1	From Gregor Mendel's 1865-lectures to his 1866-masterpiece
2	
3	
4	
5	Peter J. van Dijk, Keygene N.V., Agro Business Park 90, 6708 PW Wageningen, The Netherlands,
6	peter.van-dijk@keygene.com
7	
8	
9	and
10	
11	T.H. Noel Ellis, Department of Biochemistry and Metabolism, John Innes Centre, Norwich Research
12	Park, Norwich, NR4 7UH, United Kingdom,
13	thnoelellis@gmail.com
14	
15	

# From Gragor Mondol's 1965 losturos to his 1966 mastorniaso

## 16 Abstract

17 The two lectures Gregor Mendel gave in the spring of 1865 to the Natural Science Society in Brno can 18 be considered the ultimate origin of genetics. Here we reconstruct these lectures and their settings 19 using digitized historical newspapers, and we compare these to Mendel's 1866-paper "Experiments 20 on plant hybrids". The newspapers explained to their readers that Mendel used the term "Hybriden" 21 in the sense of "Bastarden". Naturalists commonly used the latter term to describe hybrids between 22 species in nature. Mendel's use of "Hybriden" and the avoidance of "Bastarden" in the 1866-paper 23 and early letters to Nägeli regarding Pisum are particular. In English translations, both German words are translated as "hybrids" so that Mendel's differentiated use of words is no longer noticeable. We 24 argue that with the use of "Hybriden" Mendel did not need to take a position on whether 25 26 the Pisum parental forms were species or varieties, as Mendel considered these as extremes of a 27 continuum. That Mendel probably started his pea crossings as a breeder may also have played a role; 28 "Hybriden" was commonly used in horticulture. Mendel's use of "Hybriden" was unusual for the 29 naturalists in the Natural Science Society, and newspaper reports indicate that this led to confusion. 30 According to the Brünner Zeitung, legumes were not suitable for studies on hybridisation because such 31 interspecific hybrids were rare in nature. However, in his 1866-article, Mendel explained that the 32 garden pea was highly suitable for experimental hybridization due to its flower structure. In the 33 Concluding Remarks of the 1866-article, Mendel showed that his findings were relevant for hybrids 34 between wild species by reviewing the work of Gärtner and Kölreuter. We conclude that it is probable 35 that this section was not part of the lectures and was added later to the paper to accommodate points 36 raised in the discussion after the lectures.

38 Introduction

39 On Wednesday, February 8, and a month later, on Wednesday, March 8, 1865, Gregor Mendel 40 presented the results of his crossing experiments in Pisum in two lectures to the Natural Science 41 Society (NSS) in Brünn (nowadays Brno, Czech Republic). These lectures were the climax of the 42 experiments, which he had begun ten years earlier in 1856. The lectures were the only public 43 presentations Mendel made about his pea crosses. Likewise, the long paper "Experiments on Plant 44 hybrids" published in 1866, said to be based on the lectures, was Mendel's only written report of his 45 results and interpretation; that paper constituted the basis for the science of genetics when it was 46 read and understood in the year 1900. Thus – two lectures alone, presented in one paper, laid the 47 foundation of a revolutionary science.

48 Mendel's research was unique for the 19<sup>th</sup> century. Because the 1866 publication did not 49 generate response in his time, and his notes were destroyed after his death in 1884, it is difficult to 50 perceive his thought process and the development of his research programme.

51 We have earlier analysed the central question of *why* Mendel started making his crosses and 52 what he hoped to achieve with them (VAN DIJK *et al.* 2018, VAN DIJK *et al.* 2022). As with all research 53 projects, his questions and approaches changed direction in the course of achieving interesting results. 54 As can be expected, not many of these changes are explicitly described in the resulting paper, but 55 careful analysis of remaining sources can provide some insight into how the research evolved.

However, achieving interesting results and presenting them to an understanding audience is very different from getting a paper based on the same results written and published. This is the topic of our concern here: How did Mendel present his results? What were the reactions? How did Mendel himself react to these when finalising his manuscript together with his own insights that he had obtained from presenting and arguing for his results?

61 We have assembled available historical data and added some new pieces of information, to 62 answer some of these questions. We find, as expected, that the standard view that his famous 63 publication copies precisely what Mendel said in his two lectures is incorrect. In the writing of his

paper, many factors – internal and external – influenced Mendel. By identifying at least some of them,
we get a clearer picture of the making of this scientific masterpiece.

66

67 The premises

68 The NSS had been in existence for three years and was founded as an offshoot of the 69 Agricultural Society to promote fundamental science. The monthly meetings of the NSS were held on 70 the second Wednesday of the month in a classroom of the *Realschule* (secondary school), in the center 71 of Brünn, made available by the municipality. The *Realschule* was a new imposing building with 26 72 classrooms in a Florentine palace style (ANONYMOUS 1902) on the Johannesgasse (now Jánská), 73 which had opened at the end of 1859. Here, during the day, for 18 to 27 hours per week, Mendel 74 taught natural history and physics as a supply teacher for the second and third grades (WEILING 1991). 75 The society's library and collections were housed in rooms on the third floor and NSS members had 76 the opportunity to consult the collections and the library on Wednesday and Saturday afternoons. The 77 monthly meetings started at 6.00 pm and ended between 8.30 pm and 9.00 pm. The meetings were 78 held in German and announced in the German newspapers Neuigkeiten, the Brünner Zeitung and the 79 Mährischer Correspondent and in the Czech newspaper Moravská Orlice.

80 How many members attended the monthly meetings? The annual report of 1866 stated that 81 always 1/4 to 1/3 of the members living in Brünn were present. In 1865 there were 161 members from 82 Brünn, equating to 40-55 participants. As there was a steady increase in 1866, the average number of 83 participants by the beginning of 1865 would have been around 40. The meetings started with a 84 housekeeping section listing the new books and journals for the library obtained through exchanges 85 with other societies or donations from individual members. This was followed by an overview of new 86 acquisitions for the collections of animals, plants, rocks, and minerals. Then there was time for one 87 main or several shorter lectures. The topics of these were diverse.

In the early years of the NSS, nearly all lectures were given by the executive committee and
the board. The following issues were addressed in the three meetings before and after Mendel's

90 lectures. In November: coal deposits, the fluorescence of liquids and solid materials; and newly found 91 plant species in Moravia. In December: new theories in organic chemistry; large-scale production and 92 utilization of magnesium; newly found plant species. It is of particular interest and relevance that in 93 January Alexander Makowsky, Mendel's colleague at the Realschule, spoke about Darwin's theory of 94 "organic creation". In March, after Mendel's second lecture, there was a talk on peculiar stones. In 95 April, there was a lecture on meteors, and in May, a lecture on the mathematical shape of the earth. 96 Demonstration material was often shown at the lectures. Original experimental research, as in 97 Mendel's lectures, was rarely a subject; the lectures mainly covered new developments in a scientific 98 field, or the speaker's findings, for example, of plants or types of rock in Moravia. After the lecture, 99 new members were elected. Generally, a few days later, brief reports of the lectures appeared in the 100 three local German-language newspapers.

101

## 102 Earlier descriptions of Mendel's lectures and new material

103 Hugo Iltis (1924) gave a largely fictitious dramatized description of the two meetings in his 104 1924 Mendel biography<sup>1</sup>. He based his account on the recollections of two board members of the NSS, 105 Gustav von Niessl-Mayendorf (1839-1919) and Alexander Makowsky (1833-1908), almost 40 years 106 after the event. In 1966 Joseph Sajner discovered two 1865-reports of the meetings in the local 107 newspaper Neuigkeiten. These Neuigkeiten articles were discussed by De Beer (1966b), Olby and 108 Gautrey (1968), and lately by Zhang et al. (2017). Searching in digitized historical newspapers<sup>2</sup>, we 109 have found additional newspaper reports of the meetings in two other local newspapers: the Brünner 110 Zeitung and the Mährischer Correspondent. We use all these articles to reconstruct the contents of 111 the lectures. We also extracted information from these newspapers about the settings of the lectures.

112

## 113 The February lecture

According to the newspapers, Wednesday, February 8, was a sunny and clear day. However, by late afternoon the sky quickly became cloudy. The sun was already setting at 5 pm, and it was minus 116 8.5 degrees Celsius in the evening. The moon was almost full but probably not visible because of the 117 clouds. Brünn's more than 900 street gas lanterns (DEUTSCH 1865) were lit early in the evening by the 118 lamplighters. The newspapers had announced Mendel's lecture on plant hybrids the day before. The 119 Brünner Zeitung had written in July 1861 that Mendel was trying "to approach the truth in a practical 120 manner", suggesting that the research he was going to present was not a complete surprise to all 121 attendees. The *Realschule* was in the city centre, less than half an hour's walk from the Augustinian 122 monastery in the suburb Altbrünn, a journey which Mendel made at least twice daily, but Mendel may 123 have used the monastery's carriage this time, especially if more priests came to listen to the lecture. 124 From St. Thomas Abbey, Thomas Bratranek and Benedikt Fogler were members of the society; Abbot 125 Napp, Mendel's patron, and Johann Lindenthal and Alipius Winkelmayer, who assisted Mendel in the 126 pea experiments, may also have been present.

127 Inside, the building was lit with gas lamps. The NSS lectures were held in classroom nr. 7, on 128 the 2nd floor. The stairs will probably have cost Mendel some effort, given his predisposition to 129 corpulence (Mendel reflected on this with self-deprecation two years later in a letter to Nägeli)<sup>3</sup>.

