THE LIFE OF GREGOR JOHANN MENDEL —TRAGIC OR NOT?

By *ÅKE GUSTAFSSON*

DEPARTMENT OF FOREST GENETICS, STOCKHOLM AND INSTITUTE OF GENETICS, UNIVERSITY OF LUND, SWEDEN

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1.

IT is my privilege to discuss here some conflicting evidence concerning the life of Gregor Johann Mendel, the founder of modern genetic thought, and his lectures at Brünn in February and March 1865, just over a century ago. The rough outlines of his life, as well as his work, are well-known to every biologist of to-day. We are, however, still puzzled by the incapacity of his contemporaries to apprehend the precise analysis he made of the traits studied: their independence of one another, their free combination, their particulate constancy through generations.

Moreover, we often consider his life as "tragic". He died on January 6, 1884, at the age of 61 years, embittered we say. His funeral procession three days afterwards at 9 o'clock in the morning was followed, Hugo Iltis, his biographer, declares, by a huge concourse of mourners: state officials whom he had opposed in the latter so-called embittered part of his life, city representatives, professors and teachers, catholic clergymen, but (since he was broad-minded in his religious beliefs) also by the Protestant pastor and the Jewish rabbi, delegates of the numerous societies which Mendel supported by work and money, members of the fire brigade of Heinzendorf (his birth place), and scores of poor people whom he had helped in their poverty. ILTIS (1932, p. 280) concludes that even though hundreds of participants in the procession mourned the death of a charitable friend, and hundreds came as in duty bound

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or from curiosity to witness the interment of a dignitary, not a single one of those present on the occasion knew that a great scientific investigator, a man of imperishable reputation had passed away.

Seen in the sharp light of our own time all this clearly looks tragic. The apparent tragedy is deepened even more by Iltis himself and by numerous geneticists of this century who retell Mendel's life in an often sentimental way, complaining about the oblivion of his discoveries, and attacking his contemporaries Nägeli, Kerner, Focke for not understanding him. We talk about the enormous loss to science because Darwin had no cognizance of his publications. But we now know that Darwin himself is to blame for his failure to trace Mendel's writings.

In a publication on Linné, Darwin, Mendel, the Swedish botanist and geneticist HERIBERT NILSSON (1930), in splendid fancy, twisted this so-called tragic event into a more natural, but still fateful incident. He quoted from the Icelandic poem Havamal:

> Small are the grains of sand
> Small are the drops of water
> Small are the thoughts of men.
> Not all men were made equally wise;
> Each century only bears a man.

Linné belonged, Heribert Nilsson tells us, to the eighteenth century, Darwin to the nineteenth. So Mendel and his discoveries simply had to be removed from the nineteenth to the twentieth century. Mendel himself assured a friend of his, the distinguished scholar Gustav von Niessl, about the value of his experiments: "My time will come." There is no tragedy in this. It is the obvious and modest self-assuredness of a great man ranking high even according to the Havamal standard.

2.

Let us listen to the suspenseful description (Iltis, p. 176) of the remarkable meeting, February 8, 1865, when Mendel presented the first part of his discoveries:

"On a clear, cold evening in February 1865 several men are walking along the Johannesgasse in Brünn towards the Modern School, a big building, still new. One of these men, stocky and rather corpulent, friendly of countenance, with a high forehead and piercing blue eyes, wearing a tall hat, a long black coat, and trousers tucked into top-boots, is carrying a manuscript under his arm. This is Pater Gregor

Mendel, a professor of the Modern School, and with his friends he is going to a meeting of the Brünn Society for the Study of Natural Science, where he is to read a paper on *Experiments in Plant-Hybridisation.* In the room where the meeting is to be held about forty persons get together. The lecturer is welcomed by the secretary of the society, G. von Niessl, the astronomer and botanist. Other members of the audience are Professor Makowsky, the botanist and geologist, Nave, the authority on cryptogams, Dr. Kalmus, another expert in the same branch of research, Theimer the botanist, and Czermak the chemist; all of them are able scientists, helping to give weight to the small (!) audience. For about an hour Mendel reads from his manuscript (!) an account of the results of the experiments in hybridisation which have occupied him during the last eight years" (in fact nine years).

"His hearers, who were personally attached to the lecturer as well as respecting him for his original observations in various fields of natural science, listened with considerable astonishment (!) to his account of the seemingly invariable ratios in accordance with which certain characters had appeared among the hybrids. At the close of this evening's address, Mendel said that at the next monthly meeting he would tell them the explanation he had formulated to account for the peculiar and regular way in which the segregation of characters took place among his hybrids.

There was a goodly audience once more at the next month's meeting. It must be admitted, however, that the attention of most of the hearers was inclined to wander (!) when the lecturer was engaged in rather difficult mathematical deductions; and probably not a soul among them really understood what Mendel was driving at. His main thought (implied) a new and uncongenial notion.

