III. GREGOR MENDEL'S LIFE AND ACHIEVEMENTS

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The contributions of Mendel to biological science have been recognized so generally during the last two decades that in many parts of the world during the past year scientific men have joined in celebration of the centennial of his birth. Bateson, one of the foremost students of heredity of the present day has made an extensive study of the life of Mendel and the events connected therewith. From his account*, many of the facts in the present

During the period from 1853 to 1868, Mendel was a teacher especially of physics in the Realschule at Brunn, and during a certain part of this period he carried on experiments in the large garden of the cloister there. This institution which was the Aug-

ustinian house of St. Thomas in Bruenn was generally spoken of at Koenigskloster. He had long been interested in watching the behavior of various plants cultivated in the garden in experimental conditions, and took great pleasure in this sort of work. The views of Darwin on natural selection had just come into prominence when Mendel, who did not fully agree with Darwin, began his experiments on peas. These experiments were conducted for eight years and Mendel's account of them, "Experiments in Plant Hybridization" was published in 1866, one year after they had been communicated to the Bruenn society. In translation this paper occupies 44 pages. In it are detailed the results of his experiments on peas and his conclusions regarding them. Another paper of importance was communicated in 1869 and published the following year in volume VIII, of the same journal. This paper is entitled "On Hieracium-hybrids Obtained by Artificial Fertilization" and is his last publication on plant breeding. Besides these two papers we have only two other notes published earlier in Verh. Zool. Bot. Verein. Wein, on Scopolia margaritais in 1853 and on Bruchus pisi in 1854. In 1868 he was elected abbot of the Koenigskloster and during the rest of his life he was devoted to other than scientific interests.

His papers seem to have been known to one scientist only, the botanist Nageli, and he did not appreciate their importance. A single reference to this work occurs in the scientific literature before 1900. It is in a publication of Focke, "Pflanzenmischlinge" published in 1881. It was to this reference that is due the rediscovery of Mendel's papers in 1900.

In 1900 three investigators DeVries, Correns, Tschermak, independently came upon his two papers and perceived their importance. The time, 16 years after his death, was now ripe for their appreciation and for the application of the discoveries he had made, and wide recognition has since been accorded Mendel. No field of work is now of greater consequence than that of genetics and of this field his work is the cornerstone.

Mendel's discoveries were undoubtedly contributions of the highest order to the science of heredity, and upon them has been built the superstructure which has made the subject not only a commanding one in biological research but of the greatest significance for the social sciences. As the result of his experiments Mendel recognized first the principles of the purity of the germ cells and their segregation unmodified in the second generation, and second the principle of dominance.

†Vahr. Naturf. in Bruenn, Abhandlung. IV., 1865.
The meaning of this principle of dominance and segregation may be best illustrated from Mendel's own work. He relates that in experiments in crossing individuals differing in regard to a single pair of characteristics it was found in many cases that "One of the two parental characters is so preponderant that it is difficult, or quite impossible, to detect the other in the hybrid." The following quotations are from Mendel's paper entitled "Experiments on Plant Hybridization."

"This is precisely the case with the Pea hybrids. In the case of each of the seven crosses the hybrid-character resembles that of one of the parental forms so closely that the other either escapes observation completely or cannot be detected with certainty. This circumstance is of great importance in the determination and classification of the forms under which the offspring of the hybrids appear. Henceforth in this paper those characters which are transmitted entire, or almost unchanged in the hybridisation, and therefore in themselves constitute the characters of the hybrid, are termed the dominant, and those which become latent in the process recessive. The expression "recessive" has been chosen because the characters thereby designated withdrew or entirely disappear in the hybrids, but nevertheless reappear unchanged in their progeny, as will be demonstrated later on."

"Of the differentiating characters which were used in the experiments the following are dominant:

1. The round or roundish form of the seed with or without shallow depressions.
2. The yellow colouring of the seed albumen (cotyledons).
3. The grey, grey-brown, or leather-brown colour of the seed-coat, in association with violet-red blossoms and reddish spots in the leaf exils.
4. The simply inflated form of the pod.
5. The green colouring of the unripe pod in association with the same colour in the stems, the leaf-veins and the calyx.
6. The distribution of the flowers along the stem.
7. The greater length of stem.

With regard to this last character it must be stated that the longer of the two parental stems is usually exceeded by the hybrid, a fact which is possible only attributable to the greater luxuriance which appears in all parts of plants when stems of very different length are crossed. Thus, for instance, in repeated experiments, stems of 1 ft. and 6 ft. in length yielded without exception hybrids which varied in length between 6' ft. and 7½ ft."

In discussing "The Generation From the Hybrids," he says,
"In this generation there reappear, together with the dominant characters, also the recessive ones with their peculiarities fully developed, and this occurs in the definitely expressed average proportion of three to one, so that among each four plants of this generation three display the dominant character and one the recessive. This relates without exception to all the characters which were investigated in the experiments. The angular wrinkled form of the seed, the green colour of the albumen, the white colour of the seed-coats and the flowers, the constructions of the pods, the yellow colour of the unripe pod, of the stalk, of the calyx, and of the leaf venation, the umbel-like form of the inflorescence, and the dwarfed stem, all reappear in the numerical proportion given, without any essential alteration. Transitional forms were not observed in any experiment."