Gradually more listeners arrived, of whom teachers, roughly a third, made up the largest group<sup>4</sup>. All were amateur naturalists, although some, especially the board members, took their hobby very seriously, for example, several were working on the publication of the cryptogam flora of Moravia.

For Mendel's first lecture, the chairman was Carl Theimer, the vice-president of the society and a pharmacist in daily life. Theimer was an amateur botanist and three years before, at one of the new society's first meetings in February 1862<sup>5</sup>, had given a lecture on hybrids in the wild

Thus, Theimer was knowledgeable concerning the topic of the meeting. The "recent experiments" that Theimer had mentioned in that lecture most likely referred to Gärtner's, described in his 1849 standard work, which summarized the results from more than 10,000 artificial plant crosses. Natural plant hybrids were an important topic in the first ten years of the NSS. At the December 1864 meeting,

two months before Mendel's first lecture, von Niessl had reported on a *Verbascum Bastard* which he
had found in nature in the vicinity of Brünn (VON NIESSL 1864).

According to the newspaper *Neuigkeiten*, the February meeting was very well attended, like Makowsky's lecture on Darwin's "organic creation" a month before. The *Mährischer Correspondent* was somewhat less generous and spoke of being "reasonably well attended".

Gregor Mendel took the floor for a lecture of probably 1.5 hours at maximum. He had presented his meteorological data in several lectures for the NSS before, but this was his first botanical lecture. He read his lecture from a script, which was later the basis for his 1866-paper (see 2<sup>nd</sup> letter to Nägeli, CORRENS 1905). He would have explained the numbers, ratios, and formulas using the chalkboard; perhaps he had written them beforehand. Mendel was an experienced teacher with excellent didactic qualities<sup>6</sup>. We can assume that Mendel presented the lecture clearly and that the algebra would have been well understood by the audience<sup>7</sup>.

153 *Neuigkeiten* reported on the meeting two days later, on February 10. Almost a month after 154 the lecture, on March 3, the *Brünner Zeitung* published an extract of the meeting minutes made by 155 the secretary of the NSS, Gustav von Niessl. The *Neuigkeiten* report clearly differs from that and must 156 have been made by an unknown person attending the meeting.

157 The Brünner Zeitung texts have, as far as we know, not been discussed previously. They partly 158 overlap and partly complement the *Neuigkeiten* articles. Below we have combined the reports of the 159 first lecture in Neuigkeiten (indicated as NK) and the Brünner Zeitung (BZ). We also marked in bold 160 some words that are discussed later. The numbers between brackets refer to our comments below 161 the combined reports. For the Neuigkeiten articles, we use the translation of Olby and Gautrey (1968), except that we kept the German words "Hybriden" and "Bastarden" and forms thereof. Both words 162 are translated as "hybrids", but Mendel used these words very specifically, implying that for him they 163 164 had a different meaning. All other translations are ours.

- 165 NK: After the reading of the communications received, Herr Professor G. Mendel delivered a 166 long lecture, of special interest to botanists, on plant hybrids raised by artificial fertilization of 167 related species, that is by transfer of the male pollen to the seed plant.
- BZ: He gave as an introduction a brief historical review of the most important observations
  and experiments (1) in regard to plant **bastardization** (2).
- 170 NK: The lecturer emphasised the fact that the fertility of the *Pflanzenhybriden*, or **Bastarde**
- (2) was proven but did not remain constant, and that these hybrids always tended to revert
  to the stem species, this reversion being speeded up by repeated artificial fertilisations with
  the pollen of the stem plants (2).
- BZ: Subsequently, he presented his own numerous and carefully and successfully conducted
  experiments that partly agreed with previous observations and partly disagreed.
- 176 NK: On this point the lecturer drew attention to his experiments carried out over several years
  177 with success, which he had made especially with several kinds of pea (*Pisum sativum*, *P.*178 saccharatum and *P. quadratum*)(3)
- BZ: From his experiments, he drew several very interesting and important conclusions. The
  observations were mainly made on Papilionaceous plants (a family that according to wellknown researchers is not well suited for *hybridisation*) (4) and continued for a number of
  years and numerous generations.
- 183 NK: [He] exhibited examples from the generations in question, in which characters common 184 to both stem-parents were transmitted reciprocally, but differing characters gave rise to new 185 characters. The differentiating characters of the pea hybrids were seen in the form and colour 186 of the ripe seed and seed coat, in the colour of the flowers, in the form of the ripe pods and 187 their colour when unripe, in the position of the flowers and in the difference in length of the 188 stems. The numerical data with regard to the occurrence of the differentiating characters in 189 the hybrids and their relation to the stem species were worthy of consideration.

BZ: The results were so favorable that a number of mathematical formulas for the laws of hybridization could be deduced from them with reasonable accuracy. The lecture was illustrated with numerous samples (especially on fruits and seeds).(5)"

193 NK: That the theme of the lecture was well chosen and the exposition of it entirely satisfactory
194 was shown by the lively participation of the audience."

195 Our remarks to the newspaper reports of the February lecture:

196 1. The historical review in the introduction of the 1866-paper is also brief, but the discussion of 197 the work of Kölreuter, Gärtner, and Wichura in the concluding remarks section is extensive. 198 Gärtner (1849) was the standard work on plant hybridization and described both the loss of 199 fertility of hybrids over the generations (p 365 and further) and the reversion of hybrids to the 200 parental types by self-fertilization (p 422 and further) as well as the transformation of one 201 species into another by back-crossing (Rücksläge, Vorsläge). Gartner also noticed that 202 reversion by self-fertilization of the hybrids was a prolonged process (p 460 and 473). The 203 members of the NSS will have been aware of Gärtner's ideas about plant hybridization.

204
2. In the German text of the 1866-paper, Mendel used the word "*Hybriden*" with respect to
205 *Pisum*, and only four times the word "*Bastarden*" with respect to studies by others. The
206
207 *"Hybriden*" however was unusual for naturalists. Therefore, both newspaper articles begin by
208
208
209
209
209
209
209
200

In the 1866-paper Mendel refers to *Pisum sativum*, *P. quadratum* (i.e., round vs wrinkled), *P. saccharatum* (i.e., parchmented vs parchmentless) and *P. umbellatum* (flowers at the apex rather than axillary). As *P. umbellatum* is not mentioned here, Mendel may not have presented that data set.

This sentence in the *Brünner Zeitung* is remarkable because, in his 1866-article, Mendel
 praised *Pisum* as especially suitable for artificial crossing since the flower structure minimizes

the risk of contamination by foreign pollen. The *Brünner Zeitung* criticism referred to natural
hybrids, which are rare in the large legume family (Leguminosae or Fabaceae; the
Papilionaceae are a subfamily that includes the genus *Pisum*). There seems to be a mismatch
between Mendel's interests and those of the members of the NSS. We will discuss this in more
detail below.

221 5. Mendel thus illustrated his talk with different new combinations of pea seed and pod 222 characteristics in different generations, presumably of dried material, unless Mendel had 223 grown some plants in his glasshouse specifically for the purpose of this illustration. For 224 example, one progenitor variety with yellow round seeds, when crossed with another with 225 green wrinkled seeds; formed a hybrid with yellow round seeds, and the progeny of the selfed 226 hybrid generated yellow round, yellow wrinkled, green round, and green wrinkled seeds. The 227 pod ("fruit") samples will have varied in the shape of the mature dried pod: inflated or 228 constricted. The time of the year probably would not have allowed other traits, like flower 229 colour, to be shown without some special effort in the glasshouse to produce plants for 230 illustration, although, as Mendel noted, some seed colour characters are a pleiotropic feature 231 of flower colour.

At the next month's meeting, Mendel would give a cell biological explanation for the "mathematicalformulas for the laws of hybridization".

234

## 235 The March lecture

One month later, on Wednesday, March 8, it snowed all morning heavily. The snow was almost 20 centimeters deep in the fields at eight o'clock in the morning. The snow melted away in the city. During the day, the temperature fluctuated around freezing. Due to the melting snow, the water in the streams and rivers had swollen considerably. The sun was setting at a quarter to six. In the evening, it started to snow again, but lightly. Due to the bad weather, the monthly meeting was only moderately attended (*Mährischer Correspondent* 03-10-1865), so there were probably not more than

242 20 people<sup>8</sup>. That day there was another scheduled lecture by Makowsky, so Mendel's second lecture 243 will have been shorter than the first one. His second lecture focused on fertilization and pollen 244 hypothesis (cell theory). It is plausible that Mendel had discussed this topic intensely with his friend 245 Johann Nave (VAN DIJK *et al.*, 2022). However, Nave had died of tuberculosis in November 1864, only 246 a few months before the lectures.

The reports from *Neuigkeiten* (two days later) and *Mährischer Correspondent* (MC, three days later) were short. The *Brünner Zeitung* report, one and a half weeks after the meeting, discussed the content in more detail. The combined report reads as follows:

250 MC: Professor G. Mendel finished his lecture on plant hybrids. Before he gave his lecture, he 251 spoke of the cell and of the reproduction of plants by fertilization (1).

252 NK: Taking up the thread of last month's lecture, he spoke about cell formation, fertilization 253 and seed production (2) in general, and in the case of hybrids in particular, alluding to his 254 experiments undertaken with as much care as success, which he declared he would continue 255 next summer.

