild ones in the relationship of heredity and environment.

4. In the next and last chapter 11, "Concluding remarks", as I mentioned before, Mendel took up some problems which had been treated by his predecessors. By additional experiments, he extended his theory and applied it to the interpretation of these problems. The passage in which Mendel stated it is very remarkable and interesting to me. It runs: "Gärtner, by the results of these transformation experiments, was led to oppose the opinion of those naturalists who dispute the stability of plant species and believe in a continuous evolution of vegetation. He perceives in the complete transformation of one species into another an indubitable proof that the species are fixed within limits beyond which they cannot change. Although this opinion cannot be unconditionally accepted we find on the other hand in Gärtner's experiments a noteworthy confirmation of that supposition regarding variability of cultivated plants which has already been expressed."

Even from the above which I cited and referred to, we may get some idea of the pea paper, in which I intended to show that Mendel's concern on evolution is discernble as he conducted the experiments.

As to the paper on hieracia, as I said before, this study might have been Mendel's attempt at solving the problem of diversity of the species in this genus in the light of hybridization, and this paper may be regarded as one dealing with evolution rather than heredity. At the end of the paper, after explaining that hieracia are different from peas in their ability to produce constant hybrids and that this phenomenon is not very peculiar, for instance, as observed by Wichura in the willow, he stated as follows: "It is supposed from this instance that Hieracium also shows a case similar to it. As such is the case, whether or not the hypothesis that the polymorphism observed in the willow and hieracia has something to do with the peculiar behavior of their hybrids can be formulated is yet to be determined. This problem is worth discussing, but has not been solved." Although this paper of Mendel on hieracia seems to have been overlooked, I think it is a remarkable piece of the classic literature of evolution in view of what I mentioned in the above.

It may also be pointed out that various comments have been made as to

Mendel's selection of *Hieracium* as the experimental material, such as "he was kidnapped by Nägeli," "it was a mishap for Mendel himself as well as for the development of science and the history of science", or "it was the cause of his failure that he wrestled directly with a complicated matters as *Hieracium* without following Descartes' way of thinking as he did with peas."

But I don't agree with these criticisms. Here too, keeping the attitude of adopting the consistent method of experiment as the way of problem solving, Mendel patiently faced a new problem as it arose. No one but Mendel himself chose hieracia with more than enough knowledge of this group which is a genus with many problems, and so is a proper material for the study of the problem of evolution. It cannot be denied that such a contemporary specialist as Nägeli was of some help to Mendel in selecting this plant.

As Mendel mentioned in the paper, our attention is drawn to the fact that this study had progressed no further than the first step. It should also be noted that at that time parthenogenesis of this plant had not yet been discovered and neither Nägeli nor Mendel knew the phenomenon, which was discovered as late as 30 years after. If Mendel had known the phenomenon, many of his questions would have been solved and his work made easier. But I feel that Mendel would have reached this point with his brilliancy, if he had been given 10 more years or even a shorter time for its study. Because, judging from this second paper and also from other data such as found in his letters to Nägeli, Mendel already had the idea of self-pollination in connection with the second and later generations of hybrids which are sterile and constant. It seems likely that a person of Mendel's ability could have managed to reach the conclusion concerning the mathematical relation between the sterility rate of pollen and self-pollination rate, and furthermore the discovery of parthenogenesis itself might not have been impossible. It is even felt that he was just on the verge of an important discovery. The term "mishap" or "unlucky", must not be used for Mendel's selecting hieracia as his experimental material, but it may be applied to the fact that he was too busy to secure the time for study, holding the office of high-ranking holy order, and moreover, being involved in a tax problem, etc. To the contrary, I believe, this second paper confirmed the Mendel's attitude and intention of study as a scholor of evolutional

problems. This fact interests us together with the work of the Mendelians who, in later years, came to develop the population genetics which is intimately related to evolution.

In short, these two papers may be the results of Mendel's attempt to find some solution to the problems of evolution by discovering laws in the course of analysing the offspring in their numbers and behaviors of hybrids in successive generations. For this purpose, he at first made experiments on peas and then applied the laws found to other plant groups including hieracia in order to generalize them.

