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Gregor Mendel as Entomologist – A Historiographical Reminiscence

Gregor Mendel als Entomologe – eine historiographische Reminiszenz

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Summary: Approximately 150 years ago, the Augustinian monk Gregor Mendel first published his articles on the rules of heredity, which became the founding stone of genetics and are today known as Mendelian laws. However, Mendel also intensively worked on numerous other scientific topics such as meteorology and entomology. Even though his interest in bees is often used as an anecdotal reference in accounts on Gregor Mendel, his deep interest in entomology has been explored seldom in detail. Mendel worked on several entomological topics, such as investigating the effect of two herbivorous insects (*Botys margaritalis* and *Bruchus pisi*) which caused havoc in local fields. Furthermore, he also worked on cross-breeding of different bee species. The present article gives a more detailed account on Mendel's works on insects.

Keywords: Entomology, history of science, pea-weevil, bees

Zusammenfassung: Vor etwa 150 Jahren publizierte der Augustinermönch Gregor Mendel seine Arbeiten über die Regeln der Vererbung, welche den Grundstein für die heutige Genetik legten und die heutzutage jedermann als Mendel'sche Regeln bekannt sind. Daneben hat sich Mendel aber auch intensiv mit anderen wissenschaftliche Themengebieten wie Meteorologie und Entomologie befasst. Auch wenn beispielsweise sein Interesse an Bienen oftmals eher am Rande erwähnt wird, so ist doch sein besonderes Interesse an der Entomologie eher selten genauer untersucht worden. So hat Mendel an zwei herbivoren Insektenarten (*Botys margaritalis* und *Bruchus pisi*) gearbeitet, welche in örtlichen Felder großen Schaden verursachten. Zudem beschäftigte er sich ausführlich mit der Kreuzung von verschiedenen Bienenarten. Der vorliegende Artikel gibt eine detailliertere Darstellung der Arbeiten von Mendel an Insekten wieder.

Schlüsselwörter: Entomologie, Wissenschaftsgeschichte, Erbsenkäfer

1. Introduction

Today Gregor Mendel (1822-1884) is practically universally known due to his two scientific articles on quantitative hereditary rules in peas, hawkweed and other plant species (Mendel 1866, 1870). The derived laws on the propagation of discrete traits later formed the basis of the Mendelian laws, which were named after him. First presented at two consecutive lectures held in 1865 in Brno/Brünn and published a year later (Mendel 1866), the printed volumes containing his first article were distributed in early 1867 (Mielewczik et al. 2017), but their contents were not fully recognized by the scientific community (Mielewczik et al. 2017) before they were rediscovered in parallel by Hugo de Vries (1848-1935), Carl Correns (1864-1933), Armin (1870-1952) and Erich von Tschermak-Seysenegg (1871-1962) in 1900 (Simunek et al. 2011, 2017a, b).

However, Mendel's other scientific works have remained relatively forgotten. Beside his works on hereditary traits in plants,

which he performed over several years (FISHER 1936), he also published several meteorological observations, which in part were not less meticulous and detailed than his studies on plants (DUBEC & OREL 1980; WEILING 1993). MENDEL also worked on several entomological topics, which most typically have been highlighted as biographical anecdotes (ILTIS 1924; RICHTER 1943), even though it has been clear for some time that his entomological interest especially in bees was quite prominent (WEILING 1993, 1994). Discussions and many speculations have focussed on MENDEL's original intentions and ambitions, when he started his hereditary experiments in peas, but his early entomological works have been largely ignored in this context (ILTIS 1924; RICHTER 1943), even though they give some additional ideas on MENDEL's scientific focus. The present essay that includes some literal citations (translated by the author) acknowledges MENDEL's entomological efforts.