256 BZ: Professor G. Mendel finished his lecture on plant hybrids. He discussed the views on their 257 origin and formation, as well as the cross-fertilization, multiplication, and reproduction of 258 hybrids. The lecturer clearly reviewed the most recent research findings on the genesis and 259 development of the plant germ in general and sought to apply them to the formation of the 260 hybrids. He developed a hypothesis concerning the factors involved in this process, which, 261 confirmed by a large number of meaningful and highly successful experiments, could 262 significantly contribute to the elucidation of this hitherto inaccurately observed process. Professor Mendel intends to continue his investigations into this subject and publish the 263 264 results in the proceedings of the Natural Science Society.

265 NK: At the end he said that in the last few years he had also undertaken artificial fertilisations 266 with many other related plants, which he named, in order to raise *Bastarden*, and he felt

267 encouraged by the favourable results achieved not only to experiment further with such
268 *Bastardierungen*, but also to offer detailed reports. (3)

269 NK: Herr Professor von Niessl added to this lecture which was very well received that with the 270 aid of the microscope he had observed hybridisations in fungi, mosses and algae, and that 271 further observations of this kind not only supported existing hypotheses but will also give 272 further interesting clarifications."

273

274 Remarks on the newspaper reports of the March lecture:

The first two sentences are from the *M\"ahrischer Correspondent* and indicate that Mendel first
 gave an introduction about cells and fertilization before he presented his own experiments
 and results.

278 2. In the mid-1850s, it was clear that the embryo did not arise from the extremity of the pollen 279 tube, as Schleiden had hypothesized, and which was incompatible with Mendel's results, as 280 Mendel discussed in the 1866-paper. In contrast, the general opinion was that the embryo 281 developed from the egg cell after the pollen tube made contact. The nature of this interaction 282 remained a mystery for decades. It was thought that the pollen tube tip might contain 283 spermatozoa, or possibly small openings in the membranes allowed the mixing of the pollen's 284 fertilizing substance with the contents of the germinal vesicle, or it may have been diffusion 285 through intact cell membranes (SACHS 1875). That the nucleus of the pollen tube would enter 286 the embryo sac and fuse with the egg cell's nucleus was not known until much later, with the 287 aid of better microscopes and staining methods (1884, STRASBURGER). In the 1866-paper, Mendel proposed that characters for which plants had alternative forms (such as tall or dwarf) 288 289 could be represented by '*Elemente*', and these would be different in different true-breeding 290 lines. Because the offspring of hybrids between such true-breeding lines again had either one 291 or the other form, Mendel concluded that **both** types of '*Elemente*' must be present in F1 292 hybrids but that the pollen and egg cells of a hybrid could only contain **one** type of element

and that the types of reproductive cells would be formed in equal number. He also deduced
that one pollen grain united with one egg cell at random, which would produce a ground cell
from which the offspring plant would develop. This was entirely correct but completely new
in Mendel's time. Mendel tested these assumptions by three specific crosses and concluded
that his algebraic series "found rationale and explanation in the proven proposition" [p 32,
MENDEL 2016].

Three months later, at the June 1865 meeting, Mendel presented living *Verbascum*, and
 *Campanula* interspecific hybrids obtained by artificial fertilization. The parent plants must
 have been crossed the year before (in 1864), in accordance with the *Neuigkeiten* report.
 Mendel also describes these hybrids in his third letter to Nägeli. Note that the newspaper now
 uses the word "*Bastarden*" for these interspecific hybrids, whereas in the pea text above,
 "*Hybriden*" is used. Olby and Gautrey (1968) translate "*Bastarden*" in this sentence with
 "hybrids" thereby losing the distinction.

306

# 307 The reception of Mendel's lectures

308 Iltis wrote about the reception of the lectures: "The minutes of the meeting inform us that there were neither questions nor discussion." (ILTIS 1965, p178). This explains why the Brünner 309 310 Zeitung article, based on these minutes, was silent about the discussion. In contrast, Neuigkeiten 311 commented on the discussion at the first meeting: "That the lecture's topic was a good one and that 312 the execution of it was a completely satisfactory one was proven by the active participation of the 313 audience." Mendel commented on the reception of his lectures in his second letter to Nägeli: "[I] discussed the Pisum experiments at the meeting of the local society of naturalists. I encountered, as 314 315 was to be expected, divided opinion" (PITERNICK AND PITERNICK 1950). This also suggests that there 316 was a discussion about the lectures, although the discussion was not recorded in the minutes.

According to Richter (1941), Makowsky had told Iltis that the audience's reaction was "ridicule
 and laughter" (*Spott und Gelächter*), but Iltis does not write about this himself<sup>9</sup>. Some later authors

have mentioned this in their Mendel publications (WEILING 1966, GUSTAFSSON 1969). Eichling, a seed company representative, visited Mendel in Brünn in 1878 after first meeting with a client (EICHLING 1942). This client stated "while Mendel was one of the best beloved clerics in Brünn, not a soul believed his experiments were anything more than a pastime, and his theories anything more than the maunderings of a charming putterer". However, Mendel's obituary published by *Neuigkeiten* in January 1884 called his plant research "epochmaking", arguing against the idea that Mendel was not taken seriously.

326 It is interesting to recall another historical gathering of great significance: the reading of 327 Darwin and Wallace's essays on evolution by natural selection at the Linnean Society of London 328 meeting on Thursday, July 1, 1858. The essays were communicated by Darwin's friends Lyell and 329 Hooker and read by the secretary (DARWIN AND WALLACE 1858). Then there was no discussion afterward because the ideas were too innovative (DARWIN 1887). The president of the society, 330 331 Thomas Bell, made in his 1859 presidential address the famous misjudgement: "The year which has 332 passed has not, indeed, been marked by any of those striking discoveries which at once revolutionize, so to speak, the department of science on which they bear." (BELL 1859)<sup>10</sup>. Mendel's ideas may also 333 334 have been too new and original to bring about much discussion.

Another important factor determining the reception of the lectures will have been the interest of the audience. Adolf Oborny, a fellow teacher of Mendel's at the *Realschule*, a *Hieracium* (hawkweed) expert, and a member of the NSS since its foundation in 1861, reflected on the lectures in 1922 in general terms:

"Among his [Mendel's] close circle of friends at home, nobody had been involved in biological
studies. The botanists and zoologists were mainly taxonomists, and many of them will have
been astonished that Mendel restricted himself to the narrow range of some cultivated
species, such as peas, beans, *Aquilegia, Dianthus*, and *Nicotiana* species, and to a few wild
species." (OBORNY 1922)(see the appendix for the original German text)<sup>11</sup>

As Mendel was requested to submit a manuscript for the Proceedings of the NSS, it is evident that the board was convinced of the importance of Mendel's work. However, as is explained below, parts of the concluding remarks are likely to have been added after the lectures, to meet the interest of the members of the NSS.

348

349 *Confusion about* "Hybriden" *and* "Bastarden"

350 In the 1866 paper, Mendel consistently used the word "Hybriden" with respect to peas. 351 "Bastarden" was used only two times to describe the work of others; the members of the NSS were interested in hybrids between species in the wild and therefore "Bastarden". The Proceedings of the 352 NSS contain reports of the topics at the monthly meetings and articles, such as that of Mendel from 353 354 1866. In the first ten years since the founding of the NSS hybridization was a frequently recurring topic. 355 Figure 1 shows the number of times the words "Bastarden" and "Hybriden" were used per year 356 between 1862 and 1871. The term "Bastarden" (or variants thereof) is used 61 times, whereas, if we exclude Mendel's 1866 paper, the word "Hybriden" (or variants thereof) is used only twice. These two 357 358 instances of the use of "Hybriden" are in a paper about a supposed wild fern hybrid Asplenium adulterinum, however in that paper "Bastarden" is used much more frequently (14 times, VON NIESSL 359 1868). The naturalists were interested in interspecific hybrids and used "Bastarden" to indicate a 360 361 morphologically intermediate growth form of a hybrid between two species growing in the wild. They 362 were not interested in intraspecific hybrids between varieties (NEILREICH 1851).





Figure 1. The use of the German words "*Bastarden*", "*Hybriden*" and "*Blendlingen*" and variants thereof in the first 10 volumes of the Proceedings of the NSS. The coloured bar is scaled to the fraction of usage and the actual number is given. Note that the proceedings were published one year later. For example, Mendel's *Pisum* paper appeared in Volume IV (1865), which was published in 1866. Mendel's use of "*Hybriden*" is very exceptional. The frequent use of "*Bastarden*" in 1869 is due to Mendel's *Hieracium* paper. Searches were performed with the search function in the Biodiversity Heritage Library.

369

370 Mendel's use of "Hybriden" in his 1866 paper was thus very unusual for the naturalists of the NSS. In the two spring lectures of 1865, he also used "Hybriden". Both Neuigkeiten and the Brünner Zeitung 371 felt is necessary to clarify that this was the same as "Bastarden". Since Mendel used the term 372 373 "Hybriden" that was uncommon for naturalists, there must have been a difference between them. One reason could be that "Bastarden" were often considered to be hybrids between species. For 374 375 example, the German translation of Darwin's Origin, of which Mendel possessed a copy, used the word 376 "Bastarden" for hybrids between species and "Blendlingen", for hybrids between varieties (Darwin 377 1863). Focke (1881) in his monumental reference work on plant hybrids (Die Pflanzen-mischlinge), also defined "Bastarden" as hybrids between two species and Blendlingen as hybrids between varieties. 378 379 "Hybriden" however could be used to describe both inter and intraspecific hybrids (Focke 1881).

