REMARKS ON MENDEL'S MATHEMATICS

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Abstract
Mendel's seminal paper Versuche über Pflanzen-Hybriden *has been studied thoroughly from many aspects and in all manner of contexts. However, mathematics and the mathematical context to Mendel's work seem to have received only superficial attention. In this paper we concentrate exclusively on Mendel's mathematics. We treat this aspect of Mendel's work in its full complexity, both in its historical context and from the point of view of present-day mathematics, and give consideration to Mendel's education, mathematical knowledge, and influences. We believe that in mathematics lies the key to resolving some of the enigmas that remain over Mendel's work.*

Introduction

Mendel's paper *Versuche über Pflanzen-Hybriden*[0] was published in 1866. It reports on experiments with peas (*pisum* in Latin) and therefore we will refer to it as the *Pisum* paper. The *Pisum* paper was based on two lectures given in 1865 for the Natural Science Society in Brno (Der naturforschende Verein in Brünn). The dates are very important and so is the place: Brno, capital of Moravia, one of the two Czech lands, was during the 19th century part of the Austrian (since 1867 Austro-Hungarian) Empire. Mendel himself was a member of the prestigious Augustinian monastery of St. Thomas in Brno, a monastery with a long tradition and centre of cultural and educational activity in Brno and the whole of Moravia. Mendel's membership of this distinguished society lasted from 1843 until his death in 1884. He became a respected personality among his peers, was elected abbot (in 1868) and also accepted other public responsibilities (chairman of a bank etc.). This limited his time toward the end of his life. He was considered a wise man in a circle of wise people. All this is well documented in the literature and we refer to the books of Iltis[1], Orel[2], Olby[3] and more recently of Klein[4], to name just a few. And there was another, very special side to Mendel's personality: From 1854 to 1865 and even after, but more sporadically, he performed one of the largest biological experiments of the 19th century. On the premises of the monastery (and in the greenhouse which he later had built) he treated more than 25,000 plants in a well controlled and systematically organised way. His experiment was revolutionary, both in its design and its outcome. It was so revolutionary that Foucault in his famous inaugural address at the Collège de France called Mendel a "monster" not "living in the truth."[5] Mendel was not understood by his contemporaries. His work had to wait another 34 years before it was independently rediscovered in three places. Then Mendel's work became famous almost instantly. It was only a matter of ten years before a life-sized statue of him was erected in Brno (now situated in the garden of St. Thomas Monastery). "My time will come," Mendel assured one of his friends,[6] and this is what happened. Well, a little later…

Mendel became the father of genetics, one of the principal branches of modern science. Genetics has brought and continues to bring some of the most spectacular scientific results of modern history, and has had a profound impact on our lives. These claims are documented by many sources and for the purpose of this paper it is not necessary to repeat them. We just remark that recently M. Gromov, a leading scientist of our day, included Mendel in his list of greatest thinkers of all time. This alongside Plato, Aristotle, Newton, Darwin, Gödel, Einstein, …[7]

In Mendel's case (as well as in the cases of some of the other great men just mentioned) the major breakthroughs were highly concentrated:

- Mendel wrote a single (1866) paper,
- his discovery was singular and seminal,
- his discovery was isolated in time and space, its priority indisputable.

This is nicely formulated in the laudatory address of de Beer at the centenary of the *Pisum*: "It is not often possible to pinpoint the origin of a whole new branch of science accurately in time and space … But genetics is an exception, for it owes its origin to one man, Gregor Mendel, who expounded its basic principles at Brno on the 8th February and on the 8th March 1865." [8] What makes Mendel's paper so singular, so novel, so revolutionary? What are its origins?

There are numerous answers to this question and discussion is particularly abundant in the biological literature. "Each generation, perhaps, found in Mendel's paper only what it expected to find; in the first period a repetition of the hybridisation results commonly reported, in the second a discovery of inheritance supposedly difficult to reconcile with continuous evolution. Each generation, therefore, ignored what did not confirm its own expectations." [9]

The biological literature related to Mendel is extensive. The history of genetics is treated in many books and nearly all of them discuss Mendel's work. But not only that, the *Pisum* paper is truly a landmark of science in general and as such it has been and it continues to be investigated and scrutinised from all possible angles and in many different contexts. To name just a few: genetics,[10] history,[11] history of science,[12] rhetoric,[13] sociology,[14] semiotics,[15] even (good) comics and catalogues.[16] It is therefore surprising that one of the striking aspects of the *Pisum* paper — namely its mathematical contents, its mathematical style and, yes, its mathematical elegance and rigour — seems to be absent in the existing literature.[17] We would like to make this hiterto overlooked aspect the subject of our paper (and of its companion paper[18]). What we would like to document is the extent and quality of the mathematical content of the *Pisum* paper in the context of Mendel's time as well as in the the context of present-day mathematics. The paper consists of the following parts:

1. Easy mathematics of structural change.
2. Counting, probability and trees.
3. Mendel’s semiotics.
4. Mendel’s algebra.
5. Mathematical experience and influences.
6. Final remarks.
7. References and comments.

We treat Mendel’s mathematics in the full complexity of its time (pointing to new high school curricula sources), providing new evidence and comments on Mendel’s education and influences (in particular highlighting the influence of Ettingshausen’s book on combinatorics). We illustrate our findings by analysing Mendel’s possible approaches to generation counting (Section 2) and Mendel’s algebraic “Gesetze” (Section 4), thus contributing to the “*AA* vs *A*” debate by giving new mathematical aspects. It is here where we point to some very recent mathematics evolving and inspired by Mendel’s ideas. In Section 5 we comment on possible Mendel’s mathematical knowledge both from his studies and from his teaching. Particularly we want to reverse the traditional opinion that Doppler (as opposed to Ettingshausen) was a prime source for Mendel’s mathematics. The paper ends with final remarks and bibliography with comments.

1. Easy mathematics of structural change

It has been stressed in many places that one of the fundamental novelties of the *Pisum* paper was its use of mathematics and statistics. However statistics had been mentioned by other researchers even earlier. Other people before Mendel had counted ratios of hybrids and species in general. Moreover, Mendel’s statistics was subject to speculative criticism (which started with R.A.Fisher and continues busily until this day[19]). Thus we will not consider the statistical aspects of Mendel’s work here. However, the mathematical aspects are a very different story. On the one hand, the mathematics of the *Pisum* paper is simple, or, better, it seems to be simple. We are going to comment on it in depth in this paper and we hope to demonstrate that it is worth investigating both the explicit and the implicit mathematics in Mendel’s paper, from an historical as well as a factual point of view. But there is more to it than meets the eye. Exactly because, per se, the mathematics of the *Pisum* paper is simple, the weight of importance is to be shifted to the context of how and for what purpose the mathematics is used. The context has to be revolutionary: a change of paradigm, a change of concepts, a change in the whole conceptual structure. As an example, just imagine that one would like to support a new theory by Euclid's postulates. Or by elementary graph theory. Yes, it is (very rarely) possible, but then interpretation and context play a pivotal role in such situations. The world cannot be changed by simple mathematics alone, but even simple mathematics can help to turn attention in a new direction, and by this change the viewpoint taken.

This is exactly what Mendel did:

- he turned attention to details, to isolated characteristics, which he treated as individual units;
- he turned attention to local aspects: how characteristics are transmitted from one generation to another;
- he brought rigour and exactitude to a subject which previously had been woolly, inexact.