2. Early works on pests of horticultural plants (1852-1854)

It is noteworthy that GREGOR MENDEL's interest in entomological topics first started already before he began his experiments on peas. While still a student at the university in Vienna he held a small lecture on the caterpillar of *Botys margaritalis*, a pest of the garden radish (*Raphanus sativus*), which had pillaged a local garden in his home town Brno (MENDEL 1853). MENDEL described the damage of the *R. sativus* pods caused by the caterpillars and, encouraged by his academic teacher VINCENZ KOLLAR[1], tried to raise the caterpillars. Further, MENDEL added some information on the morphology of these caterpillars in this article and highlighted that *B. margaritalis* then was common in Germany, Hungary and the Ukraine. Most interestingly, he also explained, why this little insect might have been of interest to him: "*The damage, which they had caused in the present case, is important enough to draw the attention of the economist*" and that it is "*therefore important to study the economy of the animal in more detail*" (MENDEL 1853 p. 117). This economical interest he shared with V. KOLLAR, who often focussed on similar topics (see for example KOLLAR 1850, 1858).

In the following year MENDEL obviously did not continue his studies on *B. margaritalis*. He became more interested in another economically relevant pest, the pea-weevil (*Bruchus pisi*). This beetle was first described in the late phase of the colonization of America (KALM 1754) and was afterwards found in Europe, where it caused several severe losses of pea-harvests in different regions throughout the 19th century.[2] Already in the early 1850s there were several severe outbreaks in Hungary (PABST 1854), Bavaria (ANONYMOUS 1853) and Austria. In 1853 this outbreak also started to affect pea plantations in Moravia. In a letter, which was read by V. KOLLAR in 1854 before the Zoological-botanical Society in Vienna, MENDEL emphasized that in the last two years (1852 and 1853) the pee-weevil had caused severe damage in the local area around Brno and that especially in 1853 the pea-weevil "*had destroyed a large part of the peas on the field, also rendering the harvested fruit inedible for humans*" (MENDEL 1854, p. 27). Due to the fact that larvae overwinter in the pea MENDEL failed to clarify even the gross raw life-cycle of *B. pisi*. He only gave a very general description of the pea-weevil, however again he highlighted his general motivation: "*Indeed it would be desirable to know the economy of this animal in its most detail ...*" (MENDEL 1854, p. 28), closing with the statement that important landowners were already considering "*to stop growing peas in the coming summer*" (MENDEL 1854, p. 28). This economical problem was also underlined in the session of the Society by KOLLAR himself, who emphasized earlier reports that in colonial North America pea culturing was already given up in large areas

due to infestations with *B. pisi* (s. Mendel 1854). As a matter of fact, concerning pea cultures already in 1854 real economic problems existed in Moravia, as it was suggested that Silesian agriculture should avoid importing pea-seeds from affected Austrian areas (Letzner 1854). *B. pisi* infestations remained a serious problem in Moravia for several years (Hofmann 1861).

Probably Mendel, who was not sure how and where pea-weevils survived the winter, continued his work on pea with imported pea-seeds and tried to investigate artificial cross-pollination (Mendel 1866). Fact is that he seriously considered the influence of *B. pisi* on his pea crossing experiments by transferring pollen (Mendel 1866). His fear that these beetles might contaminate his experiments and might cause cross-pollination even hindered him to send pea seeds to Carl Nägeli[3], who asked for them, as he wanted to verify Mendel's experiments. Nägeli considerably influenced Mendel's work in the following years (Correns 1924; Sohn 1996).

From a biological perspective Mendel's entomological articles are not very rich in morphological details. This is especially obvious when comparing his two articles (Mendel 1853, 1854) with those on *B. pisi* published by some of his contemporaries (Letzner 1854; Kollar 1858; Elditt 1860). In fact, even his teacher Kollar seriously criticized some of Mendel's observations (Kollar 1858), among other things that some of the larvae observed inside the pods did not belong to *B. pisi*. Already in this early study Mendel showed a keen interest in new practical ideas. In his article on *B. margaritalis* (Mendel 1854) he suggested that the infestation problem of pods might be solved or at least reduced by later sowing, while most authors then favored older approaches including the use of two-year-old seeds, the heating the seeds before sowing or using special fertilizers (Mendel 1854; Kollar 1858; Kolenati 1860; Haberlandt 1863, 1865, Temple 1872). Mendel's suggestion was rather unusual for his time; it is remarkable, that this suggestion was practically tested in Moravia in a large field experiment concerning *B. pisi* only a few year later (Hofmann 1861). Although Hofmann did not cite Mendel, it is clear from a later detailed study that Kollar collaborated with both Hofmann and Mendel on *B. pisi* (Kollar 1858). In short, Mendel was not the only one in Brno interested in this topic and an anonymous author (Pseudonym: V-g-l) (Anonymous 1854) made similar suggestions, therefore Mendel's work might have been embedded in a larger research discussion.