380 In the 1866 paper, Mendel leaves it open whether his *Pisum* forms were species or varieties:

381 "Incidentally, to the experiments in question, the hierarchical position that one assigns to them382 [the various types of pea] in the system is of no concern at all. As little as one can draw a sharp383 distinguishing line between species and varieties, so little has anyone succeeded so far to establish a384 thorough difference between the hybrids of species and varieties." (MENDEL 2016, p6)

385 Mendel's use of "*Hybriden*" avoided the problem of the taxonomic rank of the pea forms.

Mendel's use of the word "*Hybriden*" instead of "*Bastarden*" may also reflect the fact that Mendel initiated his experiments for breeding peas as a vegetable crop (VAN DIJK *et al.* 2022). In horticulture, where artificial crosses were made, it was more common to speak of "*Hybriden*" than of "*Bastarden*" (see, for example, *Hamburger Garten- und Blumenzeitung* (Figure 2). Neither botanists nor horticulturalists commonly used *Blendlingen*.



391

Figure 2. The use of the German words "*Bastarden*" and "*Hybriden*" and variants thereof in the same period as Figure 1
 (1862-1871) in volumes of the horticultural journal *Hamburger Garten- und Blumenzeitung*. Searches were performed with
 the search function in Google Books.

Also, in his letters to Nägeli (CORRENS 1905), Mendel uses "*Hybriden*" and "*Bastarden*" differently (Figure 3). Consistent with the newspaper reports of the lectures and the 1866-paper, in his early letters to Nägeli, dealing with mainly *Pisum*, Mendel almost exclusively uses "*Hybriden*". In contrast, in his later letters, dealing with *Hieracium*, Mendel exclusively uses "*Bastarden*", probably because here he was crossing wild plant species, instead of cultivated forms. In the title and text of the 1870 paper "On some *Hieracium-Bastarde* obtained by experimental fertilization" Mendel only uses the word "*Bastarden*" (see Figure 1, the year 1869).

Mendel's use of "*Hybriden*" was correct but was unusual for the members of the NSS and led to confusion. This is reflected in the *Brünner Zeitung's* comment about Mendel's first reading that "according to well-known researchers, Papilionaceous plants were not well suited for hybridization". In contrast, in the 1866-paper, Mendel argued that the Leguminosae were particularly convenient for his experiments, due to their special flower structure.

408 Who were these prominent researchers that the Brünner Zeitung referred to? Certainly, 409 Gärtner, who wrote: "Incidentally, the reluctance of legumes to produce hybrids does not seem to us 410 to be at all in doubt" (GÄRTNER 1849). Gärtner had even stated that successful crosses between pea 411 varieties such as those Mendel made should not be considered as evidence for Bastardization in the legume family: "Indeed, the combinations of the different varieties of *Pisum sativum* succeed easily 412 413 and perfectly ..... but these are mere varieties and not pure species (p 173)". About the same time as 414 Mendel's lectures, other prominent botanists also wrote that hybridization in the legume family was rare (KERNER 1865; NÄGELI 1866). 415

In the section "Selection of the Experimental Plants" of the 1866 article, Mendel wrote that *Pisum* fulfilled all the requirements of a plant suitable for experimental hybridization. "The experimental plants must of necessity: 1. Possess constantly differing traits, 2. Their hybrids must be protected, or be easily protectable, from the influence of all alien pollen during the flowering period, 3. Hybrids and their descendants should suffer no noticeable disturbance in their fertility in successive generations ...... On account of their particular flower structure, particular attention was paid to the

Leguminosae right from the start. Experiments which were performed on several members of this family led to the result that the genus Pisum sufficiently meets the posited requirements." (MENDEL 2016, p5). The hybridization comment in the *Brünner Zeitung* suggests that Mendel did not mention this advantage in his lectures.





Figure 3. Mendel's use of the words "*Hybriden*" and "*Bastarden*" in the ten letters to Nägeli that have survived (CORRENS 1905), displayed cumulatively. In the first three letters, Mendel mainly uses "*Hybriden*", rarely "*Bastarden*". In the last three letters, the preferred word use is reversed.

431

427

432

# 433 Were the Concluding Remarks of the 1866-paper part of the lectures?

If we look at the 1866-paper with the criticism that Leguminosae species were not well suited for hybridization, there is another striking contrast. In the Concluding Remarks, Mendel discussed Kölreuter and Gärtner's experiments in detail and showed how his pea findings might explain the observations of these two hybridizers *e.g.*, reversion (through selfing of the F1) and transformation (by repeated back-crosses of the F1 to the parents). Kölreuter is mentioned four times in this section and Gärtner 15 times. If Mendel would have said this during his lectures, the criticism that the Papilionaceous plants were not well suited for hybridization would be hard to understand. An obvious explanation is that Mendel added this section later to counter the criticisms expressed after thelectures.

443 It, therefore, seems unlikely that the 1866-paper is identical to the content of the lectures Mendel 444 gave. De Beer (1966) concluded that the lecture and the paper were exactly the same because Mendel wrote to Nägeli in his 2<sup>nd</sup> letter: "The paper presented is an unaltered reprint of the concept for the 445 mentioned lecture..."12. However, it is important to keep in mind the context of Mendel's remark. In 446 447 his reply to Mendel's first letter Nägeli wrote that he could not judge Mendel's experiments well 448 because he did not know the experimental details: "I refrain from going into other points of your 449 communications since I could only speak conjecturally without knowing the details of the experiments on which they are based."<sup>13</sup> When Mendel replied that it was an unaltered reprint of the concept, he 450 451 referred to the limited details about the experiments; his comment does not necessarily apply to the 452 whole text, for example, to the concluding remarks.

453 From the newspaper reports, it is clear that the long first lecture dealt with the algebraic series 454 and the second short one with the cell biology and fertilization process. Mendel had to present all this 455 within about two hours. The 1866-paper is 45 pages long. We determined the number of words in the 456 German text of the Versuche as about 13,200. The normal "Read Out Loud" rate of German in 457 Microsoft Edge is 138 words per minute. Therefore, reading the full text of the 1866-paper would take 458 about 1 hour and 35 minutes. This reading speed, although fine for a novel or other forms of 459 entertainment, is too fast for a lecture that also needs thought processing. Since Mendel had to 460 explain his tables, formulas and calculations and demonstrate the pea samples, it is difficult to see 461 how the whole 1866-paper could be presented within two hours. For reasons of limited time alone, it is likely that Mendel did not present the entire last two sections of the 1866 paper (Experiments with 462 463 Hybrids of Other Species of Plants and the Concluding Remarks) during the lectures.

464

465 Did Mendel make use of Nägeli (1865) in the Concluding Remarks?

466 In the first paragraph of the Concluding Remarks of the 1866-paper, Mendel wrote that it 467 would be interesting to compare his results with those of Kölreuter and Gärtner. The last sentence of 468 this paragraph also commented on variety hybrids and species hybrids: "The hybrids from varieties 469 behave just like species-hybrids, except that they possess even greater mutability of conformations 470 and a more pronounced tendency to revert to the parental forms" (MENDEL 2016, p38). The content 471 of this paragraph shows striking similarities to the end of Nägeli's article Die Bastardbildung im 472 Pflanzenreiche (1865) in which he summarized the work of Kölreuter and Gärtner and tried to draw 473 generalizations (see Appendix). Nägeli had given this lecture on December 15, 1865, in Munich for the Royal Bavarian Academy of Sciences<sup>14</sup>. In paragraphs on p438-432, Nägeli described the intermediate 474 475 form and the two parental forms in the progeny of the hybrid, the comparison between species and 476 variety hybrids, and the greater tendency of the latter to revert to the parental forms. However, most 477 striking is the phrase: "Diess gilt aber nicht für alle Varietätenbastarde "("This, however does not apply 478 to all variety hybrids" p234) which is almost identical to Mendel's "Das gilt jedoch nicht von allen 479 Hybriden ohne Ausnahme" ("This, however, is not the case with hybrids without exception") and which 480 in both texts refers to the occurrence of non-segregating, constant hybrids. Constant hybrids, "hybrids 481 which remain constant in their descendants and propagate themselves in the same way as pure 482 species." (MENDEL 2016, p40), which Mendel discussed in the paper as a different type from the 483 variable hybrids (such as *Pisum*), were not mentioned in the newspaper reports. This specific phrase 484 in the context of constant hybrids is unlikely to be due to chance. More likely, Mendel had read Nägeli 485 (1865) and used it for his manuscript. This is not unique; elsewhere in the 1866-paper there are also 486 indications for influences by other authors<sup>15</sup>.

487 Mendel's manuscript was discussed in the meeting of the NSS board in February 1866 488 (OPPENHEIM 1932). Mendel, therefore, had almost a year after the lectures to complete his 489 manuscript. On the monthly meeting of April 11, the issue of the Proceedings of the Royal Academy 490 of Sciences of Bavaria, 1865, Volume 2, containing Nägeli's *Bastardbildung*, was among the 491 communications received (ANONYMOUS 1867, p19). In it, Nägeli wrote that "[hybridization] sheds 492 some light on reproduction, more specific on how traits from the parents are transmitted to the 493 progeny". This was precisely what Mendel had studied. It is likely that Mendel read Nägeli's 494 *Bastardbildung*, around the end of March, possibly alerted by his friend, Gustav von Niessl, the 495 secretary of the NSS, who also had an interest in hybridization. At the board meeting on June 9, 1866, 496 it was decided to include Mendel's meteorological observations also in the Proceedings of 1866. Thus, 497 the submission deadline had not yet passed in June.