"Expt. 1. Form of seed.—From 253 hybrids 7,324 seeds were obtained in the second trial year. Among them were 5,474 round or roundish ones and 1,850 angular wrinkled ones. Therefrom the ratio 2.96 to 1 is deduced."

"Expt. 2. Colour of albumen.—258 plants yielded 8,023 seeds, 6,022 yellow, and 2,001 green; their ratio, therefore, is as 3.01 to 1."

"Expt. 3. Colour of the seed-coats.—Among 929 plants 705 bore violet-red flowers and grey-brown seed-coats; 224 had white flowers and white seed-coats, giving the proportion 3.15 to 1."

"Expt. 4. Form of pods.—Of 1,181 plants 882 had them simply inflated, and in 299 they were constricted. Resulting ratio, 2.95 to 1."

"Expt. 5. Colour of the unripe pods.—The number of trial plants was 580, of which 428 had green pods and 152 yellow ones. Consequently these stand in the ratio 2.82 to 1."

"Expt. 6. Position of flowers.—Among 858 cases 651 had inflorescences axial and 207 terminal. Ratio 3.14 to 1."

"Expt. 7. Length of stem.—Out of 1,064 plants, in 787 cases the stem was long, and in 277 short. Hence a mutual ratio of 2.84 to 1. In this experiment the dwarfed plants were carefully lifted and transferred to a special bed. This precaution was necessary, as otherwise they would have perished through being overgrown by their tall relatives. Even in their quite young state they can be easily picked out by their compact growth and thick dark-green foliage."

"If now the results of the whole of the experiments be brought together, there is found, as between the number of forms with the dominant and recessive characters, an average ratio of 2.98 to 1, or 3 to 1."
"The ratio of 3 to 1, in accordance with which the distribution of the dominant and recessive characters results in the first generation, resolves itself therefore in all experiments into the ratio of 2:1:1 if the dominant character be differentiated according to its significance as a hybrid-character or as a parental one. Since the members of the first generation ($F_2$) spring directly from the seed of the hybrids ($F_1$) it is now clear that the hybrids form seeds having one or other of the two differentiating characters, and of these one-half develop again the hybrid form, while the other half yield plants which remain constant and receive the dominant or the recessive characters (respectively) in equal numbers."

If we seek to apply the Mendelian principles to human inheritance, as is done by modern eugenists, the knowledge of the stock from which a man comes assumes importance. In the case of Mendel himself we would be glad to know how the traits which characterize him, and which of course enabled him to achieve so largely in the scientific realm, may have appeared among his progenitors. He was born July 22, 1822 at Heinzendorf, in Austrian Silesia. His father was a small peasant proprietor. The family name Mendel, or Mandel as it is frequently written, appears in the church register in the 17th century. The suggestion that the name suggests Jewish origin is probably incorrect since it can be traced back of the time when the Jews in Austria assumed definite surnames. Owing to the fortunes of war the Kuhland district in which Heinzendorf is located was at one time protestant, and among Mendel's ancestors were several of that faith. His four grandparents were all of local Heinzendorf stock; that is members of a German colony which was surrounded by Slavonic population. We are indebted to Bateson for the collection of many facts regarding his life. Of him Bateson says:

"It is recorded of his father that he took special interest in fruit-culture, initiating his son at an early age into the methods of grafting. Mendel's maternal uncle, Anton Schwirtlich, was evidently a man of intellectual tastes, which is shown by the fact that he started private classes for the children of Heinzendorf who could not walk so far as the neighboring village, for in Heinzendorf itself there was at that time no regular school. Mendel was thus able to say with some pride that he came from an educational family.

"On the death of Schwirtlich a government school was established which Mendel attended as a young boy. His talent was noticed and encouraged by the master. At this time also two
older boys who had gone away to the school at Leipnik fell in with Mendel during their holidays, and excited his ambition, with the result that he asked his parents to let him study, and eventually he too was sent to Leipnik at eleven years old, though this involved considerable sacrifice on the part of the family. Here he distinguished himself so much that it was decided to continue his education at the gymnasium at Troppau, a course made possible through the generosity of a younger sister, who voluntarily contributed a part of her dowry for this purpose. In after years he repaid her advance many times over, himself providing the education of her three sons, his nephews.

At the end of his study at the gymnasium Mendel became a candidate for admission to the Koenigkloster in Bruenn. His application was successful and he was selected with the expectation that he would take part in the educational work of the institution. His baptismal name was Johann but on admission to the cloister he became known as Gregor. He was ordained as priest in 1847 and was sent at the expense of the cloister to the University of Vienna 1851-53 where his study was chiefly devoted to sciences. After his election as abbott 1868 he hoped for better opportunity for study and experiment, but his opportunity never came. The government in 1872 imposed a tax on the properties of religious houses. Mendel believed this tax unjust and set himself in opposition to it. This involved him in litigation and prolonged trouble, so that the last ten years of his life were years of great disappointment. His cheerful, friendly, disposition was changed and he became suspicious and embittered. He died January 6th, 1884, as a result of chronic nephritis. It is of interest to record that the government without debate removed the special tax on the properties of religious institutions a few years after his death.