3. Mendel's work on bees (1871-1877)

After finishing his experiments on hereditary traits in plants, Mendel had less time for scientific studies, because he had become the prelate of the Brno monastery (Iltis 1924). Yet, he continued to work scientifically but again focussed on entomological topics with an emphasis on bees (Alperton & Oral 1979; Matalova & Kabala 1982; Matalova 1988; Weiling 1994). In 1870 he became a member of the Moravian bee society and started experimental works after completion of the monastery bee house (Fig. 1) in late 1871 or early 1872 (Weiling 1994). His main interest was to improve apiculture, to study foreign bee species and to experiment with crossings of bee species (Weiling 1994). Mendel gave several lectures at the meetings of the society and some of them were mentioned or even summarized in the magazine of the Society ("Die Honigbiene in Brünn"; see Fig. 2). Mendel experimented with several foreign bee species, including the Italian, Egyptian and Krainian bee, and even with tropical bees (Weiling 1994). In this context he noticed in 1877 the assets of the Cyprian bee (*Apis mellifera cypria* Pollmann, 1879), which according to him was "*well suited to improve breeding stocks*" and "…*could even be*

Fig. 1: MENDEL's bee-house, erected in 1871 (Source: Department for the History of Science (Mendelianum), Moravian Museum Brno).
Abb. 1: MENDELS Bienenhaus, das 1871 errichtet wurde (Quelle: Abteilung für Geschichte der Genetik (Mendelianum) des Mährischen Landesmuseum Brünn).

Die
Honigbiene von Brünn.

Organ der Bienenfreunde Mährens.

Nr. 9. September 1875. Jahrgang IX.

Inhalt: Mittheilung der Vereinsleitung. — Bericht über die am 29. Juli 1875 abgehaltene Monatsversammlung. — Anweisung zum Methbrauen. V. Hefstbech. — Die Witterung und ihr Einfluß auf die Bienenzucht. V. Jedlička. — Apistische Notizen. V. Temple. — Wasser als Besänftigungsmittel der Bienen. V. Klettenhofer. — Beiträge zur Živansky-Stiftung. — Anzeige.

Mittheilung der Vereinsleitung.

31. Nachdem die Berichte der Herrn Bezirksleiter und korrespondirenden Mitglieder sehr spärlich einlaufen, sieht sich die Vereinsleitung genöthigt, dieselben zu ersuchen, ihre Berichte als schätzenswertes Material für das Vereins-Organ ehemöglichst einzusenden.

Fig. 2: Title page of an issue of the journal "Die Honigbiene von Brünn", in which lectures of MENDEL are summarized.
Abb. 2: Titelseite einer Ausgabe der Zeitschrift „Die Honigbiene von Brünn", in der Vorträge von Mendel zusammengefasst sind.

used to get a so much aspired and hotly desired cultural race"[4] (Anonymous 1877, p. 82). Mendel had received a queen and ca. 50-60 companion bees of this variety from a Bohemian bee-hive in Tábor[5] (Anonymous 1875b).

A fact often overlooked is, that Mendel was also very interested in local meteorological influences. After a cold spring he remarked in one of the Society meetings, that "*after a cool May, there will always be a good honey-year*"[6] (Anonymous 1877, p. 27).

In several instances Mendel tried to improve apicultural procedures. In 1875 he described results on experiments to overwinter bee stocks (Anonymous 1875a). In earlier years, Mendel tried to store his stocks in a specially built dry cellar, yet in spring he always found the hive wet and full of mold (Anonymous 1875a). Mendel then stopped using the cellar for overwintering, but by accident he found, that a "weak" stock that should be stored for a short time in the cellar, but then was forgotten, was not affected by wetness and mold, probably because it was stored in the cellar with a slight inclination from the ground. Encouraged by this Mendel started a winter-experiment, in which he stored both "strong" and "weak" bee-hives in the cellar and found that only the "strong" hives had problems, but not the "weak" ones. Mendel believed that these problems were caused by the higher temperatures in "strong" bee stocks. He thus suggested that hives are best stored outside, but that "weak" hives can be stored in cold rooms. The little report also highlights how much efforts Mendel put in his bee experiments. For example, the monastery had not only build a bee house and a winter cellar, but there was also a special "ventilation appliance" installed.