498 Mendel may even have had more time to rewrite his manuscript. On June 26, there was an 499 additional extraordinary monthly meeting because of the Austrian-Prussian war; at this meeting, it 500 was decided to postpone all NSS activities until October. Mendel's letter to his brother-in-law dated 501 31-08-1866 tells us that Brünn was occupied by 50,000 Prussian troops from mid-July till early 502 September (MATALOVÁ 2009). This caused a delay in the publication of the Proceedings, according to 503 the annual meeting report in December 1866 (ANONYMOUS 1867, p71-87). The delay in publishing 504 will have given Mendel the opportunity to modify the manuscript to include some ideas he had read 505 in Nägeli (1866). It is hard to believe that Mendel would not have grasped that opportunity, and the 506 first paragraph of the *Concluding Remarks* suggests that he did.

507 Mendel probably received the reprints shortly before the end of 1866, as he sent a reprint 508 with a long covering letter, explaining his experimental results as well as revealing his future plans, to 509 Nägeli on New Year's Eve. In contrast, the reprint he sent to Kerner the next day had only a short cover 510 letter – a copy of the first formal paragraph of the letter to Nägeli. This reveals Mendel's eagerness to 511 enter into correspondence with Nägeli, a renowned Botany professor interested in inheritance.

512

513 Conclusion

We have argued that the extensive discussion of interspecific hybrids in the 'Concluding Remarks' section of Mendel's 1866-paper is not consistent with the newspaper reports of his 1865 lectures but is consistent with a response to the discussion of his lectures. This proposal suggests that Mendel intended to show that his findings were relevant for hybrids between wild species. It is also

518 striking that the constant hybrids, which "propagate themselves in the same way as pure species." 519 (MENDEL 2016, p40), which Mendel discussed in the paper as a different type from the variable 520 hybrids (such as *Pisum*), are not mentioned in the newspaper reports. Interspecific hybrids, both 521 constant and variable, were of greater interest to the members of the NSS than inter-varietal hybrids, 522 considered as of interest in horticulture. Such a broader relevance may have been required for 523 publication of the manuscript in the NSS journal rather than in a horticultural journal. In conclusion, it 524 is likely that much of the text of the concluding remarks was added after the lectures, and these 525 comments do not indicate the subject for which the pea experiments were initially conducted.

526

#### 527 Acknowledgements

528 We are very grateful to Adrienne Jessop, Bengt Bengtsson, and Julie Hofer, for their comments and

529 suggestions on this paper's draft versions and to Franjo Weissing for improving our translations.

530

## 531 References

ANONYMOUS, 1862. Verzeichniss der in Oesterreich lebenden Botaniker. Oesterreichische botanische
 Zeitschrift 12: 395-403.

ANONYMOUS, 1863. Meeting on February 12 1862. Verhandlungen des naturforschenden Vereines
in Brünn 1: 19.

536 ANONYMOUS, 1866. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-

537 Naturwissenschaftliche Classe Abt. K.K. Hof und Staatdruckerei, Wien.

538 ANONYMOUS, 1867. Verhandlungen des naturforschenden Vereines in Brünn 5: 71-87.

539 ANONYMOUS, 1902. Festschrift zur Erinnerung an die Feier des fünfzigjährigen Bestandes der

540 Deutschen Staats-Oberrealschule in Brünn. Verlage der Schülerlade der deutschen Staats-

541 Öberrealschule, Carl Winiker, Brünn.

542 BATESON, W.,1902. Mendel's principles of heredity: a defence. Cambridge University Press, 543 Cambridge.

- 544 BELL, T. 1859. Address of Thomas Bell, ESQ, F.R.S., The President, read at the annual meeting of the
- Linnean Society, on Monday, May 24, 1859. Taylor and Francis, London.
- 546 DARWIN, C., WALLACE, A., 1858. On the Tendency of Species to form Varieties; and on the
- 547 Perpetuation of Varieties and Species by Natural Means of Selection. Communicated by C. Lyell and
- 548 J.D. Hooker. Journal of the Proceedings of the Linnean Society of London. Zoology, 3: 46–62,
- 549 doi:10.1111/j.1096-3642.1858.tb02500.x
- 550 DARWIN, C., 1863. Über die Entstehung der Arten im Thier- und Pflanzen-Reich durch natürliche
- 551 Züchtung, transl. Bronn H. G. E., Schweizerbart'sche Verlagshandlung und Druckerei, Stuttgart.
- 552 DARWIN, F., 1887. The Life and Letters of Charles Darwin, Vol 1, Murray, London.DE BEER, G., 1966a.
- 553 Genetics: the centre of science. Proc. R. Soc. Lond. B.164: 154–166.
- 554 DE BEER, G., 1966. Mendel, Darwin, and Fisher. Addendum. Notes Rec. Roy. Soc. 21: 64–71.
- 555 DEUTSCH, E., 1865. Führer durch Brünn und Umgebung. Fr. Karafiat, Brünn.
- 556 https://books.google.nl/books?id=Jek22a-K-cMC&hl=nl&source=gbs\_navlinks\_s
- 557 EICHLING, C., 1942 I talked with Mendel. Jour. Heredity 33:243-246.
- 558 FAIRBANKS D., J., RYTTING B., 2001. Mendelian controversies: a botanical and historical review.
- 559 Am. J. Bot. 88: 737–752.
- 560 FAIRBANKS, D., J., ABBOTT, S., 2016. Darwin's influence on Mendel: evidence from a new translation
- of Mendel's paper. Genetics 204: 401–405.
- 562 FOCKE, W., O., 1881. Die Pflanzen-Mischlinge. Gebrüder Borntrager, Berlin.
- 563 GÄRTNER, C., F., 1849, Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich.
- 564 Hering, Stuttgart.
- 565 GUSTAFSSON, A., 1969. The life of Gregor Johann Mendel tragic or not? Hereditas 62: 239-258.
- 566 HOPPE, B., 1971. Die Beziehung zwischen J.G. Mendel und C.W. Nägeli auf Grund neuer Dokumente.
- 567 Folia Mendeliana 6: 123–138.
- 568 ILTIS, H., 1924. Gregor Johann Mendel: Leben, Werk und Wirkung. Springer, Berlin.
- 569 ILTIS, H., 1966. Life of Mendel. (Translated by Paul E. and Paul C. George), Allen and Unwin, London.

- 570 KERNER, A., 1865. Aus dem botanischen Garten in Innsbruck. Oesterreichische botanische Zeitschrift
- 571 15: 205-213.
- 572 MATALOVÁ, A. 2009. Primary sources to Johann Gregor Mendel's early years. Folia Mendeliana 42-43:
  573 7-82.
- 574 MENDEL, G. 2016. Experiments on Plant Hybrids (1866). Translation and commentary by Staffan
- 575 Müller-Wille and Kersten Hall. British Society for the History of Science Translation Series. 576 <u>http://www.bshs.org.uk/bshs-translations/mendel</u>.
- 577 MENDEL, G. 1871. Über einige aus künstlicher Befruchtung gewonnenen Hieracium-Bastarde.
- 578 Verhandlungen des naturforschenden Vereines in Brünn 8: 26-31.
- 579 NÄGELI, C., 1865. Die Bastardbildung im Pflanzenreiche. Sitzungsberichte der Königl. Bayerischen
- 580 Akademie der Wissenschaften, Vol 2: 395-443. F. Straub, München.
- 581 NEILREICH, A. 1851. über hybride Pflanzen der Wiener Flora. Verhandlungen des Zoologisch582 Botanischen Vereins in Wien, 1: 114-131.
- 583 OBORNY, A., 1922. Erinnerungen an Gregor Mendel. Znaimer Tagblatt, 22-12-1922, p25.
- 584 OLBY, R., Gautrey, P., 1968. Eleven references to Mendel before 1900. Ann. Sci. 24: 7–20.
- 585 OPPENHEIM, J., 1932. Aus dem Archiv des Naturforschenden Vereins in Brünn. Tagesbote 19.7.1932.
- 586 PETERS, J., 1959. Classic Papers in Genetics. Prentice-Hall, London.
- 587 PITERNICK, L., K., PITERNICK, G., 1950. Mendel, G. 1950. Gregor Mendel's Letters to Carl Nägeli.
  588 Genetics, 3: 1–29.
- 589 RICHTER, O., 1941. 75 Jahre seit Mendels Großtat und Mendels Stellungnahme zu Darwins Werken
- 590 auf Grund seiner Entdeckungen. Verhandlungen des naturforschenden Vereines in Brünn, 72: 110-
- 591 173.
- 592 SACHS, J., 1875. Geschichte de Botanik vom 16. Jahrhundert bis 1860. K. Oldenburg, München.
- 593 SAJNER, J., 1966. Neue Forschungen über Gregor Mendel. Schriften Ver. Verbreitung naturwiss.
- 594 Kentnisse in Wien 106: 163 182.
- 595 SCHLEIDEN, M., J., 1846. Grundzüge der wissenschaftlichen Botanik. Engelmann, Leipzig.