Many of Mendel's auditors must have been repelled (!) by the strange linking of botany with mathematics, which may have reminded some of the less (!) expert among them of the mystical numbers of the Pythagoreans, or of the natural philosophy of the schools of Schelling and Oken which had been fashionable some half century before to the detriment both of science and of philosophy . . ."

So far Iltis. It is not difficult to detect his dramatisation of the events. But this is not the end. What took place has become even more dramatised.

At a meeting (January 11) preceding the one when Mendel read his paper, Professor Alexander Makowsky, one of the leading members of the society, referred with the utmost enthusiasm to Darwin's theory

of the origin of species. "Since the consciousness of the epoch was entirely filled by the flood of ideas contained in the Darwinian theory and its consequences, people would not trouble themselves to make place in their minds for the profound and peculiar ideas of Mendel, even though these were concerned with a kindred field" (Iltis, p. 178).

According to information said to be given by the named Makowsky, one of Mendel's associates, to Iltis personally, Mendel's presentation would even have been received by scornful laughter (RICHTER, 1941, p. 132; WEILING, 1966 a, p. 274).

In his letter to Nägeli, April 18, 1867, Mendel himself formulated his audience's reaction in the following way: "I encountered, and nothing else could (of course) be expected, very divided opinions; repetition of the experiments was, however, as far as I know, undertaken by nobody." Mendel says nothing of scornful smiles or laughter.

The Brünn "News" (Neuigkeiten) of the time contained, according to a report by SAJNER (1965), some details about the meetings of February 8 and March 8, and the lectures given by Mendel. Here it was clearly indicated that Mendel's presentation was indeed accompanied by demonstrations, not a long tedious reading from a manuscript. "Well worth considering was the compilation of ratios (numbers) with regard to the distinguishing traits of the hybrids and their relation to the parent types" (quoted from Sajner, *l. c.*, p. 201). Also the first session, on February 8, was indeed well attended.

Mendel was a trained teacher, logical, earnest, at the same time also friendly and humorous, "an excellent teacher" (according to RICHTER, 1943, p. 65). We can expect him to have delivered a fine presentation of his data, without dramatisation, and we can expect the audience to have listened carefully and respectfully. The audience certainly did not understand the fine interpretations and the ingenuity of the talk. This is true. But the same might surely happen in a similar situation again and again, here and there. If there were some open laughter, it would not have been from scorn of Mendel or his ideas but caused rather by somebody in the audience, perhaps Mendel himself, joking harmlessly.

In fact, we may safely assume that his colleagues and friends, of high intellectual standard, even if they did not understand the epoch-making conclusions, would find his experiments truly interesting. His lecture was indeed published in the Brünn Proceedings and Mendel wrote about this to Nägeli (April 18, 1867): "When, last year, I was *requested* (German: aufgefordert) to publish my lecture in the Proceedings of the Society, I agreed to do so, after having re-examined my records for

the various years of experimentation and not having been able to find a source of error. The paper which was submitted to you is the unchanged reprint of the draft of the lecture mentioned; thus the brevity of the presentation, as it simply has to be in the society lectures" (slightly changed from the translation in STERN and SHERWOOD, 1966, p. 61). Mendel was asked (or requested) to publish his lecture, this could not imply scorn or ridicule.

3.

Mendel, like many European botanists at the time, was greatly intrigued by the complex genus *Hieracium,* the hawkweeds, characterized by a fantastic multitude of forms, specially in Middle Europe. (See his paper on *Hieracium* (1869/1870), Stern and Sherwood, p. 49). That these hawkweeds are parthenogenetic in reproduction, nobody would of course know or guess at the time, not even the ingenious Mendel. Nägeli, an expert on the genus, was also intrigued by the complexity. It is quite understandable that he immediately grasped upon the project outlined by Mendel in his first letter (December 31, 1866). Indeed he proposed certain "species" for hybridisation mentioned by Mendel. In a letter of April 1869, Nägeli stressed the *great importance* of Mendel's hawkweed hybrids. On May 30, 1871 Nägeli sent his photograph to Mendel. After Mendel's last letter to Nägeli (November 18, 1873) the latter, one of the foremost German professors at the time, and professor at the famous University of Munich, too, wrote at least two letters (in 1874 and 1875) without getting any reply. We do not know the reason for Mendel's impoliteness. Was it tiredness, travelling, illness (his eyes were in terrible shape after the strenuous hawkweed emasculations), or the onset of state taxation worries? In his letters Nägeli was keenly interested to learn whether the polymorphous *Hieracium* hybrids "in addition to an identical mother parent also had an identical father".