His sensitivity and great courage to follow the magic provided by mathematics is overwhelming. Take for example his famous ratio 3:1. Where in the whole of nature can we find such simple *integral* parameters? Of course, Mendel did not find *exactly* such a ratio, as it varied from experiment to experiment: sometimes it was 3.15:1, sometimes 2.95:1, or 2.82:1, sometimes 3.14:1 (see the *Pisum* paper). Where did Mendel find the courage to set it just to 3:1? Why not 3.14 ($\doteq \pi$) or 2.72 ($\doteq e$) or even $\frac{1}{2}(e+\pi) \doteq 2.92993724$, which all seem to be more reasonable „natural" constants? *Why should nature choose an integer?* This is the true magic and the true genius of Mendel (and, of course, a key case in the discrete versus continuous, or Mendel–Darwin debate). And whenever we come across magic, we seek an explanation, and Mendel found it. Mathematics gave him the clue and provided the golden thread in the darkness. It is fitting to quote here C. Stern and E.R.Sherwood (1966): "Gregor Mendel's short treatise '*Experiments on Plant Hybrids*' is one of the triumphs of the human mind. It does not simply announce the discovery of important facts by new methods of observation. Rather, in an act of highest creativity, it presents these facts in a conceptual scheme which gives them general meaning. Mendel's paper is not solely a historical monument. It remains alive as a supreme example of scientific experimentation and profound penetration of data." [20]

In doing so, Mendel really stands apart along with Galileo, Newton, Einstein and others. No doubt his contemporaries were not impressed, particularly as there was another revolution in progress: Darwin's theory of evolution. To reconcile these two theories took another sixty years (as nicely described by any of the books already cited above). It is often said that Mendel's "rediscovery" had to wait for thirty years. However, an interesting detail (which seems to be generally overlooked) is quoted in V. Orel book: In 1902 the *Verhandlungen des naturforschende Vereins in Brünn* (i.e. in the same journal where the *Pisum* appeared) printed a report on its annual meeting. It contains the following lines (admittedly defensive lines from Mendel's colleagues):

"It is not correct to state that Mendel was "rediscovered" only now. His works were well known, but were obscured in the context of others, at those times more accepted theories." [21]

An interesting and speculative question is why Darwin did not discover Mendel laws.[22] Darwin was not just philosopher of evolution, he, in fact, conducted research with plants and counted ratios (later than Mendel). And with Primula auricula he arrived (implicitly) to 3:1 ratio. However, as nicely formulated in an article by Howard,[22] "Darwin was in no way programmed to see the critical meaning in these numbers." Yes, life is simply — mathematics is simple — just 3:1. But what a courage.

2. Counting, probability and trees

The mathematics of the Mendel's principal opus is easy to describe. Only on p.17 of the *Pisum* paper, after introducing all the necessary notions and presenting some experimental results, does Mendel start to employ mathematical notation, using A, a for (dominating and recessive) traits (now known as alleles) and gives various combinations AB, ABb, AaB, … etc. and their semantic meaning in his experiment. In the whole paper we only have expressions of the form $A + 2Aa + a$ and similar for more traits. The most complicated explicit expression is for three traits on p.22: $ABC + ABc + AbC + Abc + aBC + aBc + abC + abc + 2ABCc + 2AbCc + 2aBCc + 2abCc + 2ABbC + 2ABbc + 2aBbC + 2aBbc + 2AaBC + 2AaBc + 2AabC + 2Aabc + 4ABbCc + 4aBbCc + 4AaBCc + 4AabCc + 4AaBbC + 4AaBbc + 8AaBbCc$. Mendel calls this a "combination row" or a developmental (or evolutionary) series.[23] The combination of A and a is also denoted by $\frac{A}{a}$ (p. 30, the *Pisum* paper) and this is probably motivated by the famous diagram in Figure 1, (yes, Markovian)

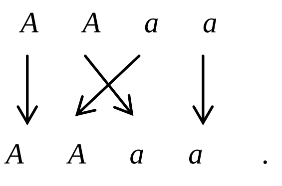


Figure 1. Mendel's diagram illustrating fertilisation

And formally, this is about all. No proofs, no mathematical explanation, not even for the iterative formula for n-generation hybrids on p. 18 of the *Pisum*. Could this be called a basis for a revolution? For an outsider (non-mathematician) this is perhaps too modest a contribution to warrant attention.

An investigation and thus discussion of the *Pisum* mostly concerns solely its biological aspects. However, the whole *Pisum* paper is written in a lucid, modest, yet exact "mathematical" style. (especially when compared with writing of contemporaries[24]). It is thus evident that the mathematical evidence cannot be bypassed so simply. And yes, there is more to see on the mathematical side itself. Each line has a history and an interesting (possibly important) context. Of course, primary sources are scarce, but every field of science (and mathematics particularly) has its logic of discovery.

Take, for example, the table of successive generations (Table 1) and counting of hybrids (*Pisum,* p. 18). Here Mendel verifies the statement of Gärtner and Köhlreuter that the hybrids seem to be few in subsequent generations. The key table and text look as follows (*Pisum,* p. 18). Mendel writes:

				put in proportion:				
Generation	*A*	*Aa*	*a*	*A*	:	*Aa*	:	*a*
1	*1*	*2*	*1*	*1*	:	*2*	:	*1*
2	*6*	*4*	*6*	*3*	:	*2*	:	*3*
3	*28*	*8*	*28*	*7*	:	*2*	:	*7*
4	*120*	*16*	*120*	*15*	:	*2*	:	*15*
5	*496*	*32*	*496*	*31*	:	*2*	:	*31*
n				$2^n -1$	:	*2*	:	$2^n -1$

Table 1. Distribution of Traits (Constant Dominating, Recessive and Hybrids) over Successive Generations

"In the tenth generation, for example, $2^n – 1 = 1023$. There thus exist among 2048 plants respectively that originate in this generation, 1023 with the constant dominating trait, 1023 with the recessive trait, and only 2 hybrids." Very nicely formulated. Probability is evident (and equiprobability of all forms assumed), but how did Mendel prove this? What possibly could have been his reasoning? Let us give it a try:

First proof (trees):
Let us assume with Mendel that each plant forms only four seeds in each generation. Among new plants which originate from those four seeds is exactly one with constant dominating trait *A*, one with recessive trait *a* and two are hybrids *Aa* (*Pisum*, p.18). This can be visualised by the genealogical tree in Figure 2.

Figure 2. Genealogical tree showing successive generations in the hybridisation process; hybrids (heterozygotes) are indicated by thin lines

In the above tree the hybrid descendants are indicated by thin lines. Note that according to careful selection by Mendel the descendants of constant traits (i.e. thick lines in the above scheme) are again constant traits. Thus in the n-th generation we have 4^n plants out of which 2^n are hybrids (i.e.descendants of the tree formed by thin lines) and $(4^n – 2^n)$ are constant traits *A* and *a* (in the equal amount). So the number of constant traits is $4^n - 2^n$ and thus the number of traits *A* is

$$\frac{1}{2}(4^n - 2^n) = 2^{2n-1} - 2^{n-1} \quad .$$

The number of traits a is also $2^{2n-1} - 2^{n-1}$ and the number of *Aa* hybrids is $2 \cdot 2^{n-1}$. By dividing by 2^{n-1} we obtain the Mendel's results and the ratio $2^n - 1 : 2 : 2^n - 1$, as claimed.