- 596 STERN, C., SHERWOOD, E., 1966. The Origin of Genetics. A Mendel Source Book. Freeman, San 597 Francisco.
- 598 STRASBURGER, E., 1884. Neue Untersuchungen über den Befruchtungsvorgang bei den 599 Phanerogamen, als Grundlage für eine Theorie der Zeugung. Gustav Fischer, Jena.
- 600 VAN DER POST, C., C., 1866. Overzicht van de boeken, kaarten, penningen enz. ingekomen bij de
- 601 Koninklijke Akademie van Wetenschappen te Amsterdam, ten geschenke of in ruil ontvangen in de
- 602 maand mei 1866. De Roever en Kröber, Amsterdam.
- VAN DIJK, P., J., WEISSING, F., J., ELLIS, T., H., N., 2018. How Mendel's Interest in Inheritance Grew out
  of Plant Improvement. Genetics, 210: 347–355.
- VAN DIJK, P., J., JESSOP, A., P., ELLIS, T., H., N., 2022. How did Mendel arrive at his discoveries? Nat.
  Genet. 54, 926–933.
- VON NIESSL, G., 1864. Floristic Notes. Verhandlungen des naturforschenden Vereines in Brünn 3: 8588.
- 609 VON NIESSL, G., 1868. Ueber Asplenium adulterinum Milde und sein Vorkommen in Mähren und
- 610 Böhmen. Verhandlungen des naturforschenden Vereines in Brünn 6: 165-176.
- 611 WEILING, F., 1966. J. G. MENDELS ,, Versuche über Pflanzen-Hybriden" und ihre Würdigung in der Zeit
- bis zu ihrer Wiederentdeckung. Züchter, 36: 273-282.
- 613 WEILING, F., 1991. Historical Study: Johann Gregor Mendel 1822-1884. American Journal of Medical
- 614 Genetics 40: 1-25.
- 615 ZIRKLE, C., 1958. The First Recognized Plant Hybrid? Journal of Heredity, Volume 49: 137-138.
- 616 ZHANG, H., CHEN W., SUN K., 2017. Mendelism: New Insights from Gregor Mendel's Lectures in Brno.
- 617 Genetics 207:1-8. doi: 10.1534/genetics.117.201434.

#### 618 Appendix

- All translations are made by the authors, unless otherwise indicated. In some cases, only the passages
- about Mendel's lectures are translated. Untranslated parts of the German text are indicated by [....].
- 621 I. First lecture article in *Neuigkeiten*
- 622 II. First lecture article in the *Brünner Zeitung*
- 623 III. First lecture report in the *Märischer Correspondent*
- 624 IV. Second lecture article in *Neuigkeiten*
- 625 V. Second lecture article in the *Brünner Zeitung*
- 626 VI. Second lecture article in the *Märischer Correspondent*
- 627 VII. Original German text (OBORNY, 1922)
- 628 VIII. Possible influences from Nägeli (1865) on Mendel's 1866-paper
- 629
- 630
- 631
- 632 I. First lecture article in *Neuigkeiten* February 10, 1865.

Nach bekanntgabe der Einlaufe hielt Herr Prof. G. Mendel einen längeren, besonders für Botaniker 633 interessanten Vortrag über Pflanzen-hybriden, welche durch künstliche Befruchtungen 634 635 stammverwandten Arten und zwar durch Übertragung des männlichen Blüthenstaubes auf die Samenpflanze hervorgebracht werden. Er hob darbei hervor, dass die Fruchtbarkeit der 636 637 *Pflanzenhybriden, oder Bastarde zwar erwiesen sei, aber nicht konstant bleibe und das dieselben stets* 638 geneigt waren, zur Stammart rückzukehren, welche Rückkehr eben auch durch wiederholte künstliche 639 Befruchtungen mit dem Blüthenstaube der Stammpflanzen beschleunigt werden kann. Der Vortragende betonte hierauf seine durch mehrere Jahrer mit Erfolg gemachten Versuche die er 640 namentlich mit mehreren Erbsengattungen (Pisum sativum, P. sacharatum und P. quadratum) 641 642 anstellte und zeigte die Proben aus bezüglichen Generationen vor, wonach gemeinsame Merkmale 643 gegenseitig uebergangen waren, Differenzmerkmalen aber ganz neue Charaktere hervorbrachten. Die Differenzmerkmalen der Erbsenhybriden zeigten sich im Gestallt, dann Färbung des reifen Samens, und
der samenschale, in der Farbe der Blüthen, in der Form der reifen und in der Farbe der unreifen
Samenhüllen, in der Stellung der Blüthen und im Unterschiede der Achsenlänge. Beachtenswerth
waren die ziffermaessigen Zusammenstellungen mit Rüksicht auf die eingetretenen Differenz
Merkmale der Hybriden und deren Verhältnis gegenüber der Stammarten. Dass der Vorwurf des
Vortrages ein glücklicher und die Durchfürung desselben eine ganz befriedigende war, bewies die rege
Theilname des Auditoriums.

[Über Antrag des Vereins-Ausschusses wurde ferner beschlossen, die Pfarrhauptschule in Weißkirchen
auf ihre Bitte mit einer Kollektion von Pflanzen und Käfern zu beschenken, dann mit einer Wiener und
Leipziger Pflanzentauschanstalten behufs Komplettirung der Vereinsherbariums in Verbindung zu
treten. Der Verein selbst erhielt schließlich durch die Wahl von fünf neuen Mitgliedern einen weiteren
Zuwachs.]

656

657 Translation by Olby and Gautrey (1968):

658 After the reading of the communications received, Herr Professor G. Mendel delivered a long 659 lecture, of special interest to botanists, on plant hybrids raised by artificial fertilization of related 660 species, that is by transfer of the male pollen to the seed plant. The lecturer emphasised the fact that 661 the fertility of the plant hybrids [*Pflanzenhybriden*], or crossbreds [*Bastarde*] was proven but did not 662 remain constant, and that these hybrids always tended to revert to the stem species, this reversion 663 being speeded up by repeated artificial fertilisations with the pollen of the stem plants. On this point 664 the lecturer drew attention to his experiments carried out over several years with success, which he had made especially with several kinds of pea (Pisum sativum, P. saccharatum and P. guadratum) and 665 666 exhibited examples from the generations in question, in which characters common to both stem-667 parents were transmitted reciprocally, but differing characters gave rise to new characters. The 668 differentiating characters of the pea hybrids were seen in the form and colour of the ripe seed and 669 seed coat, in the colour of the flowers, in the form of the ripe pods and their colour when unripe, in

670 the position of the flowers and in the difference in length of the stems. The numerical data with regard 671 to the occurrence of the differentiating characters in the hybrids and their relation to the stem species 672 were worthy of consideration. That the theme of the lecture was well chosen and the exposition of it 673 entirely satisfactory was shown by the lively participation of the audience.

- 674
- 675

## II. First lecture article in the Brünner Zeitung (Brünner Morgenpost) March 6, 1865.

676 Monats-Versammlung des Naturforschenden Vereins in Brünn am 8. Februar 1864 [sic!].

677 (Auszug aus dem Sitzungsprotokolle)

678 [Nach Eröffnung der Sitzung durch den zum ersten Male den Vorsitz führenden Herrn Vicepresidenten 679 C. Theimer und Mittheilung der feit der letzten Versammlung eingegangenen Geschenke und 680 Sendungen] hielt Professor G. Mendel den angekündigten Vortrag über Pflanzenhybriden. Derselbe 681 gab als Einleitung eine kurze Geschichte der vorzüglichsten in Bezug auf Pflanzenbastardirung 682 angestellten beobachtungen und Versuche und die Resultaten derselben, und ging dann auf seine 683 selbständigen zahlreichen, met eben so viel Umsicht als Erfolg angestellten Versuche über, um deren 684 zum Theil mit alteren Angaben übereinstimmende, zum Theile abweichende Ergibnisse mitzutheilen 685 und aus denselben Reihe hochst interessanter und wichticher Schlusse zu ziehen. Die einschlägigen 686 Beobachtungen würden meist an Papilionaceen (einer selbst nach namhaften Forschern zur 687 hybridisation weinig geeigneten Familie) gemacht und durch eine Reihe von Jahren an zahlreichen 688 Generationen fortgesetzt, und gaben so günstige Ergibnisse, das aus denselben mit ziemlicher 689 Genauigkeit eine Anzahl mathematischer Formeln für die Gesetze der Hybridenbildung gewonnen 690 werden könnte. De Vortrag wurde durch zahlreiche Belegfünde (namentlich Früchten und Samen) 691 erläutert erklärt. [Auf Antrag des Ausschusses wurde beschlossen, die Pfarrhauptschule in Weißkirchen 692 mit Naturalien zu betheilen und zur Vervollständigung des Vereinsherbars mit den 693 Pflanzentauschanstalten in Wien und Leipzig in Verbindung zu treten. Als Mitglieder wurden gewählt 694 die Herren: Leopold Haupt, Großhändler; Dr. Robert Heym, Secretär der Handelskammer; J. U. Dr. Adolf 695 Promber, Finanzprocuratursbeamter; J. ü. Dr. Carl Koch, Bezirksgerichtsadjunct, und Adolf Heißler,
696 Sudmeister in Brünn.]

697

698 (Extract from the minutes of the meeting)

699 Professor G. Mendel gave the announced lecture on plant hybrids. He gave as an introduction a brief 700 historical review of the most important observations and experiments in regard to plant 701 bastardization. Subsequently, he presented his own numerous and carefully and successfully 702 conducted experiments that partly agreed with previous observations and partly disagreed. From his 703 experiments, he drew several very interesting and important conclusions. The observations were 704 mainly made on Papilionaceous plants (a family that according to well-known researchers is not well 705 suited for hybridization) and continued for a number of years and numerous generations. The results 706 were so favorable that a number of mathematical formulas for the laws of hybridization could be 707 deduced from them with reasonable accuracy. The lecture was illustrated with numerous samples 708 (especially on fruits and seeds).