It is possible that Nägeli, as said so often, considered Mendel a sort of amateur or dilettante but he nevertheless called him "Most esteemed *Colleague*" (German: Verehrtester Herr *Kollege*), "Honorable Sir and *Friend*" (German: Hochgeehrter Herr und *Freund*). That he took a considerable interest in Mendel's *Hieracium* work cannot be doubted. The results on *Hieracium* and on *Pisum* were in conflict. The reason for the conflict was not understood until 30 years later, when Danish and Swedish scientists found out about the parthenogenetic behavior of *Hieracium.*

ZIRKLE wrote of Nägeli in 1964: "Mendel's letters to him have been published, and this has given him a form of immortality he would not otherwise have had. He will be remembered as the great biologist who could not understand Mendelism even when he had the advantages of Mendel's own personal assistance." This is a malicious statement and not truthful. Nägeli cannot be blamed for failing interest in Mendel and his work; nor can he be blamed for his failure to understand the extraordinary *Pisum* analysis. "I believe also to remember that he told me of Mendel, but certainly only of the *Hieracium* investigations, in which alone he was permanently interested" (CORRENS, in Stern and Sherwood, p. 137).

Mendel also sent a copy of his article to Kerner von Marilaun. It was known long ago that at least one letter from Mendel to Kerner was in existence but had been lost. It now is deposited in the University library of Uppsala. According to a guess by my friend and colleague Diter von Wettstein (professor of genetics in Copenhagen), a great-grandson of Kerner, the letter was probably inherited by Richard von Wettstein, the son-in-law of Kerner, purchased by the plant exchanger Ignaz Dörfler in Vienna and sold by him to Uppsala together with books and herbaria (v. STUBBE, 1965, p. 133, also 1963, for this lost and refound letter). Kerner answered on March 5, 1867 (according to an annotation on Mendel's original letter).

Whether there was any further correspondence between Mendel and Kerner is not (yet) known. But Kerner, a famous professor of Innsbruck and Vienna, must also in some respects have held a high opinion of Mendel's ability. Kerner, too, was intrigued by the hawkweeds and in a letter to Gustav von Niessl he wrote about some *Hieracium* specimens (December 6, 1872; Iltis, p. 205): "Perhaps next summer, Herr Mendel will be able to obtain a greater number of specimens of this plant, and if so I hope he will not forget me . . ."

4.

The first outside quotation of Mendel's *Pisum* article was made by the professor of Botany at Giessen, H. HOFFMANN. He had for a series of years studied the variation within different species and genera, especially in *Phaseolus* and in *Pisum*. In his book (1869), "Untersuchungen zur Bestimmung des Werthes von Species und Varietät. Ein Beitrag zur Kritik der Darwinschen Hypothese" (Studies to determine the value of species and variety. A contribution to the criticism

of Darwin's hypothesis), Hoffmann quoted Mendel's article five times, three times with regard to species hybrids in *Aquilegia, Geum* and *Lavatera*, which Mendel himself had quoted from the work of C. F. Gärtner, who in 1849 published a book on hybridisation experiments. Hoffmann refers to the successful species crossings that Mendel achieved in *Phaseolus* (p. 52). With regard to *Pisum* he speaks about Mendel's six years of observations, quotes the Brünn Proceedings and discusses his findings on floral biology and crossing technique. He also briefly stated: "Hybrids are inclined to revert to the original species in the following generations" (*l.c.*, p. 136).

This is the most interesting item of the whole 19th century story. Darwin could have entered the scene here. In his book on "The Effects of Cross- and Self-fertilization in the Vegetable Kingdom" (1876) Darwin referred to Hoffmann's treatise with regard to hybridisation in *Phaseolus* (PUNNETT, 1925), just the place where Hoffmann's own and Mendel's studies are mentioned closely one after another. Darwin must have seen Mendel's name. He, the careful reader, the patient collector of data in experimentation and from the literature, refrained from looking up Mendel's original paper in the Brünn Proceedings. Darwin also owned the famous compilation by W. O. Focke "Die Pflanzenmischlinge" (1881), where Mendel was quoted 18 times (*v.* below). He lent this book to J. G. Romanes with the remark that he would read the historical part as a preparation for his contribution about hybridization in Encyclopedia Britannica (9th Edition) (*v.* OLBY, 1966, p. 195). In fact, the Proceedings of the Brünn Society, year 1866, containing Mendel's *Pisum* article, is still in the possession of the Royal Society of London and the Linnaean Society. In volume 8 (1879) of the Royal Society Catalogue of Scientific Papers, the *Pisum* article, the *Hieracium* paper and Mendel's description of the Brünn Tornado in 1870 are cited.

What would have happened if Darwin had cared to look up Mendel's *Pisum* article?

We know that Mendel, on his side of the fence, already at an early date had read Darwin's books in translation (Iltis, p. 103), (Origin of Species, Animals and Plants under Domestication, On the Various Contrivances by which Orchids are Fertilised by Insects, The Effects of Cross- and Self-fertilization in the Vegetable Kingdom), and made notes, comments and references to pages specially interesting to him (RICHTER, 1943). According to Niessl (RICHTER, 1941, p. 168), Mendel "had hoped to fill a gap in Darwin's system with his experiments". "Always when Darwin's name came up, he said that the theory was

inadequate, that something was still lacking" (Iltis, p. 103). Mendel also commented on Lamarck's views on the direct environmental influence on inheritance (later on accepted by Darwin) that "this much already seems clear to me, that nature does not modify species in any such way, so some other force must be at work". (And Mendel here, no doubt, meant a "natural" force, not a divine one.)