Well, perhaps easy to see in 1866, and perhaps even today. This is the proof Mendel could have had in mind. He was dealing with trees in various forms as we shall see shortly.

Second proof (probability):
For a given hybrid plant the probability that one of its fours seeds gives A-plant is 1/4, the probability of *a*-plant is 1/4 and the probability of *Aa* hybrid is 1/2. Thus, in the n-th iteration (n-th generation) the probability of obtaining hybrid is 2^{-n} (as hybrids descend only from hybrids). Thus probability of *A* is 1/2(1 - 2^{-n}) and the same is true for the probability of *a*. As the total number of plants in the (whole) n-th generation is $4^n = 2^{2n}$, we obtain the desired ratios.

Even this second proof could have been the one Mendel had in mind. There are still other possibilities. The proof could be, for example, obtained by summing up a geometric series, and even this might have been the one in Mendel's mind. But in each case this place in the *Pisum* indicates Mendel's mathematical fluency and skill.

There are no proofs in the *Pisum* paper. Why? Well, proofs somehow do not fit in to a biology paper. But there are other reasons. In the 19th century proofs were often omitted. Authors would claim a result and indicate just a few cases by which one could convince oneself of its validity. One might mention here Euler's formula and Cayley's formula as examples.[25] The closing sentence of the *Pisum* (above) perhaps indicates that the probabilistic proof was the closest one to Mendel's heart. However, the tree-proof (which could be also called a genealogical proof) is quite interesting. Tree and tree-like structures were, of course, known and understood from medieval times, and they also naturally appeared in botany and biology. For example, Wichura[26] uses many illustrations to express the range of possibilities of various combinations of hybrids. A typical example from Wichura's book is shown in Fig. 3.

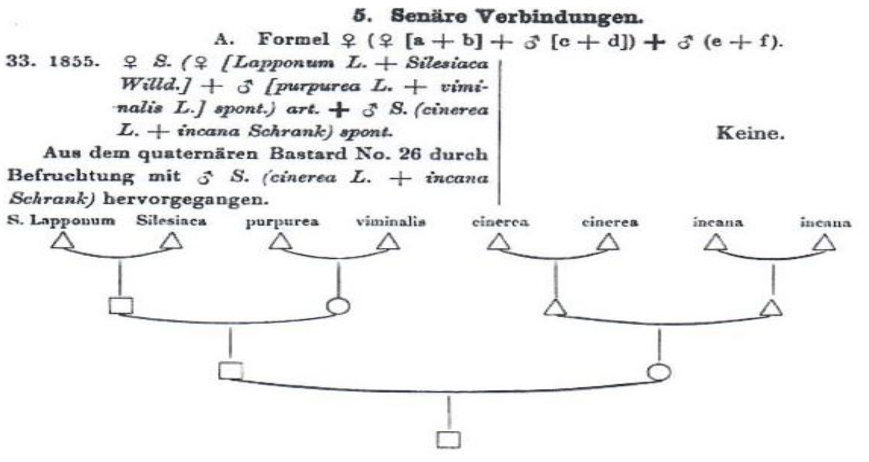
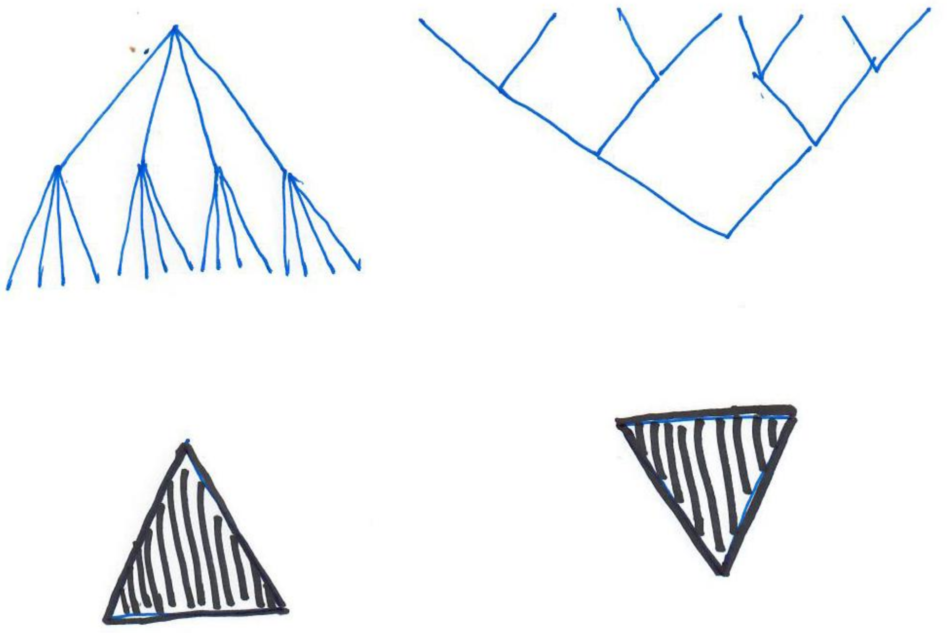


Figure 3. An example of a tree in Wichura's book[26], p. 21.

Wichura is quoted in the *Pisum* in a very respectful way ("… and most recently, Wichura published thorough investigations on the hybrids of willows.", *Pisum*, p. 3). What the schemata such as that of Fig. 3 mean is clear. If we compare the schema of Mendel's experiment, we see that Mendel flipped Wichura's trees. He started with a single (fully tested) hybrid and by self-fertilisation produced subsequent generations: in practice sometimes to the 7th generation, abstractly to the n-th generation. This is in the contrast to all previous research which started with plants gathered from nature and proceeded (in a controlled way and elaborately many types of cross-fertilisations). So in this respect one of the fundamental contributions of Mendel is that by isolating traits he flipped the tree. In mathematical terms, he considered the dual problem. We have tried to express this symbolically in Figure 4.



Mendel Kohlräuter, Gärtner, Wichura

Figure 4. The conceptual change in usage of genealogical trees by Mendel (compared to his predecessors)

This schema symbolises the radical change of perspective on the whole area.

While stating this, we wish to stress the contribution of Wichura. In 1851–1854 he studied hybrids of willows (following the research of Wimmer and Franz). Wichura reported on his investigations in 1853.[27] In this paper he is interested in the problem that hybrids seem to be just a small proportion of the population, and he stresses two facts:

(i) the problem could be solved by artificial crossing of plants,

(ii) he considers more complex combinations (not just binary) in the crossing process.