709

## 710 III. First lecture article in the Märischer Correspondent, February 10, 1865.

[Der gestrigen Versammlung von 9 Februar war ziemlich zahlreich besucht. Der Sekretär, Med. Dr.
Kalmus, berichtete zuerst über die Einlaufe seit der letzten Sitzung; unter den letzteren befanden sich
auch 1500 Exemplare Conchylien, welche dem Vereine von Herrn Ullepitsch in Kärnten geschenkt
wurden, und 4000 geordnete Pflanzen-Exemplare welche ein Geschenk des hierortigen Apothekers
Herrn Theimer sind.] Hierauf hielt Hr. Realschullehrer P. Gregor Mendel einen Vortrag über die
Künstiche Befruchtung der Pflanzen und theilte die gelungenen Resultate seiner Versuche auf diesem
Gebiete mit.

Subsequently, *Herr* high school teacher P. Gregor Mendel gave a lecture about artificial fertilization in
plants and communicated the successful results of his experiments on this subject.

## 721

## IV. Second lecture article in *Neuigkeiten* March 10, 1865.

722 Sitzung des naturforschenden Vereins. Brünn 8. Marz,

723 Nach Eröffnung der Sitzung durch den Vizepräsidenten Theimer und Mitteilung der seit der letzten 724 Versammlung eingegangenen Geschenke und Sendungen hielt Herr Professor G. Mendl seinen zweiten 725 Vortrag über Pflanzenhybriden, Anknüpfend an die bezüglichen Mittheilungen in der letzten 726 Vereinsversammlung am 8. V. M. sprach er über Zellenbildung, Befruchtung und Samenbildung 727 überhaupt und bei den hybriden insbesondre unter Hinweisung auf sein bei Pisum (Erbse) mit eben so 728 viel Umsicht, als Erfolg angestellten Versuche, welche er auch im nächsten Sommer fortzusetzen 729 erklärte. Zum Schlusse theilte er mit, das er auch mit vielen anderen, namentlich angezeigten, 730 stammverwandten Pflanzen künstliche Befruchtungen zur Erzielung von Bastarden in den letzten 731 Jahren vorgenommen habe, und sich durch die erlangten günstigen Resultate aufgemuntert fühle, derlei Bastardierungen nicht nur weiter zu versuchen, sondern auch hierüber eingehende Berichte zu 732 733 erstatten. Diesem mit vielfacher Anerkennung belohnten Vortrage fugte Herr Professor v. Niessl bei, 734 dass auch von ihm bei Pilzen, Mosen und Algen mit Hilfe des Mikroskopes Hybridisationen beobachtet 735 worden seien, und dass weitere diessfällige Beobachtungen nicht nur bisherige Hypothesen 736 begründen, sondern auch weitere interessante Aufklärungen bringen werden.

737

738 Translation by Olby and Gautrey (1968):

After the opening of the meeting by the Vice-President, Herr Theimer, and the notifying of the gifts and communications received since the last meeting, Herr Professor G. Mendel gave his second lecture on plant hybrids. Taking up the thread of last month's lecture he spoke about cell formation, fertilisation and seed production in general, and in the case of hybrids in particular, alluding to his experiments undertaken with as much care as success, which he declared he would continue next summer. At the end he said that in the last few years he had also undertaken artificial fertilisations with many other related plants, which he named, in order to raise hybrids, and he felt encouraged by the favourable results achieved not only to experiment further with such hybridisations, but also tooffer detailed reports.

Herr Professor von Niessl added to this lecture which was very well received that with the aid of the
microscope he had observed hybridisations in fungi, mosses and algae, and that further observations
of this kind not only supported existing hypotheses but will also give further interesting clarifications.

- 751
- 752

## V. Second lecture article in the *Brünner Zeitung*, March 20, 1865.

753 Monats-Versammlung des naturforschenden Vereins in Brünn am 8. März 1865.

754 (Auszug aus dem Sitzungsprotokolle)

755 [Der Sekretär Dr. Kalmus erstattete Bericht über die seit der letzten Monatsversammlung 756 eingelaufenen Geschenke. Unter denselben sind namentlich eine reiche Sammlung russischer und 757 französischer Pflanzen von dem Mitgliede Herrn Dr. Paul von Kühlewein, k. russischen Collegienrathe, 758 ferner Mineralien und Bücher von demselben und Herrn C. Bauer, die neuesten Hefte der Bryotheca 759 europaea, von dem Herausgeber Herrn Dr. Ludwig Rabenhorst in Dresden und eine Collection 760 Arachniden von Herrn Julius Mueller, hervorzuheben.] Herr Professor G. Mendel beendete seinen 761 Vortrag über Pflanzenhybriden. Derselbe besprach die Ansichten über die Bildung und das Entstehen 762 derselben, sowie die Kreuzung, Vermehrung und Fortpflanzung derselben. Nach einer übersichtlichen 763 Darstellung der neuesten Ergebnisse der Untersuchungen über die Entstehung und Entwicklung des 764 Pflanzenkeimes im Allgemeinen, suchte der Vortragende dieselben bei der Bildung der Hybriden zu 765 verwerthen und stellte in Bezug auf die bei diesem Acte wirksamen Factoren eine Hypothese aus, 766 welche durch eine große Anzahl sinnreicher, vom besten Erfolge gekrönter Versuche getragen, nicht 767 wenig zur Aufklärung dieses bisher noch ungenau beobachteten Processes beitragen dürfte. Herr 768 Professor Mendel gedenkt seine Untersuchungen über diesen Gegenstand fortzusehen und seiner Zeit 769 das Resultat der selben in einer im Jahreshefte des naturforschenden Vereines zu veröffentlichenden 770 Arbeit bekannt zu geben.

772 (Extract from the minutes of the meeting)

773 Professor G. Mendel finished his lecture on plant hybrids. He discussed the views on their origin 774 and formation, as well as the cross-fertilization, multiplication, and reproduction of hybrids. The 775 lecturer clearly reviewed the most recent research findings on the genesis and development of the 776 plant germ in general and sought to apply them to the formation of the hybrids. He developed a 777 hypothesis concerning the factors involved in this process, which, confirmed by a large number of 778 meaningful and highly successful experiments, could significantly contribute to the elucidation of this 779 hitherto inaccurately observed process. Professor Mendel intends to continue his investigations into 780 this subject and publish the results in a paper published in the proceedings of the Natural Science 781 Society.

782

## 783 VI. Second lecture article in *Märischer Correspondent* March 11, 1865.

Auf der Tagesordnung stand ein Vortrag des Herrn Realschullehrers P. Gregor Mendel über PflanzenHybriden. Ehe derselbe den von ihm angekündigten Vortrag hielt, sprach er über die Zelle und über die
Fortpflanzung der Gewächse durch Befruchtung. Die Versammelung war diesmal wegen der
ungunstigen Wetters nur schwach besucht.

On the agenda was a lecture by the real school teacher P. Gregor Mendel about plant hybrids. Before he gave his lecture, he spoke of the cell and of the reproduction of the plants by fertilization. The gathering was only weakly visited this time because of the unfavourable weather.

791

## 792 VII. Original German text (Oborny, 1922)

793 Unter seinem engeren Freundeskreis in der Heimat fand sich niemand, der sich mit biologischen 794 Studien beschäftigt hatte. Die Botaniker wie auch Zoologen waren durchwegs Systematiker und 795 mancher von ihnen dürfte sich gewundert haben, dass Mendel sich nur mit dem engen Kreise einiger 796 Kulturgewachse, wie Erbsen, Bohnen, Aquilegia, Dianthus und Nicotiana-Arten wie auch nur mit 797 wenigen wildwachsenden Pflanzenarten so eingehend beschäftigt hat. Among his close circle of friends at home, nobody had been involved in biological studies. The botanists and zoologists were mainly taxonomists, and many of them will have been astonished that Mendel restricted himself to the narrow range of some cultivated species, such as peas, beans, *Aquilegia, Dianthus,* and *Nicotiana* species, and to a few wild species.

- 802
- 803

# VIII. Possible influences from Nägeli (1865) on Mendel's 1866-paper

804 The underlined and numbered sentences in Mendel's and Nägeli's papers correspond.

805

806 Mendel (2016, p 38):

## 807 Concluding Remarks, first paragraph

808 It might not be without interest to compare the observations made in Pisum with the results 809 that the two authorities in this area, Kölreuter and Gärtner, arrived at in their researches. According 810 to the concurring view of both, hybrids either keep the middle form between the parent-species with 811 regard to external appearance, or they approach the type of one or the other, sometimes being hardly 812 distinguishable from the same. From the seeds of these hybrids, if fertilisation happened through their 813 own pollen, various forms usually originate that deviate from the normal type. As a rule, the majority 814 of individuals resulting from a fertilisation retain the form of the hybrid, whilst a few others become 815 more similar to the seed plant and one or the other individual comes close to the pollen plant. This is 816 however not valid for all hybrids without exception (1). With some individual hybrids the descendants 817 partly approach one, partly the other parental plant more closely, or they lean more towards one or 818 the other side all together; but in some, they remain perfectly similar to the hybrid, and propagate 819 themselves without being changed (2). The hybrids from varieties behave just like species-hybrids, 820 except that they possess even greater mutability of conformations (3) and a more pronounced 821 tendency to revert to the parental forms (4).

822

824 Nägeli (1865, p438-432):

825 Final paragraphs

826 9. In general, the hybrids in the first generation [F1] vary less the further apart the parental forms are 827 in the kinship, i.e., the species hybrids less than the variety hybrids; the former are often characterized 828 by great uniformity, the latter by great diversity (3). When the hybrids are self-fertilising, the variability 829 increases in the second and succeeding generations the more completely it is lacking in the first; and 830 indeed, the farther apart the ancestral forms are, the more certain three different varieties appear, 831 one corresponding to the original type, and two others which are more like the ancestral forms. But 832 these varieties have little constancy, at least in the next few generations; they easily transform into 833 each other. <u>A real reversion to one of the two parent forms (in the case of pure inbreeding) takes place</u> 834 primarily when the parent forms are very closely related, i.e., in the hybrids of varieties and variety-835 like species (4) [as Mendel had found albeit with reversion to both parental forms]. When it occurs in 836 other species hybrids, it seems to be confined to those cases where one species has exerted a greater 837 influence in hybrid fertilization.