Practical aspects were especially important to Mendel. In another lecture, Mendel described new packaging ways which allowed sending bee queens unharmed to other destinations (Anonymous 1875c).

Mendel was quite proud of his work with bees, which is reflected in his descriptions of his own bee-hive: "*I am quite pleased with my bee-hive. The annual cohort might have been to be called very good, if the linden flowering had been better; but thus I can count it under those being good. But it is not possible to judge one [local] stand from another. Other local conditions produce other results. For example, for the bees in Alt-Brünn the fruit-bloom today was exquisite. Especially the cherry plantations at the Red Hill provided much honey. During the cherry blossom at my stand there was a scent in the air, like fresh baked bread, so one nearly might have got a head-ache…*"[7] (Anonymous 1875b, p. 130).

This quote also underlines, that Mendel was not only interested on hereditary traits of the phenotype, but also in environmental factors that may influence them. This is also emphasized by his work on a tropical bee species (*Trigona lineata* Lepeletier, 1836, today *Paratrigona lineata*), which he tried to acclimatize to local conditions (Tomaschek 1879, 1880; Alpatov & Orel 1979; Beranek & Orel 1988).

Some of Mendel's experiments on bees also show his deep interest in quantitative investigations. For example, he studied the flight activity of bees and tried to estimate the amount of "honey" that they can bring into the hive (Anonymous 1877). In this study, which he continued for four years (Weiling 1993), he found that every year in June at maximum 69 to 85 bees per hour flew and landed at the hive (Anonymous 1877).

His main interest though was to improve bee lines by crossing of different species (Iltis 1924). Unfortunately, no primary documentation and notes of those experiments have survived (Iltis 1924). Known is that at the height of these studies Mendel supervised up to 50 hives (Beranek & Orel 1988; Weiling 1993). Interesting details on his crossing experiments were found by Beranek & Orel (1988) in an historical Hungarian bee journal (Kühne 1881). Based on a letter from Mendel to the author, Kühne describes, that Mendel invented a "*very ingenious mating-apparatus*",

which allowed "*forcing the mother to mate with the required drone*" (KÜHNE 1881; BERANEK & OREL 1988). Despite extensive efforts MENDEL's interspecies crossings were rather unsuccessful (ILTIS 1924; BERANEK & OREL 1988) and mating experiments often failed (KÜHNE 1881; BERANEK & OREL 1988). Nevertheless, at his time MENDEL was rather renowned for his apicultural interest and skills. Since 1872 he acted as co-director of the Apicultural Society and in this position, he was in contact with several well-known apiarists. He also participated in at least one international conference, while also visiting other apiarists (LAUPRECHT 1966; DITTMAR 1972; WEILING 1993).

One of the most interesting questions, which remains unanswered, is whether MENDEL had already read accounts on the possibility of quantitative rules of hereditary traits and discrete ratios, before he started his works on peas. Recently it was discussed that MENDEL might have had access to NÄGELI's theoretical works on hereditary traits, in which the author mentioned the now famous 3:1 ratio (MIELEWCZIK et al. 2017), before MENDEL published his final manuscript. Furthermore, it was emphasized, that discussions on rules of inheritance might have been started in scientific circles directly connected to MENDEL[8] already in the 1850s (MIELEWCZIK et al. 2017). Yet early accounts of discrete ratios and rules in artificial crossing are quite rare and difficult to find in the literature published before the rediscovery. In regard of insects such data are even rarer. Some authors suggested that MENDEL might have known of works of the famous Silesian apiarist JOHANN DZIERZON (WHITING 1935; ZIRKLE 1951; WEILING 1994), who had found an 1 : 1 ratio (yellow : black) in drones resulting from unfertilized eggs of an Italian/German bastard queen (DZIERZON 1856). However, based on the timeline it is very unlikely that MENDEL was aware of this study when he started his pea-experiments (WEILING 1994), but nevertheless he might have learned from this work during his work on bees (WEILING 1994). The only other note on fixed segregation ratios that has been found in the older entomological literature (see LAUSSMANN et al. 2012) before the rediscovery of the Mendelian laws comes from POULTON (1887), who found a nearly 3 : 1 ratio in the color of warts of the caterpillars of butterfly *Saturnia pavonia* after crossing.