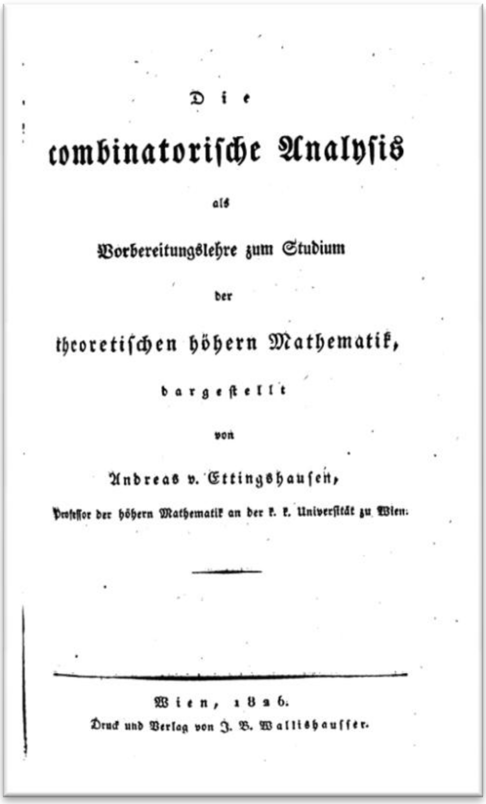
Wichura lists 6 basic types and divides them further into 10 sub-cases of concrete types of willow combinations (as in the example in Fig. 3). This Wichura (rightly) considers (in 1854!) as his main contribution. It seems that for these points one cannot find predecessors (of either Wichura or Mendel) and Wichura writes: "I believe that through these complicated hybrid forms on which formation take part more than two species, I brought a new contribution to the theory of hybrid fertilisation".[28] Yes, Wichura helped to prepare the stage for *combinatorial complexity*.

3. Mendel's semiotics

Let us add a few comments on Mendel's style, particularly on his notation — on the formal way in which he presented his results. From today's point of view (of mathematics and biology) there seems to be nothing special: Mendel uses capitals $A, B, C, \ldots$ and lower case letters $a, b, c, \ldots$, very few algebraical signs, and brackets. Nothing unusual. But 150 years ago the situation in biology was different and we may see here the key to Mendel's radical approach. For what is the meaning of A (and $a, B, b, \ldots$)? This is a single property, a single trait which Mendel isolated and then studied experimentally. Simple symbols $A, a, B, b, \ldots$ standing for colour, shape, height, … . This is not to be found anywhere in the texts of Mendel's contemporaries. Almost all botanists before Mendel use verbal descriptions of plants and never symbols as simple as letters.[29] We believe that this abstraction is one of Mendel's fundamental ideas. Where does this stem from? Where did Mendel find inspiration and encouragement for this? As we cannot find any sources in contemporary biology and botany, we have to look elsewhere, and where else should we look to but mathematics.

Mendel's education and experience in mathematics will be discussed in the sequel. Here we are interested in the formal symbolics – semiotics.[30] Of course, abstract symbols are abundant in mathematics. For combinatorics (as a part of mathematics) this holds too, but sources are much less frequent. Combinatorics can be traced back to antiquity (for example the Pascal Triangle is documented in China as early as around 1100),[31] however the more coherent development is related to the emergence of probability in the 17th and 18th centuries. And one of the first books dealing *entirely* with this emerging branch of mathematics is the book by Andreas von Ettingshausen published in 1826.[32] This is an interesting book with a title which is interesting even today *Combinatorial Analysis as Preparatory Science for Studies of Theoretical Higher Mathematics*. This book is not often quoted[33] and the importance of Ettingshausen is perhaps overlooked (in comparison with Dopppler; there is more about it in Section 5 below).

Ettingshausen's book could arguably be the first book dealing exclusively with combinatorics which has *combinatorics* in its title. It entered the history of mathematics by introducing the notation $\binom{n}{k}$ for binomial coefficient.[34] Ettingshausen's book is full of expressions similar in style to those in the *Pisum* paper. An example is shown in Figure 5.



Die

combinatorische Analysis

als

Vorbereitungslehre zum Studium

der

theoretischen höhern Mathematik,

dargestellt

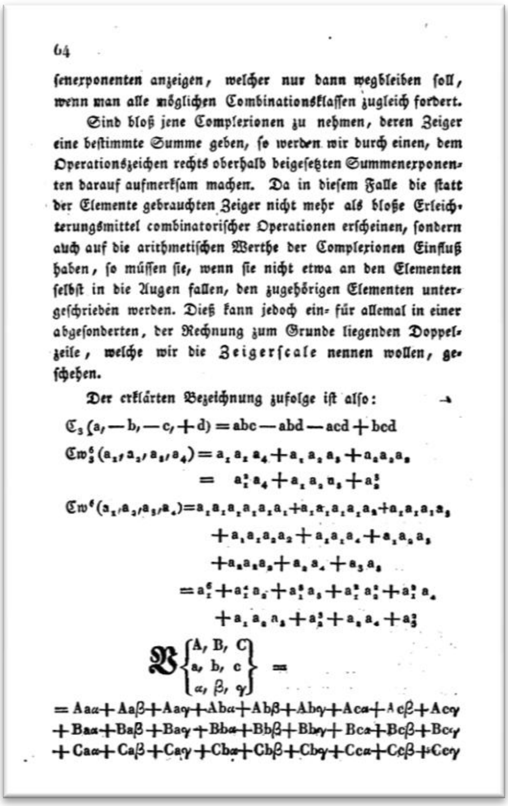
von

Andreas v. Ettingshausen,

Professor der höhern Mathematik an der k. k. Universität zu Wien.

Wien, 1826.

Druck und Verlag von J. B. Wallishausser.



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senexponenten anzeigen, welcher nur dann wegbleiben soll, wenn man alle möglichen Combinationsklassen zugleich fordert.

Sind bloß jene Complexionen zu nehmen, deren Zeiger eine bestimmte Summe geben, so werden wir durch einen, dem Operationszeichen rechts oberhalb beigesetzten Summenexponenten darauf aufmerksam machen. Da in diesem Falle die statt der Elemente gebrauchten Zeiger nicht mehr als bloße Erleichterungsmittel combinatorischer Operationen erscheinen, sondern auch auf die arithmetischen Werthe der Complexionen Einfluß haben, so müssen sie, wenn sie nicht etwa an den Elementen selbst in die Augen fallen, den zugehörigen Elementen unterschrieben werden. Dieß kann jedoch ein- für allemal in einer abgesonderten, der Rechnung zum Grunde liegenden Doppelzeile, welche wir die Zeigerscale nennen wollen, geschehen.

Der erklärten Bezeichnung zufolge ist also:

$$\mathfrak{C}_3(a, -b, -c, +d) = abc - abd - acd + bcd$$

$$\mathfrak{Cw}_3^6(a_1, a_2, a_3, a_4) = a_1 a_1 a_4 + a_1 a_2 a_3 + a_2 a_2 a_2$$
$$= a_1^2 a_4 + a_1 a_2 a_3 + a_2^3$$

$$\mathfrak{Cw}^6(a_1, a_2, a_3, a_4) = a_1 a_1 a_1 a_1 a_1 a_1 + a_1 a_1 a_1 a_1 a_2 + a_1 a_1 a_1 a_3$$
$$+ a_1 a_1 a_2 a_2 + a_1 a_1 a_4 + a_1 a_2 a_3$$
$$+ a_2 a_2 a_2 + a_2 a_4 + a_3 a_3$$
$$= a_1^6 + a_1^4 a_2 + a_1^3 a_3 + a_1^2 a_2^2 + a_1^2 a_4$$
$$+ a_1 a_2 a_3 + a_2^3 + a_2 a_4 + a_3^2$$

$$\mathfrak{V}\begin{Bmatrix} A, & B, & C \\ a, & b, & c \\ \alpha, & \beta, & \gamma \end{Bmatrix} =$$

$$= Aa\alpha + Aa\beta + Aa\gamma + Ab\alpha + Ab\beta + Ab\gamma + Ac\alpha + Ac\beta + Ac\gamma$$
$$+ Ba\alpha + Ba\beta + Ba\gamma + Bb\alpha + Bb\beta + Bb\gamma + Bc\alpha + Bc\beta + Bc\gamma$$
$$+ Ca\alpha + Ca\beta + Ca\gamma + Cb\alpha + Cb\beta + Cb\gamma + Cc\alpha + Cc\beta + Cc\gamma$$