The variability of the hybrids, i.e. the variety of forms belonging to the same generation, and their behavior in single or repeated reproduction by self-fertilization, constitute two points in the theory of hybridization which are as yet least established, and which also seem to be least subject to fixed rules.

The hybrids of the varieties are exceedingly apt to vary (3). [apparently Nägeli refers to varieties that are not true breeding] When one variety is fertilized by another, the progeny are often so varied and polymorphic that no plant resembles any other perfectly. Therefore, hybrid pollination within species is often employed by gardeners to obtain new forms. If the variety hybrid reproduces by inbreeding, the variety increases in the following generations; at the same time, however, some individuals revert to the parent varieties. The hybrid form degenerates, as the gardeners say.

848 <u>However, this does not apply to all variety hybrids</u> (1) [Mendel used almost the same 849 sentence]. There are also those that are still uniform in the first generation and only become variable in the following [variable hybrids between true-breeding parents; *Pisum*], <u>and those that retain their</u>
uniformity through several generations (2) [constant hybrids; *Hieracium*].

Among the species hybrids there are also those which show a marked variability even in the first generation. These are especially those which descend from very closely related species, such as the hybrid of *Lychnis diurna* Sibth. and *L. vespertina* Sibth.

855 The least variability is found, as a rule, in the hybrids of those parental species which are 856 mutually related. If these hybrids are fertile, they will produce offspring with greater diversity, which 857 can increase in the following generations. The change first affects the flowers, but then also the other 858 organs and the whole habitus. Varieties are formed. Among them, one retains the (intermediate) type 859 of the original hybrid form (A+B), a second approaches one parent species (A), a third the other parent 860 species (B). One of the last two can be absent, or both. In the latter case the original hybrid form 861 remains uniform and constant. This is observed e.g., in some very fertile Dianthus hybrids (2) 862 [Mendel's constant hybrids].

If a second-generation species hybrid with some individuals has more closely approximated one progenitor (A), the offspring of the same (third generation) may be even more similar to that progenitor A. However, they can also change back to the original type (A+B) or, in rarer cases, even to the opposite, in other words they can approach the other parent species (B).

867 As we have just seen, the species hybrids approach the parent species as individual varieties in the 868 course of the generations. However, whether they really achieve them and whether they can, as they 869 say, return to the parental species (zurückschlagen) still needs to be confirmed. In the case of the 870 variety hybrids, however, the complete return is a fact (4); it occurs irregularly and in leaps and bounds. In the case of the species hybrids, an irregular and abrupt changeover of their varieties into 871 872 one another is observed. In any case, there is no question of a constant approximation to a parent 873 species through a series of generations. Incidentally, Gartner also claims that the reversion is merely an exceptional phenomenon that affects only a few species hybrids and among these only a few 874 875 individuals.

#### 877 Endnotes

<sup>1</sup> Iltis' narrative contains some obvious errors, such as that Mendel's friend Johann Nave was one of the attendants. However, Nave had died from tuberculosis two months before the meetings. The 1966-English translation of Iltis (1924) erroneously mentions that "at the very same [first] meeting Alexander Makowsky......referred with the utmost enthusiasm to Darwin's theory of the origin of species", and that this "must have held the minds of biologists captive." Therefore, people would not trouble themselves to make a place in their minds for the profound and peculiar ideas of Mendel". However, Makowsky's lecture on Darwin's theory was in January, not in February.

<sup>2</sup> We searched in the following databases: DIFMOE (Digitales Forum Mittel- und Osteuropa;

<u>https://www.difmoe.eu/</u>), the Digital Library of the Moravian Library (<u>https://www.digitalniknihovna.cz/mzk</u>) and ANNO (AustriaN Newspaper Online; <u>https://anno.onb.ac.at/</u>)

<sup>3</sup> "I am no longer very fit for botanical field trips, for heaven has blessed me with an excess of avoirdupois, which becomes very noticeable during long travels afoot, and, as a consequence of the law of general gravitation, especially when climbing mountains." (6-10-1867, p12 PITERNICK AND PITERNICK, 1950)

<sup>4</sup> 33%, followed by civil servants with 16%, doctors with 14%, technicians and chemists 8 %, and lawyers with 6%.

<sup>5</sup> "The pharmacist Carl Theimer spoke about the formation of *Bastards* in the plant kingdom and showed a *Bastard* plant *Cirsium praemorsum* Michl (*Cirs. Oleraceo-rivulare* Dc), which was new to Moravia and which he discovered near Adamsthal in August 1861, as well as *Cirsium cano-oleraceum* Koch known earlier from the Moravian flora. At the end of the lecture, the speaker remarked that infertility ascribed to the *Bastard* plants has not been confirmed in recent experiments with various *Bastard* plants and that these *Bastards* often produce germinable seeds". (ANONYMOUS 1863)

<sup>6</sup> In the second letter to Nägeli he mentioned the importance of not presenting every detail (18-04-1867, p 5 PITERNICK AND PITERNICK 1950)

<sup>7</sup> It is sometimes suggested that the algebra was too complex for the listeners, but combination theory and the binomial were standard elements of *Realschule* curriculum. Its application in biological processes, however, was indeed new.

<sup>8</sup> This is in contrast with Iltis (1924) who wrote that that the second meeting in March was well attended.

<sup>9</sup> This characterization goes back to third-hand information from Richter (1941): "after an oral statement by Professor Makowsky to Hugo Iltis, from which Professor Dr. A. Fietz informed me" (*Nach einer mündlichen Äußerung H. Professors Makowsky and Hugo Iltis, von der ich durch Herrn Dozenten Dr. A. Fietz erfuhr*; p132).

<sup>10</sup> Bell's paragraph continues: "it is only at remote intervals that we can reasonably expect any sudden and brilliant innovation which shall produce a marked and permanent impress on the character of any branch of

knowledge or confer a lasting and important service on mankind. A Bacon or a Newton, an Oersted or a Wheatstone, a Davy or a Daguerre, is an occasional phenomenon, whose existence and career seem to be especially appointed by Providence, for the purpose of effecting some great important change in the condition or pursuits of man."

<sup>11</sup> That Mendel was not a botanist in the sense of a taxonomist/florist is also clear from his absence from the list of 274 living Austrian botanists that was published in the *Oesterreichische botanische Zeitschrift* in 1862. In contrast, eight other members of the NSS, including Alexander Makowsky, Johann Nave, Gustav von Niessl, and Carl Theimer, were on this list (ANONYMOUS 1862).

<sup>12</sup> "Die überreichte Abhandlung ist eine ungeänderte Abdruck des Conceptes für den erwähnten Vortrag…"

<sup>13</sup> Ich unterlasse es, auf andere Punkte ihrer Mittheilungen einzugehen, da ich ohne die Versuche, die denselben zu Grunde liegen, in allen Einzelheiten zu kennen, doch nur vermutungsweise sprechen könnte. (Hoppe 1971)

<sup>14</sup> Although Nägeli's lecture was held ten months after Mendel's lectures, it is unlikely that Nägeli knew about Mendel's work since besides, in the local newspapers, there were no accounts published.

<sup>15</sup> Fairbanks and Abbott (2016) have shown by text analysis that the part of the 1866-article preceding the Concluding Remarks session contains many words from the German 1863 translation of Darwin's Origin of species. Sometimes, in his 1866-paper, Mendel copied expressions from other authors. For example, the strictest definition of a species that Mendel gives in the introduction is literally from Schleiden (1846): "If one wanted to apply the strictest definition of the species concept, according to which only those individuals belong to one species which under entirely identical circumstances also exhibit entirely identical traits,....." (MENDEL, 2016 p6). ("Wollte man die schärfste Bestimmung des Artbegriffes in Anwendung bringen, nach welcher zu einer Art nur jene Individuen gehören, die unter völlig gleichen Verhältnissen auch völlig gleiche Merkmale zeigen, so könnten nicht zwei davon zu einer Art gezählt werden."(p6). Schleiden (1846) wrote: To one species belong all individuals who exhibit, independent of time and place, and under the same circumstances, precisely the same characters." ("Zu Einer Art gehören alle Individuen, die, abgesehen von Ort und Zeit, unter völlig gleichen Verhältnissen auch völlig gleiche Merkmale zeigen." (p518). Also, the phrase in the introduction of the 1866-paper "To this task, careful observers such as Kölreuter, Gärtner, Herbert, Lecoq, Wichura and others have sacrificed part of their lives with untiring endurance" (MENDEL 2016, p3), "Dieser Aufgabe haben sorgfältige Beobachter, wie Kölreuter, Gärtner, Herbert, Lecocq, Wichura u. a. einen Theil ihres Lebens mit unermüdlicher Ausdauer geopfert."), maybe based on Nägeli (1866) ("who devoted the work of their lives to solving this problem, "die die Arbeit ihres Lebens auf die Lösung dieses Problems verwendeten.", p398) or the German translation of Darwin (1863) ("who have devoted almost their whole lives to this subject; "welche fast ihr ganzes Leben diesem Gegenstande gewidmet haben." (p275).