Mendel understood Darwin's revolutionary theory, referred his own results to it and took the evolution (transformation) of species for granted (KRIZENECKY, 1965, p. 27). It is, I think, a dangerous counter-conclusion when BATESON (1909) declares: "I rest easy in the certainty that had Mendel's paper come into his (Darwin's) hands, those passages would have been immediately revised" (p. 289) and "Had Mendel's work come into the hands of Darwin, it is not too much to say that the history of development of evolutionary philosophy would have been very different from that which we have witnessed" (p. 316). These, as well as a couple of conclusions in FISHER's artful paper "Has Mendel's work been rediscovered?" (1936), are after-constructions. Darwin was a man of high collecting ability, besides being a genius, and time was ripe for his thesis of natural selection and origin of species. I sincerely doubt, however, whether he, more than the no less intelligent, but less ingenious scientists Nägeli, Kerner von Marilaun and Focke, would have grasped Mendel's deductions, so brilliantly simple and outstanding in the history of science.

The second scientist to quote Mendel repeatedly in a scientific treatise was the botanist, A. BLOMBERG, from Uppsala in Sweden. This happened in a doctor's thesis of 1872 "On hybrid formation in phanerogamous species" (in Swedish; the reference was published by ROBERT LARSSON (1915), later on Editor for "Hereditas" during more than 35 years). For its time the thesis is a good and honest compilation. Quite emphatically Blomberg stated (p. 37) that "Mendel supposes that two kinds of characters are transmitted to the hybrid when it is formed: 'dominant' are those which in the first generation determine the appearance of the hybrid, and 'recessive' those which in the beginning are latent". The phenomena of dominance and recessiveness were thus correctly emphasized. The fact that Mendel was quoted in Uppsala is perhaps not so strange. Mendel himself mentioned in his second letter to Nägeli some *Hieracium* groups characterized by the Swedish taxonomist and fungus specialist Elias Fries, famous Uppsala professor. In his *Hieracium* paper, published in the Brünn Proceedings 1869 (1870), Mendel stated that Fries "will have nothing to do with hybrids in Hieracia"

(Stern and Sherwood, p. 51). The distinguished Uppsala botanists of the time must have noticed also this article, interesting to many of them.

The young Russian botanist I. Schmahlhausen was, then, in his doctor's thesis of 1874, even more precise in his evaluation of Mendel's work. This contribution has been overlooked in the international literature, although it was referred to by Philiptchenko 1925; Vavilov 1935 and, quite extensively, by Gaissinovitch 1935 (*v.* WEILING, 1966 a, p. 279). Schmahlhausen discussed the segregation ratios, the phenomena of dominance and recessivity (as did Blomberg) and stressed the importance of Mendel's mathematical method: "I learnt to know Mendel's 'Experiments on plant hybrids' at a time when my own work was just in printing. However, I consider it necessary to direct attention to this article, because the method of the author and the strict way, in which he presents the results of his work (German: formelmässig), should receive full attention and be developed further. The procedure of the author, carried out with mathematical precision, was to determine the number of different forms after fertilization of the hybrids and the proportions of the individuals of these forms to one another."

This and the subsequent analysis implies, in full sense, a clear description of Mendel's solution of the problems of inheritance. But how many biologists in other countries read Russian texts at the time? And even less did they read Russian dissertations by unknown young scientists.

5.

Mendel was quoted by the German W. O. FOCKE in his big compilation "Die Pflanzenmischlinge" (The Plant Hybrids) (1881), a gold mine for hybridizers. Anyone interested in hybridization should have come across and been able to pick up Mendel's work for detailed reading. (Apparently, Darwin did not.) *Pisum, Phaseolus* and *Hieracium* were quoted genera. In his paper "Has Mendel's work been rediscovered?", previously mentioned, Ronald A. Fisher refers to Focke's book with a definite lack of enthusiasm. "The fatigued tone of the opening remark would scarcely arouse the curiosity of any reader, and in all he has to say Focke's vagueness and caution have eliminated every point of scientific interest . . . It is not an accident that Focke was vague. In this case, as perhaps in others, he had not troubled to understand the work he was summarizing" (Stern and Sherwood, p. 170).