Figure 5. Ettingshausen book[32], front page and p. 64

It may be that Ettingshausen's rigour and notational effectiveness attracted the young Mendel and in his mature years contributed to the style of his *Pisum* paper. We comment further on this in Section 5, restricting ourselves here to remarking that Ettingshausen's name was possibly a life-long companion for Mendel.[35]

4. Mendel's algebra

It is often said that Mendel was one of the first people to introduce combinatorial mathematics into biology (which is correct) and that he used the binomial formula. This second statement is not so clear, as we wish now to demonstrate and explain. Mendel gives immediately after defining *A*, *a* and *Aa* the expression

$$A + 2Aa + a\ . \tag{1}$$

This is often viewed as a consequence of binomial formula. Of course, by the rudimentary binomial formula,

$$(A+ a)\ \times (A+a)= AA + Aa + aA + aa,$$

and assuming commutativity of multiplication (i.e. $Aa = aA$) this is equal to

$$AA + 2Aa + aa\ . \tag{2}$$

Thus binomial formula or not? Various authors consider this question and they mostly interpret the difference between (1) and (2) as consisting in omission or shorthand notation.[36] We believe that this is the principal issue underlying the correct biological interpretation. Mendel does not speak about the binomial formula (which he surely knew), instead he speaks of "combinations" and "combination series". *Mendel does not multiply, he combines*.

The formula (2) relates to genes and is an expression of how zygots in the next generation will inherit genetic information. Note that $Aa = aA$ and thus the operation of combination is commutative as Mendel (and before him Gärtner) justifies in detail.

The *zygotic multiplication table* (Table 2) then reads as follows and this table (in freshmen biology course sometimes called the Punnett square) supports formula (2).

	A	*a*
A	*AA*	*Aa*
a	*aA*	*aa*

Table 2. Zygotic multiplication table

Formula (1) is not so easy. It suggests the *Mendelian multiplication table* (Table 3), which however combines heterozygots *Aa* with gametes *A, a*. So we still need some work on our formalism.

.

	A	a
A	A	Aa
a	aA	a

Table 3. Mendelian multiplication table

Let us now consider phenotypes (i.e. expressions of genes) and we think of A as dominant and a as recessive (dominating and recessive traits by Mendel). We obtain the *phenotype multiplication table* (Table 4).

	A	a
A	A	A
a	A	a

Table 4. Phenotype multiplication table

The phenotype multiplication table was surely in Mendel's mind and it is used throughout his paper. This multiplication table is known in mathematics (particularly in combinatorial optimisation) as *MAX algebra*. If we order alleles so that $a < A$, then this table can be summarised as

$$x.y = max\{x, y\} .$$

or, otherwise,

$$A.A = A$$
$$A.a = a.A = A$$
$$a.a = a .$$

We believe that any of these multiplications could be close to Mendel's experiment. But it is a fact that in the whole *Pisum* paper one cannot find expressions containing *AA* or *aa*. Mendel however did not speculate, and he explicitly stated that he did not do so in his letter to Nägeli.[37]

The fusion of gametes during reproduction may be seen as multiplication and this was investigated thoroughly by mathematicians in an algebraic and topological context. The above Table 3 takes form of the *gametic algebra* of Table 5.

	A	a
A	A	$\frac{1}{2}\,(A + a)$
a	$\frac{1}{2}\,(A + a)$	a

Table 5. Gametic algebra

Here $aA = \frac{1}{2}A + \frac{1}{2}a$ expresses the fact that each of the gametes *A* and *a* reproduces so that half of the offsprings will inherit *A* and half of the offsprings a.

We can use this multiplication table to define a 2-dimensional algebra (say over the real numbers, ℝ) generated by *A* and *a*. This is called the *gametic algebra* (for simple Mendelian inheritance with two alleles). This interesting algebra is commutative (and this was justified by Mendel) but not associative. For example

$$A \times (A \times a) = A \times \left(\frac{1}{2}A + \frac{1}{2}a\right) = \frac{1}{2}A + \frac{1}{2}\left(\frac{1}{2}A + \frac{1}{2}a\right) = \frac{3}{4}A + \frac{1}{4}a \quad ,$$

while

$$(A \times A) \times a = A \times a = \frac{1}{2}A + \frac{1}{2}a \quad .$$

Another possibility to interpret the Mendelian table (Table 3) is to consider it as a rudimentary zygotic multiplication table, as displayed in Table 6.

	AA	Aa	aa
AA	AA	$\frac{1}{2}(AA + Aa)$	Aa
Aa	$\frac{1}{2}(AA + Aa)$	$\frac{1}{4}AA + \frac{1}{2}Aa + \frac{1}{4}aa$	$\frac{1}{2}(Aa+aa)$
aa	Aa	$\frac{1}{2}(Aa+aa)$	aa

Table 6. Zygotic algebra

The coefficients in an expression such as $\frac{1}{2}A + \frac{1}{2}a$ are interpreted as the distribution of frequencies. This algebra (generated again by *A*, *a* over ℝ) is called the *zygotic algebra.* Arguably, this is closest to the *Pisum* paper. It could be called the *Mendel algebra.* Mendel was guided by phenotypes and was led to the combination of traits and to the rudiments of gametic and zygotic algebras. To quote Wynn[13], “This added rigour to his biological arguments that appealed to his early 20th century supporters for whom mathematically describable laws quickly became the gold standard for making arguments on evolution, heredity, and variation.”

Even without being explicite (whether gametic or zygotic) and mathematically unprecise, Mendel´s formalism became the „golden standard“ as it was consistent with further development. This is another „unreasonable effectivness“ of mathematics, this time in biology.[38]

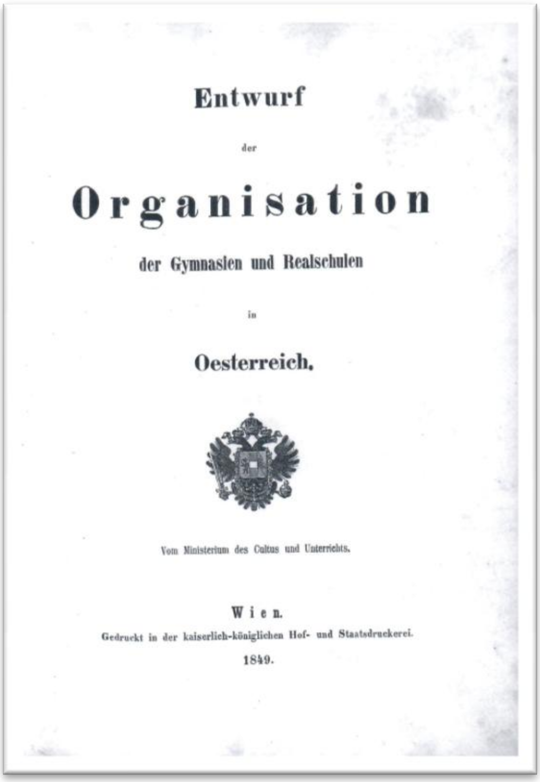
All the above algebras are interesting from the mathematical point of view. They have been generalised to a whole variety of algebras (such as “special train” algebras, “genetic” algebras, “train” algebras, “baric” algebras, etc.). Such algebras have been studied since 1939 from mathematical point of view by I. M. Etherington, R. D. Schafer, H. Gonshor. See the survey by M. L. Reed.[39]

The present-day setting of Mendel’s discovery is strikingly broad and mathematically relevant. It is interesting to note that while in biology researchers seem to concentrate on aspects of “what Mendel did not know,” mathematicians are finding broader and, yes, deeper part of mathematics related to and inspired by Mendel’s work. The fact that M. Gromov[40] relates Mendel to *Mendelian dynamics* is a simply magnificent development of which Mendel and the whole of biology should be proud. However, to go into more detail on this topic lies beyond the scope of this paper.