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Endnotes

[1] VINCENZ KOLLAR (1797-1860) was an Austrian entomologist and zoologist, who's main interest was focussed on dipteran and other insect species. KOLLAR worked in Vienna as curator and later director in Vienna's "Naturaliencabinet". KOLLAR was especially interested in species of economical relevance. Already before his collaboration with MENDEL he had established contacts to several natural scientists in Brünn (KOLLAR 1850).

[2] The origin of *Bruchus pisi* has been quite controversial and has never been fully clarified. From early accounts it was suggested, that the pea-weevil was introduced as an alien species that came from America to Europe (KALM 1754). Other authors, however, have suggested that *B. pisi* was a pest already known in ancient times (HABERLANDT 1865).

[3] CARL WILHELM NÄGELI (1817-1891) was a Swiss botanist, with whom MENDEL intensely corresponded on his plants experiments, once he had published his first article on peas. NÄGELI was very interested in MENDEL's work and was even willing to reproduce some of his results in peas; however, he was more interested in other plant species such as hawkweed, which he considered a better model organism for hybridization experiments.

[4] Translation by the author. Original German transcript: „*Der hochw. Hr. Prälat Mendel aus Altbrünn, machte auf die Vorzüge der Cypernbiene aufmerksam und meinte, dieselbe eigne sich vorzüglich zur Zuchtveredelung, ja zur Gewinnung einer so sehr angestrebten und heiß ersehnten Culturrace.*"

[5] Mendel was lucky to receive this bee quite early. The Cyprian bee was introduced first, but unsuccessfully, to Bohemia in 1866 (BUTTEL-REEPEN 1915). In 1872 and 1874 under count RUDOLPH KOLOWRAT further imports occurred and allowed since 1876 a successful distribution to partners in Germany (BUTTEL-REEPEN 1915). Probably MENDEL was one of the first, who had access to the new species.

[6] Translation by the author: Original full German transcript: „*Doch einigen Trost gewahrte nur die Bemerkung des hochw Herrn Prälaten Mendl bei der Monatsversammlung des mährischen Bienenzucht-Vereines am 1. Juni 1876, wo derselbe unter Anderem bemerkte, dass nämlich immer auf einen kühlen Mai ein gutes Honigjahr zu folgen pflegt, was sich auch zu meiner größten Freude wie mit einem Zauberschlage bewahrheitete.*"

[7] Translation by the author. Original German transcript: „*Ich bin mit meinem Stande zufrieden. Der Jahrgang wäre vielleicht sehr gut zu nennen, wenn*

die Lindentracht besser gewesen waere; so aber kann ich ihn unter die guten rechnen. Man kann aber von einem Stade auf den andern nicht urtheilen. Andere Localverhältnisse bewirken auch ein anderes Resultat. So war für die Bienen in Altbrünn die Obstblüthe gerade heuer ganz vorzüglich; besonders spendeten die Kirchplantagen am Rothen Berge viel Honig. Während der Kirschblüthe roch es bei meinem Stande, wie nach frischgebackenem Brode, so daß man fast Kopfschmerzen spürte."

[8] The possibility of hereditary rules was raised by numerous authors during the 19th century. It was especially highlighted in lectures by such authors as Carl Wilhelm Nägeli, Eduard Fenzl and August Regel (Mielewczik et al. 2017). Rules in those discussions focussed more on "rational" descriptions than on quantitative traits (Mielewczik et al. 2017). However, Mendel's teacher Eduard Fenzl already proposed to perform artificial crossing to elucidate the rules of heredity, assuming, that a continuous monitoring of rows might provide important insights (Mielewczik et al. 2017).

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