Also ROBERTS, in his "Plant hybridization before Mendel" (1929), took a clearly negative attitude towards Focke's descriptions of Mendel's

work. Indeed he accused him of having judged the scientific value of the works to which he referred by the size and length of the publications. Everybody, who has had any contact with Focke as scientist and person, must resent this type of argument. Also Fisher's statement about Focke ("not troubled to understand") is unfair. Focke was a medical man practising in Bremen. He became 88 years of age, clear-minded to the end. He was busy all his life with his dear plants, especially of the complex genera, also *Hieracium,* but above all the difficult genus *Rubus* which includes the blackberries and raspberries. Also the European (as well as the American) blackberries are apomictic with a peculiar mode of parthenogenesis, associated with the fertilization of endosperm (pseudogamy). The taxonomical handling of the genus is exceedingly difficult. Focke made not only a good but an outstanding contribution to the treatment of the genus. His honesty, his intelligence and diligence, his desire to obtain more and more precise taxonomical information is evident to everybody who has worked with this obscure genus. He was a learned man in many fields and personally a gentleman. Fisher's remarks are superficial and do not penetrate to the core of the problem: Why was Mendel's *Pisum* work not discussed more openly (it was, however, discussed, as we now know), why not understood (it was understood, for instance by Schmahlhausen)? We cannot blame Nägeli, nor Kerner, nor Focke, nor any of the Brünn contemporaries for their failure in understanding the brilliant *Pisum* analysis. *Pisum* did not interest them (more than as part of their food); they were all occupied by complex genera, natural hybridisation and the formation of species. The abbot stands there, perhaps not as the man of the highest genius in natural history, perhaps no more ingenious than Darwin, Lamarck or Linné, to mention three outstanding naturalists, but he stands there, among them and among his contemporaries, as the sharpest-minded, clearest, most clairvoyant of them all.

WEILING (1966 a) has proposed as a reason why Focke did not go into more detail about Mendel's work or penetrate it more fully that he got hold of Mendel's treatise just before the book of "Pflanzenmischlinge" was finished. In fact, Focke told this story to Iltis (Iltis, p. 285) and, incidentally, added a significant remark: "Fluttering the pages of my book I note that on p. 492 I have included Mendel among the most trustworthy observers."

It is necessary for me here to emphasize the incorrect and unjust arguments by Roberts and Fisher, the more so since Focke's name will have to be mentioned in all analyses of the rediscovery of Mendel. The

American, L. H. Bailey, also a specialist on the genus *Rubus,* had quoted Mendel's *Pisum* work in 1892, but after Focke, not from the Brünn Proceedings. Hugo de Vries, the first of the three rediscoverers, the first by a month, had either got his information about Mendel from Focke, or from Focke via Bailey, or possibly by reading the Brünn article in a reprint given to him by the Dutch scientist M. W. Beijerinck. The German rediscoverer Carl Correns got the quotation from Focke. The third one, E. von Tschermak, put aside as "rediscoverer" by Stern (Stern and Sherwood, p. X), was a young Viennese botanist, who had also found Focke's quotation of Mendel's article and looked it up. (According to Tschermak's original paper the proposition of "dominance" was a finding of "utmost importance".)

The secretary of the Brünn society GUSTAV VON NIESSL has twice in print opposed the expression "rediscovery", in the Brünn Proceedings of 1902 (p. 20) and 1905 (p. 8). "The important results of the long-lasting experiments carried out by Mendel ... were at that time in no way unknown or hidden (German: verborgen)." "His work was well-known, but owing to other views prevailing at the time it was put aside." "Mendel did not expect anything better, but I heard him in the garden, among his cultures of Hieracia and Cirsiums, express the prophetic words: 'My time will come'."

6.

Mendel became abbot of the monastery in 1868, two years after the publication of his "Experiments". Would he have been assigned such a high position, which made him an equal or perhaps even a superior to any first-rank old-time German (or Austrian) professor, if he was really tragic and misunderstood, or even as EICHLING expressed it (in J. of Heredity, 1942, p. 244) a "charming putterer"? Indeed, Mendel was excellent as teacher, high-esteemed as botanist (including his *Pisum* work) and a highly beloved and efficient citizen of his city. The "Tagesbote aus Mähren and Schlesien" announced the election with the following notice (Iltis, p. 239): "The population greets the election with undivided joy. We are informed by many of the citizens of Altbrünn that a proposal is afoot to deliver a congratulatory address to the prelate. This time at any rate, there is justification for the Latin adage: 'Vox populi, vox dei'." Indeed, a charming "putterer"!

Let us start to rediscover Mendel again! Ronald Fisher implied that he had done it. But he, like most others, missed the very essence of

Fig. 1. Members of the Augustinian Monastery in Old Brno (Brünn) in the years 1861 to 1864.

Fig. 2. GREGOR MENDEL, with a *Fuchsia*-variety. Detail of Fig. 1.