5. Mathematical experience and influences

What knowledge did Mendel have of mathematics? In the *Pisum* paper he displays great fluency and a superb command of the mathematical organisation of the whole paper. To quote R. C. Olby[10]: “No careful reader of his paper [*Pisum*] can come away without being deeply impressed with the precision of his language.” So what did he actually know?

Mendel obtained a sound rural elementary education and because of his recognised talents he continued at the gymnasium in Opava (1834 – 1840). Then during 1840 – 1843 he was a student at the Philosophical Institute in Olomouc (which was part of the University in Olomouc in those years). Mendel excelled at all of these institutions. Thanks to his brilliance he was recommended (by his Olomouc physics teacher F. Franz) to the Augustinian monastery in Brno. So Mendel’s education was very sound and long. After joining the Augustinians he obtained further education there and became a teacher at a gymnasium in Znojmo (1849 – 1850) and later in Brno (1851). Secondary education (i.e. gymnasium or Realschule, corresponding to high school) was a prestigious education in the 19th century and this is where the church (and Brno’s Augustinians) were active. Mendel was by any standard an educated man living in a milieu of scholars. This was not changed by the fact that Mendel twice failed (partly due to his fragile psyche) in passing an examination at the University in Vienna for becoming fully qualified as a high school professor. This examination covered different areas of the natural sciences (physics, geology, botany, zoology) but did not include mathematics. Mendel’s teaching activity can be seen as a further contribution to his education as the high school curricula were quite involved. The curriculum in Austria was centrally organised and compulsory educational plans were published in 1849 (perhaps as a reaction to the revolutionary year 1848) and again in 1889 without much change.[41]



Entwurf

der

Organisation

der Gymnasien und Realschulen

in

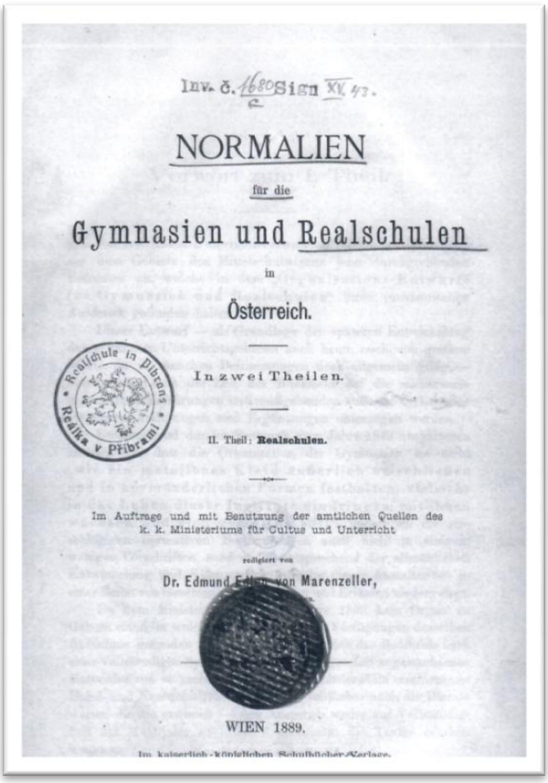
Oesterreich.

Vom Ministerium des Cultus und Unterrichts.

Wien.

Gedruckt in der kaiserlich-königlichen Hof- und Staatsdruckerei.

1849.



NORMALIEN

für die

Gymnasien und Realschulen

in

Österreich.

In zwei Theilen.

II. Theil: **Realschulen.**

Im Auftrage und mit Benutzung der amtlichen Quellen des k. k. Ministeriums für Cultus und Unterricht

redigiert von

Dr. Edmund [illegible] von Marenzeller,

WIEN 1889.

Im kaiserlich-königlichen Schulbücher-Verlage.

Figure 6. Front covers of the compulsory educational plans in Austria, 1849 and 1889 editions

The 1849 edition of the educational plans contains on p. 247 topics in mathematics for the fall semester of the third year of Obergymnasium. One of the topics reads:

"Combinatorics with applications in the binomial and multinomial theorems and the basics of probability."

In Mendel's day high school studies were planned for 7 years. For Realschulen (i.e. for more practically oriented high schools) we find the educational plans on pp. 146 – 148 of the 1889 edition. The first three years were devoted to "elementary mathematics", years 4 to 6 to "general arithmetic", year 5 to "geometry of the plane" and year 6 contains "*combinatorics and the binomial theorem for positive integral exponents*". Year 6 also includes "goniometry, trigonometry and stereometry". Year 7 repeats and expands all the previous material (of a quite demanding curriculum).

In Znojmo, Mendel was supposed to teach class 6 but he was assigned to class 4 (because of his lack of experience). However, he taught mathematics both in Znojmo and Brno. So his knowledge of basic mathematics (and combinatorics) was sound and probably sufficient for the mathematics involved in the *Pisum* paper even before his studies in Vienna.

Let us add a final remark on the curricula. It is interesting to note that both at Realschule and at Gymnasium combinatorics was taught in higher classes (which is different from present-day practice). This probably reflected (in the 19th century) its "modernity" and recent addition to the traditional curriculum. This may also explain the subtitle of the Ettingshausen book.[32]

Of course, Mendel's contact with the university in Vienna only reinforced his mathematical education. Mendel spent two years at Vienna University. Among his teachers were Christian Doppler, the already mentioned Andreas von Ettinghausen, noted botanist F. Unger, and his past examiner R. Kner.[42]

It is worth again noting that none of the lectures which Mendel listed deals with mathematics only (perhaps the only exception is the lecture by Moth: On Logarithmic and Trigonometric Tables). However, lectures on Higher Mathematical Physics (by Ettingshausen) certainly contained a wealth of mathematics. However, there is no explicit record of combinatorics or probability. Here is the rough statistics of subjects taken by Mendel during the period October 1851 – August 1853: Physics 5, Zoology 4, Chemistry 3, Botany 3, Paleontology 1.