The estimates of Mendel as a scientist have not been exclusively laudatory. By some few Mendel has been regarded as a scientific accident, a man whose results have become of great significance but not of himself to be recognized as a truly great experimenter. It is hardly probable that this estimate of Mendel will be borne out by future developments for his discovery was by no means a chance one. Plant hybridization was an old story long before Mendel's experiments. If one searches through the writings of pre-Mendelian students he is conscious of a feeling of disappointment. Their investigations had been serious and a vast amount of valuable observations had been recorded, but they missed the clue which would bring order out of a jumble of contradictions. Mendel on the other hand had proceeded in a
Mentally his traits were those of slow but penetrating analysis, of tenacious persistence, amounting almost to obstinacy, and especially of the power of pursuing an abstract idea. That his experiments were carefully thought out and planned may be seen from the following quotation from his chief work, the paper on peas.

"Those who survey the work done in this department will arrive at the conviction that among all the numerous experiments made, not one has been carried out to such an extent and in such a way as to make it possible to determine the number of different forms under which the offspring of hybrids appear, or to arrange these forms with certainty according to their separate generations, or definitely to ascertain their statistical relations."

"It requires indeed some courage to undertake a labour of such far-reaching extent; 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 over-estimated in connection with the history of the evolution of organic forms."

"The value and utility of any experiment are determined by the fitness of the material to the purpose for which it is used, and thus in the case before us it cannot be immaterial what plants are subjected to experiment and in what manner such experiments are conducted.

"The selection of the plant group which shall serve for experiments of this kind must be made with all possible care if it be desired to avoid from the outset every risk of questionable results."

"The experimental plants must necessarily—
1. Possess constant differentiating characters.
2. The hybrids of such plants must, during the flowering period, be protected from the influence of all foreign pollen, or be easily capable of such protection.

The hybrids and their offspring should suffer no marked disturbance in their fertility in the successive generations.

"Accidental impregnation by foreign pollen, if it occurred during the experiments and were not recognized, would lead to entirely erroneous conclusions. Reduced fertility or entire sterility of certain forms, such as occur in the offspring of many hybrids, would render the experiments very difficult or entirely frustrate them. In order to discover the relations in which the hybrid forms stands towards each other and also towards their progenitors it appears to be necessary that all members of the series developed in each successive generation should be without exception, subjected to observation."
"At the very outset special attention was devoted to the Leguminosae on account of their peculiar floral structure. Experiments which were made with several members of this family led to the result that the genus Pisum was found to possess the necessary qualifications.

"Some thoroughly distinct forms of this genus possess characters which are constant, and easily and certainly recognizable, and when their hybrids are mutually crossed they yield perfectly fertile progeny. Furthermore, a disturbance through foreign pollen cannot easily occur, since the fertilizing organs are closely packed inside the keel and the anther bursts within the bud, so that the stigma becomes covered with pollen even before the flower opens. This circumstance is of especial importance. As additional advantages worth mentioning, there may be cited the easy culture of these plants in the open ground and in pots, and also their relatively short period of growth. Artificial fertilization is certainly a somewhat elaborate process, but nearly always succeeds. For this purpose the bud is opened before it is perfectly developed, the keel is removed, and each stamen carefully extracted by means of forceps, after which the stigma can at once be dusted over the foreign pollen."

In short we may say that Mendel's experiments were conducted under conditions which allowed exact knowledge of the experiments and of the material with which he worked. Since the peas were self-pollinating, he had really a pedigreed stock and by producing artificial fertilization he allowed only these seeds to come to maturity over which he had definite control. Thus his method was rigorously scientific, his experiments planned for a clearly recognized purpose, and continued persistently over a period of years. Surely such procedures as these do not constitute scientific accidents, but belong only to experimentation of the highest order.

"During his period of scientific work Mendel, as we now know, was engaged on a great variety of cognate researches. In his letters to Nageli there are allusions to some of these subjects, but unhappily few statements of results. His largest undertaking besides the work on Pisum was an investigation of the heredity of bees. He had 500 hives under observation. He collected queens of all attainable races, European, Egyptian, and American, and effected numerous crosses between these races, though it is known that he had many failures. Attempts were made to induce the queens to mate in his room, which he netted in with gauze for the purpose, but it was too small or too dark, and these
efforts were unsuccessful. We would give much to know what results he obtained. In view of their genetic peculiarities a knowledge of heredity in bees would manifestly be of great value. The notes which he is known to have made on these experiments cannot be found, and it is supposed by some that in the depression which he suffered before his death they were destroyed.” “A rich harvest of discovery awaits those who may successfully repeat the work.” (Mendel’s Principles of Heredity: Biographical Notice, pps. 329-30.)