Mendel's article as he and others also missed the enormous *Hieracium* interest of the learned Europeans of the time. Fisher did not detect or at least did not discuss the first sentence of Mendel's article: "Künstliche Befruchtungen, welche an Zierpflanzen deshalb vorgenommen wurden, um neue Farbenvarietäten zu erzielen, waren die Veranlassung zu den Versuchen, die hier besprochen werden sollen." ("Artificial fertilisations undertaken on ornamental plants in order to produce new color variants initiated the experiments to be discussed here." The translations in BATESON, 1909, p. 317; ILTIS, 1932, p. 106; or STERN and SHERWOOD, 1966, p. 1, do not fully correspond to the German text.) Since his childhood Mendel had been interested in gardening and flowers. (In addition, he bred mice in his rooms, grey mice as well as white mice, crossing them. Later on in his life, he became fascinated by bees and bee breeding.) In fact, Mendel himself produced a new variety of *Fuchsia*, a variety that was marketed for a time under the name of "Mendel Fuchsia". According to Iltis (p. 210) some of his hybrid flowers were extolled by contemporary gardeners as "a positive acquisition to Austrian horticulture".

In May, 1859 there was an exhibition in Brünn with a display of excellent vegetables grown by him. In his long letter to Nägeli of April 18, 1867, he described how he crossed two genotypes bbccDDgg and BBCCddGG and obtained the recombinant BBccDDGG; with yellow albumen, white seed coat, arched pods and long stems. The recombinant was cultivated for a long time in the garden of the monastery for its large, tasty seeds. Most probably this type is the delicious pea variety mentioned by EICHLING (1942, p. 245). "I asked him how he did it and he replied: 'it is just a little trick, but there is a long story connected with it which would take too long to tell'."

Mendel also performed experiments with fruit trees. His gardener, a man named Maresch, often intemperate, bibulous, told the story that Mendel carried out buddings and graftings, as well as numerous crossings in pears, apples and cherries. It is an important fact that in the very last part of his life—filled with "bitter" fighting against the state authorities—he devoted time to his breeding program. In the fall of 1883, a couple of months before he died, he was awarded the large Vermeil medal for his exhibit of some successful stone-fruit descendants. By this time he had given up his experiments with peas, or beans, or even hawkweeds, but apparently he got on with his bee-hives, his flowers and his fruit trees to the last of his life.

In his ninth letter to Nägeli (September 27, 1870) Mendel made a

most outstanding remark concerning sex inheritance (*v.* also WETTSTEIN, 1965). Based on an apparent 3:1 segregation of male and female individuals in the genus *Melandrium* Mendel suggested that eggcells and pollen possess different hereditary factors for male and female development ("geschlechtliche Anlage verschieden"). Certainly Mendel did not discuss the hereditary basis of sex in animals (or Man), but as evidenced by the phrasing of his letter he was aware of "singular" consequences ("sonderbaren Folgerungen") of the segregation found. An association from sex inheritance in dioecious plants to that in animals (and Man) was presumably obvious to a brilliant mind like that of Mendel, already judging from the corresponding adjectives ("*männliche* Pflanzen, *weibliche* Pflanzen").

Up to his death Mendel also made accurate observations on sunspots and weather conditions, in fact he was known as a meteorologist also abroad (Iltis, p. 227). Two days before he died he was occupied in scientific studies, and dictated the results of his meteorological observations. Mendel was an amateur, in the Latin sense of the word, he loved the world around him (except state taxes on the monastery), flowers, animals, people (except, possibly, his intemperate gardener, who lied to him, but whom he nonetheless endured his whole life). He travelled much, was in Germany several times, went frequently to the Alps, went to Rome to pay his respects to the pope, took part in a huge company travel to Paris and London 1862 (but apparently he did not visit Darwin who, incidentally, was not at Down at the time; DE BEER, 1964; cf. also RICHTER, 1943, p. 173). His monastery possessed large estates, dairy farms, a ranger lodge, vineyards, and he was forced to inspect them, which he also did with a good deal of pleasure. When he wanted rest he went to the forest ranger lodge for a couple of days. He was member of several societies, also on their boards, chairman or vice chairman, curator of the Moravian Institute for Deaf Mutes, member of the Moravian Mortgage Bank, was its vice chairman and became its chairman in 1881, a post filled until shortly before his death.

The monastery was known for its good food. Mendel complained about his corpulence which prevented him from mountain climbing and botanizing. He also smoked too much, at the end of his life as much as up to 20 cigars a day. Guests were welcomed. Is it strange that he did not find time for his Pisums, Cirsiums and Hieracia or got tired of them? I think that most administrators in the scientific world would envy his capacity. And he also *was* a priest, a prelate, an abbot. In his fight with the state authorities he finally won—but then he was dead.

7.

The last few years of his life he was indeed a sick man. He died of a kidney inflammation, with hypertrophy of the heart as complication. Possibly he also had a chronic nicotine poisoning. Since Mendel was so stubborn in his fight against the state authorities, there also arose some talk about mental disorders. In 1882 and 1883 he foresaw his death, without sentimentality, contemplating it stoically as a natural necessity. He wrote several letters to his nephews, whom he loved, in good temper, humorously, up to December 26, 1883, a few days before his death. In a letter, April 1883, he wanted one grafting shoot from the Günsbirne (a pear tree), two from the Quaglich (another pear tree) and three from a good tree in the "reservation garden". "I shall be glad to make returns in kind." "Much love to Ferdinand, who has my best wishes for the dissection and all the rest of it in which his Christmastide will be fully occupied this year ... Hoping that you will very soon turn up at your old family prison here" (December 26, 1883).