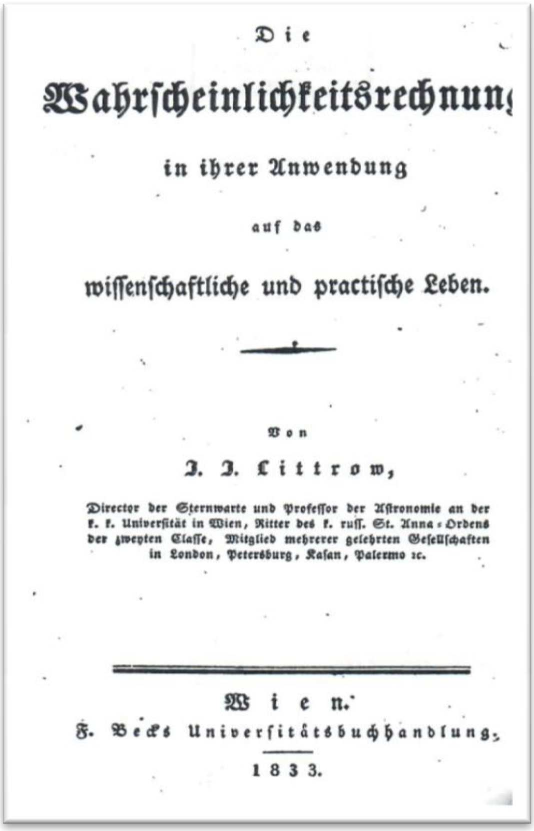
Was Doppler the primary mathematical influence on Mendel in Vienna? This is, of course, possible, but as is well known Doppler's presence at the University of Vienna only briefly overlapped with Mendel's (and his teaching was taken over by Ettingshausen). But there are other, perhaps more hidden aspects which one should consider when discussing these influences.

It is often said that the strongest impact on Mendel's mathematics came from Christian Doppler and Andreas von Ettingshausen, with Doppler's influence being stronger than Ettinghausen's (see e.g. Olby[10]). Many if not most texts on Mendel concentrate on influences from biology and neglect the mathematical context altogether. We argue that as far as mathematics was concerned the situation was more complicated and that the above order of influence should perhaps be reversed. The mathematics of the *Pisum* is entirely combinatorial so we concentrate on books dealing with this topic. Which mathematical books dealing with combinatorics were available to Mendel? At the beginning of the 19th century there were not many. There were treatises dealing mostly with probability and problems of chance (e.g. works by de Moivre, the Bernoullis, and Laplace, to name just a few). In fact, the emergence of probability and of combinatorics are closely related events, certainly in the early period of their development (e.g. think of Leibniz, Pascal, Laplace, and Cauchy: all significantly contributed to the area and produced well known texts published in several editions). But apart from an early book of Leibniz, *Ars combinatoria* (his doctoral dissertation), the only other book devoted exclusively to combinatorics (and moreover which has "combinatorics" in its title) seems to be A. von Ettingshausen's book from 1826[32]. This is (certainly for its time) an advanced book. Ettingshausen had seen renewed interest in combinatorics at the beginning of the 19th century and decided to write a book subtitled "as preparatory science for the study of higher theoretical mathematics". He aimed for originality. He classified the area and introduced concepts and notation. But it is a fact that in Vienna he was out of touch with the top mathematicians of his time. Advances in mathematics were at that time being seen mostly in Germany and France, and involved the rapid development of analysis (Cauchy, Fourier), geometry (Gauss, Riemann), and algebra (Galois, Abel), with an apparatus and level of mathematical maturity beyond the understanding of people not educated at the centres of mathematical research. This was not just the case for Ettingshausen but for the whole of Vienna (and Prague, and, for example, also England). It seems typical that brilliant researchers at these (mathematically) provincial places sought not to solve hard and complex mainstream problems but rather to develop areas which were newly emerging or which were originating from generalisations and new ideas. There are numerous examples illustrating this, such as for example Bolzano in Prague (the concept of infinity), and in England Boole, Cayley, de Morgan, Kirkman, and Hamilton (algebra, combinatorics).[43]

It is as if researchers at the mainstream centres of mathematics did not have time for such peculiarities and particularities. Only much later developments justified efforts in the latter areas. Combinatorics was certainly such a peculiarity in Mendel's time (and for many years to come). The book by Ettingshausen fits into this picture very well. His book proves nothing strikingly new but does provide a good catalogue and is well organised, introducing also notation which in some cases has survived until the present day; it also had the ambition of being a "Vorbereitungslehre" for the whole of mathematics. It seems that Mendel had to know the book.

But of course it would probably not have been Mendel's only source. For example, in 1833 J.J. Littrow (professor of astronomy at The University of Vienna) published a largely practically oriented book[44] giving many "real world" examples. Its first 41 pages, however, are devoted to "Probability in general" and the author explains the role of probability in the style of natural philosophy. In the introduction Littrow calls probability "a new science which was wholly unknown to our predecessors." In particular, he goes on to describe the method of least squares of Gauss and Laplace. There is also another (more general) book by A. Ettingshausen[45] and a book by Christian Doppler[46]. The books by Littrow and Doppler both contain combinatorics sufficient for Mendel's purposes, although both seem to be inferior to Ettingshausen's book in style and organisation of material. On the other hand, they are more practically oriented and contain many examples.

There is no doubt about the mathematical standing of Andreas von Ettingshausen, It is not possible to say the same of the great physicist Christian Doppler, who during his life faced problems not only personal but also scientific. For example his standing as a mathematician meant that he did not gain an easy acceptance among his peers. He was at first rejected and then with difficulties elected to the Royal Learned Society in Prague, where he had been strongly defended by B. Bolzano.[47] Also Doppler's mathematical books were not highly regarded: "Doppler's explanations were conducted in a very unfortunate way and demonstrated that he groped his way around uncertainly in the basics of mathematics — more so than his eminent contemporaries."[48] But he was a man of a genius and his recognition of course changed upon his most important discovery, now known as the Doppler effect (which surprisingly related two unrelated phenomena); however even then he was unable (also due to poor health) to take part in the subsequent high-level discussion of his discovery.[49]



Die

Wahrscheinlichkeitsrechnung

in ihrer Anwendung

auf das

wissenschaftliche und practische Leben.

Von

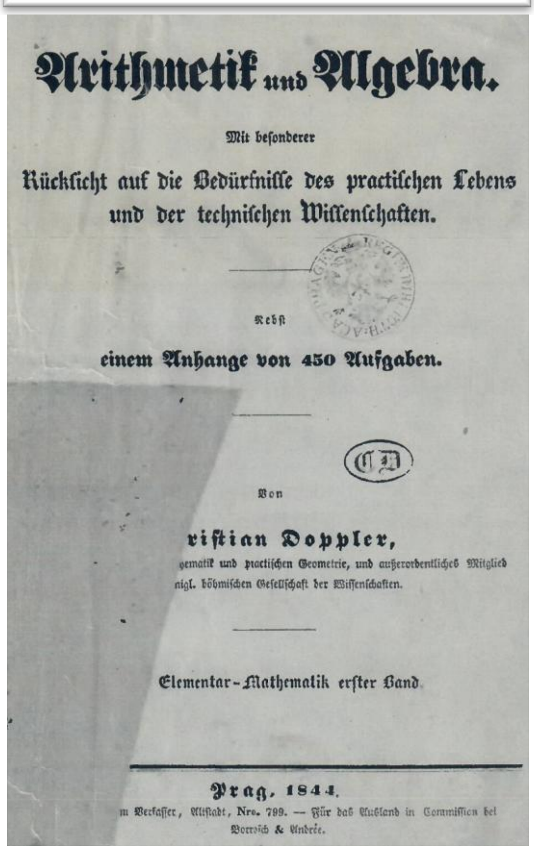
J. J. Littrow,

Director der Sternwarte und Professor der Astronomie an der k. k. Universität in Wien, Ritter des k. russ. St. Anna-Ordens der zweyten Classe, Mitglied mehrerer gelehrten Gesellschaften in London, Petersburg, Kasan, Palermo ꝛc.