It may be noted that it was not Mendel himself who extracted laws from his papers nor did he name them Mendel's laws. This fact seems to indicate to a considerable extent that Mendel was interested in the laws found in his crossing experiments merely as a means of explaining the evolution problems faced in his contemporary age, rather than in classifying heredity laws. In fact the so-called Mendel's laws were first advocated in 1900 by those whom you would call re-discoverers of Mendel's laws. At first, H. de Vries pointed out the most important part of Mendel's *heredity* laws by entitling his first re-discovery articles: "Concerning the law of segregation of hybrids " ("Sur la loi de disjunction des hybrides") and "The law of segregation of hybrids" ("Das Spaltungsgesetz der Bastarde"). The second re-discoverer C. Correns entitled his first re-discovery article as: "G. Mendels Regel über das Verhalten der Nachkommenschaft der Rassenbastarde". He discussed in this paper, rather emphasizing, the problem regarding examples of exceptions to Mendel's laws. So he seemed to have used the word Regel, not Gesetz, I presume. At any rate, Correns also must have meant Mendel's *heredity* laws by G. Mendels Regel. It may be natural that Mendel's intention or concern with elucidation of evolutional problems or evolutional implications in his papers have not come forward, because soon after the re-discovery, importance of one side of his study, that is the side concerned with heredity, in other words, the first part of the pea paper, was emphasized, and that by influential scholors, such as de Vries, Correns and Tschermak. H. Hoffmann (1869) of Germany may be regarded as the first person who quoted Mendel's pea paper, but his purpose was to criticize Darwinism and he did not deal with

Mendel's paper from the genetical or evolutional viewpoint.

It goes without saying, or it may rather be self-evident, that Mendel's works are deeply concerned with heredity and evolution. However, there seems to have scarcely been publications which discuss Mendel's two genetics papers by studying and analyzing their contents, especially emphasizing their evolutional implications.* That is why I have reported what I have long (since 1938) had in my mind at this occasion of the centennial anniversary of the discovery of the Mendel's laws held in Japan.

Reference

Bateson, W. 1909. Mendel's principles of heredity. 2. ed. The University Press, Cambridge.

The birth of genetics. Supplement to Genetics. 1950.

Correns, C. 1900. G. Mendels Regel über das Verhalten der Nachkommenschaft der Rassenbastarde. Ber. d. Deut. Bot. Gesel. 18: 158–168.

——— 1950. Gregor Mendels Briefe an Carl Nägeli. 1866–1873. Abhandl. d. Mathem.-Phys. Klasse d. Königl. Sächs. Gesell. d. Wiss. 29: 189–265.

de Vries, H. 1900. Sur la loi de disjonction des hybrides. Compt. Rend. Acad. Sci. 103: 845.

——— 1900. Das Spaltungsgesetz der Bastarde. Vorl. Mitteil. Ber. d. Deut. Bot. Gesell. 18: 83–90.

Focke, O. W. 1881. Die Pflanzenmischlinge. Berlin.

Iltis, H. 1924. Gregor Johann Mendel. Leben, Werk und Wirkung. Verlag von Julius Springer, Berlin.

Mendel, G. 1866. Versuche über Pflanzen-Hybriden. Verhandl. d. naturfors. Vereins in Brünn 4: 3–47.

——— 1870. Ueber eininge aus künstlicher Befruchtung gewonnenen Hieracium-Bastarde. Ib. 8: 26–31.

Nagashima, Y. 1942. Life of Mendel. In Japanese. Sôgensha, Tokyo.

The Publication Com. of Mendel Centennial Aniversary in Japan 1967. Upon the

* By courtesy of Dr. V. Orel in Brünn, I received a copy of "Fundamenta Genetica, 1965". Selection and commentary by Dr. Jaroslav Krízenecký, after the Mendel centennial anniversary was held in Japan in 1965. Dr. Krízenecký commented rightly on Mendel's definite standpoint towards the theory of evolution, etc.

Steps from Mendel. In commemoration of Mendel centennial aniversary. In Japanese. Shôkabô, Tokyo.

Sinotö, Y. 1938. Genetics in history——An attempt for synthesis. In Japanese. 1945. 2. rev. ed. Chikara-shobô, Tokyo.

——— 1950. Mendel. In Japanese. Kôbundô, Tokyo

——— 1955. On the development of Mendelism and its application in Japan. In Japanese with Italian, English, German and French summaries. Vol. Novant'anni d. Leggi Mendeliane, Roma: 119–143.

——— and Nagashima, Y. 1948. Re-sidcovary articles of Mendel's laws. H. de Vries, C. Correns and E. Tschermak. In Japanese translation. Chikara-shobô, Tokyo.

——— 1967. Mendel's brief biography and his two genetics papers. A memorial lecture. In Japanese. In: Upon the Steps from Mendel, commemoration of Mendel centennial anniversary: 32–40.

Stern, C. and Sherwood, E. R. 1966. The origin of genetics. W. H. Freeman and Co., San Francisco.

Tschermak, E. 1900. Ueber künstliche Kreuzung bei *Pisum sativum.* Ber. d. Deut. Bot. Gesell. 18: 232–239.