We have the eye-witness C. W. Eichling who "talked with Mendel". At the age of 22 he came to Brünn as a tradesman. At the age of 86 he described his visit to the monastery. We cannot of course rely too much on his description but nonetheless it is evident that Mendel showed no signs of bitterness at the time of Eichling's visit in 1878. "My first impression was a genuine and pleasant surprise. My customer's account had built up in my mind a picture of an old, wrinkled, spooky monk. Coming toward me was a fine looking, spectacled priest, smiling and extending a welcoming hand. His countenance expressed both determination and kindliness." "He became enthusiastic when he spoke of his own student years in Vienna and we even recalled some of our favorite songs such as 'Gaudeamus igitur'—'Vom Hoh'n Olymp'—'Edite bibite collegiales', etc." "I knew from his hearty handshake and his blessing that I had made a friend."

Mendel's life was not specially tragic. He was esteemed by colleagues in the monastery and in the city. He obtained the highest reputation during his life time that any citizen of the relatively small community could obtain. The emperor made him a commander of the order of Franz Joseph "in recognition of your meritorious and patriotic activities" (this was probably a fine award at the time). Mendel was kind and friendly, helpful to poor people, helpful to his fellow brethren. He worked hard but also travelled much and saw a considerable part of Europe. He made important discoveries recognized by his colleagues

and by famous professors (for instance Nägeli). That he was destined to become one of the very great men in this earth's history, "a man of imperishable reputation", he and nobody else could fully conceive. On the other hand, that he was really considered a great man of his time and his city there was no doubt. Brünn "Tagesbote" concluded a notice of his death with the words: "His death deprives the poor of a benefactor, and mankind at large of a man of the noblest character, one who was a warm friend, a promoter of the natural sciences, and an exemplary priest." And the Proceedings of the Horticultural Society contained the following remarkable statement in 1884 (No. 1): "His experiments with plant hybrids have in fact opened a new epoch, and what he has done will never be forgotten." This is just the opposite conclusion to the one lauched by Iltis (p. 280) and mentioned in the beginning of the lecture.

8.

There remains one sincere and mysterious thing in this great man's life and publications. He, the absolutely trustworthy and careful worker, performed and published experiments which, statistically seen, are too good to be true. This was made obvious by Fisher in 1936. The agreement with expectation is so great as 99.993 per cent. Moreover, Fisher says, there can be no doubt that the data from the later years of the experimentation have been strongly biased in the direction of agreement. "Although no explanation can be expected to be satisfactory, it remains a possibility among others that Mendel was deceived by some assistant who knew well what was expected." (Also FISHER, 1965, p. 54.) The thought goes then to some of his monastery helpers, perhaps to his intemperate gardener, not very trustworthy, or possibly to his man-servant, following Mendel like a shadow, always trying to comfort him and to simplify matters. But Josef, the man-servant, was said to be stupid; only with great reluctance did Mendel trust him to make observations (Iltis, p. 246). Even less so, of course, the gardener Maresch.

Sewall Wright has re-examined Fisher's analysis. He says (Stern and Sherwood, p. 173) that the excessive goodness of fit of Mendel's ratios is certainly one of the most disconcerting items that a historian of genetics has to deal with. Wright concludes that "in tallying those small experiments, Mendel must have been conscious of how the rows were running, especially where the expected ratio was 1:1:1:1 in the test of gametic ratios . . . and I am afraid that it must be concluded that he

made occasional subconscious errors in favour of expectation, especially in this case. Taking everything into account, I am confident, however, that there was no deliberate effort of falsification". This, apparently, must mean that also the intemperate gardener, the shadow-like manservant, and possibly other assistants are freed from the accusation. ZIRKLE (1964) raised the question: "Could the good Father Mendel have fudged his results just a little? Could he have omitted a few unusual ratios? It could be, but here we shall have to introduce an uncertainty factor" (p. 66). Neither Fisher, nor Wright want to include Mendel himself in deliberate falsification. Zirkle approaches such an accusation. But there is no indication from other sources that Mendel falsified, corrected or omitted unpleasant data. His life's great accident, the conflicting results in *Pisum* and in *Hieracium*, was in no way ignored, belittled or hidden by Mendel himself. He gave the data as he got them, in spite of the conflict. Also in his *Pisum* work deviating values were mentioned and re-analysed (Fisher, in Stern and Sherwood, p. 154).

Let us turn the evidence the other way around. If Mendel *was* correct, his data *not* falsified, what will then happen to Fisher's method of analysis? Which biological assumptions have to be made in order to consider Mendel's data correct and Fisher's analysis incorrect? Is there any truth in the (Swedish) joke that statistics is nothing but lie, lie and again lie? (Mark Twain, in his Autobiography, formulated the expression "attributed to Disraeli" that there are three kinds of lies: lies, damned lies, and statistics.) Fisher certainly referred to a pea geneticist in his study (my late friend Johan Rasmusson, whose name is misspelt by Fisher, as well as by Stern and Sherwood and J. H. Bennett), but Rasmusson participated more or less in passing. A pea geneticist would be needed for the re-analysis, with full knowledge of materials, methods, stocks, and occurrence of complete and incomplete dominance (or recessiveness) of the genes involved, and with his mathematics alert and at high level.

In fact, the few segregation data saved and listed on the famous note book page, reproduced by DARLINGTON and MATHER (1949, 1961), OLBY (1966) and LAMPRECHT (1966) (after Iconographia Mendeliana, Brno, 1965), are analysed in a recent booklet by NILSSON (1967, pp. 126—128). Here the paper by Lamprecht (*l.c.*) is fully considered, dealing with Mendel's analysis of testa colour in *Phaseolus vulgaris*. The segregation given for the two genes *P* and *V*, denoted so by Lamprecht, is 343:92:166=601, fitting a ratio of 9:3:4. This gives a χ^2 of 5.522, which (with two degrees of freedom) corresponds to a P-value less than

0.10 but greater than 0.05, a rather "normal" goodness of fit, if Mendel's data were "sophisticated systematically" (Fisher). (Mendel himself made no reference to this type of segregation.)

The discussion of the two pea geneticists (Lamprecht and Nilsson) indicates that there may still exist data and ratios in Mendel's work which could be further analysed and interpreted.

In due turn it may appear that the explanation for the excessive goodness of fit is rather simple and may lie close at hand. Wright points out (1966 and personal communication) that there are indeed possibilities for explaining the good fit; for instance, there is the likelihood that Mendel could distinguish a segregating group from a non-segregating one even in the absence of recessives and that he used seed coat genes for this reason.

In a recent paper (1966 b) WEILING has arrived at the conclusion that Fisher is incorrect in his suggestion of fraud or falsification. He points out that Fisher (and others) overlooked that the progeny available for F_3 classification could scarcely be equal to the 10 seeds planted or presumably planted in each case. Losses of seeds and seedlings occur regularly. With an assumed average number of 8 plants in these special progenies, *i.e.* 80 per cent survival, a reasonable figure, the probability of agreement with expectation is of the same order as in the experimentations with peas by Correns, Tschermak, Bateson and Killby, and Darbishire. (Weiling's interpretation needs further corroboration.)

Weiling also indicates that too great a goodness of fit will appear if the distribution of genetic segregation data, obviously different for different plant and animal species, is *not* binomial, but rather "semi-random" and that for this reason the calculated χ^2 values will be too small.

There are several possibilities in this respect. For instance, there really exist cases of mutations which for unknown reasons segregate too regularly according to expectation. I myself have found a few such cases. WEILING (1966 b, p. 361) refers to the fact that if few tetrads of pollen grains (with an exact segregation ratio of 2:2) take part in fertilization, the fit in F_2 (or F_3) will be all too good. There is, he concludes, in this respect a contrast between the autogamous and the allogamous, specially the wind-pollinating plant species.

OLBY (1966, p. 183) has another explanation of the excessively good fit. He assumed that Mendel stopped scoring the results when the totals gave a striking confirmation of a simple segregation ratio. He did not *alter* his results. He merely allowed the idea of a simple ratio between

the scores to influence the point at which he *stopped* scoring. But Olby goes a step further. Even Tschermak, in his disputed rediscovery, published segregation ratios that gave too good a fit. So he must also have acted in the same way: scoring until the totals came near the theoretically correct ratio, and then he stopped. If Fisher's idea of a "falsification" would be correct, then also Tschermak has "falsified" his data. This sounds a bit thick to me. Aren't Wright's and Weiling's interpretations more plausible? I hardly think, with all the present knowledge of this peculiar affair, that Mendel himself stopped scoring when the ratio was precise, nor did Tschermak.

It will be interesting to follow the discussions on this point. Does the Fisher method of statistical analysis really tell a lie in this case?

9.

A novice in the monastery, Pater Clemens, after Mendel's death, penned two Latin couplets characterizing him (Iltis, p. 280):

Gentle, free-handed, kindly to one and all.
Both brother and father to us brethren was he.
Flowers he loved, and as a defender of the law
he held out against injustice.
Whereby at length worn out he died from
a wound of the heart.

The diagnosis "kidney inflammation" sounds less poetic than "wound of the heart". Mendel's kidneys refused to work, his heart stopped. This is the life of Gregor Johann Mendel—reasonably long, kind, charming, great. His was a good heart. His is an imperishable fame.

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