Wien.

F. Beck's Universitätsbuchhandlung.

1833.



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Elementar-Mathematik erster Band.

Prag, 1844.

m Verfasser, Altstadt, Nro. 799. — Für das Ausland in Commission bei Borrosch & André.

Figure 7.

6. Final remark

From a mathematical point of view the *Pisum* paper is not a triviality. It looks simple but it is deeply rooted not only in biological experience but also in mathematics. We have tried to document this here.

Mendel's work has led to and finds a modern setting in dynamics (Gromov[40]). The research of this paper is not a case of l'art pour l'art, but rather a quest for the core of Mendel's thinking and discovery, a quest to isolate the essence of Mendel. This does not involve listing details and finding local improvements, but isolating the main advances and breakthroughs in knowledge of mankind. The fact that these advances are formulated by means of mathematics and the fact that this mathematics is "high" is naturally to be expected. This may be also seen as a (high-level) confirmation of the leitmotiv of this paper: core mathematics in its rigour and style is the key to understanding Mendel's paper.

Acknowledgement

We thank to Jiří Sekerák for encouragement to write this paper. We thank to Andrew Goodall for many remarks which improved the quality of this paper. We thank to Magdaléna Šustová for help in the archives of J. A. Komenský Pedagogical Muzeum and Library in Prague.

This work was supported by GAČR grant P202/12/G061.

7. Remarks and references

0. Mendel, G. J. Versuche über Pflanzen-Hybriden. *Verhandlungen des naturforschenden Vereines in Brünn for 1865*, publ. 1866, vol. 4, part Abhandlungen, p. 3 – 47.

This chief work of Mendel is available on the web in several places, and also in several English translations. We refer to the bilingual version of Gregor Mendel (2016). *Experiments on Plant Hybrids (1866).* Translation and commentary by Staffan Müller-Wille and Kersten Hall. British Society for the History of Science Translation Series. URL=http:/www.bshs.org.uk/bshs-translations/mendel. Thus the pages we give are synchronised with the original German text.

A comprehensive book containing both Mendel's papers (1866 and 1869) together with all letters of Mendel to Nägeli is: *G. Mendel , Pokusy s hybridy rostlin* (translated by A. Matalová, ed. I. Cetl), K-public, Brno, 2008, ISBN 978-80-87028-02-5.

1.Iltis, H.: *Gregor Johann Mendel, Leben, Werk und Wirkung*. Berlin: Julius Springer 1924.

Iltis, H.: *Life of Mendel*. W. W. Norton & Co. Publishers, New York,1932

2. Orel, V.: *Gregor Mendel a počátky genetiky*, Academia 2003. Orel, V.: *Gregor Mendel. The First Geneticist,* Oxford University Press 1996.

3. Olby, R.: *Origins of Mendelism,* University of Chicago Press, 2nd edition 1985.

4. Klein, J., Klein, N.: *Solitude of a Humble Genius – Gregor Johann Mendel*: Volume 1, Springer 2013

From all the above sources perhaps Iltis[1] and Orel[2] should be regarded as prime sources.

5. See Foucault, M.: The Discourse on Language, introductory lecture at the Collège de France to the course The Will to Knowledge, Dec 2nd, 1970. For a Czech reader this terminology is confusing as "To live in the truth" carries almost the opposite meanings for M. Foucault and V. Havel: For Foucault it means to act and to express oneself in the canon of one's time and thus to be understood by contemporaries. Mendel was radically different, he was a "Monster", he was not speaking "the truth of his time". For Havel this expression, of course, means to live and act according to one's conscience.

6. See Iltis[1], p. 202. In the (heavily abridged) English translation this is on p. 284. In both cases this is attributed to G. Niessl (who lived in the time of both Mendel and Iltis).

7. Gromov, M.: The Library of Mysteries. In*: Mathematics – A Beautiful Elswhere*, Fondation Cartier pour l'art, contemporain 2011, p. 70-72.

8. de Beer, G., Genetics, The Centre of Science, *Proceedings of the Royal Society of London B*, Biological Sciences, Vol. 164, No. 995 (1965), 154-166. This is the opening address to the Symposium From Mendel's Factors to the Genetic Code, 10-13 March 1965.

9. Fisher, R.A., Has Mendel's work been rediscovered? *Annals of Science 1* (1936), 115–137.

10. Olby, R.C., *Mendel, Mendelism and Genetics,* Mendelweb 1997.

11. Books by H. Iltis[1], V. Orel[2], R.C.Olby[3] and numerous further articles. Many of the important contributions were published in *Folia Mendeliana*, which under leadership of V. Orel became an international forum with several recent contributions by E. Matalová, J. Sekerák and others. See e.g. J. Sekerák, Mendel in a black box, *Folia Mendeliana 48/2*, 2012, 5-36.

12. Brannigan, A., *The social basis of Scientific Discovery,* Cambridge University Press 1981.

13. Wynn, J., *Alone in the Garden: How Gregor Mendel's Inattention to Audience May Have Affected the Reception of His Theory of Inheritance in "Experiments in Plant Hybridisation",* Written communication, Sage 24, 1 (2007), 3-27.

14. Bowler, P.J., *The Mendelian revolution: The emergence of hereditarian concepts in Modern Science and Society,* The Athlone Press 1989.

15. See e.g. Singh, R.S., *Limits of imagination: the 150th Anniversary of Mendel's Laws, and why Mendel failed to see the importance of his discovery for Darwin's theory of evolution,* Genome 58 (2015), 415-421. This paper contains some remarks on Mendel's notation (*A* vs *AA*) similar to those of Olby[10]. However, this is a very speculative essay.

16. Novelli, L., *Mendel e l'invasione degli OGM*, Editoriale Scienza 2003. See also the catalogue of a recent exhibition *DNA – Il grande libro della vita da Mendel alla genomica*, Silvana Editoriale, Rome, 2017

17. Of course, several of the quoted sources contain information and commentary on mathematics, but none seem to be devoted in depth to this aspect. The words "Mendel and mathematics" seem only to appear in the title of the book review Barton, N.H., Mendel and

mathematics (review of Bürger, R., The Mathematical Theory of Selection, Recombination and Mutation, J. Wiley&Sons, 2000, *Trends in Genetics* 17, 7 (2001), 420).

18. Nešetřil, J., Nešetřilová, H., Mendel's Mathematics (in preparation).

19. See Kalina, J., Gregor Mendel, his experiments and their statistical evaluation, *Acta Musei Moraviae, Sciential biologicae* 99 (1), 2014, 87-99, for a recent contribution which contains also the history of this discussion (which seems to be resolved by now) in favour of Mendel.

20. Stern, C., Sherwood, E.R., *The origin of Genetics; a Mendel Source Book*, W.H.Freeman (1966), p.v.

21. Vorhandlungen des naturforschende Vereins in Brünn 1903, XLI, p. 20. Annoted by V. Orel[2], p. 214. It is fitting to quote here a more recent comment of P.J.Bowler op. cit.[14], p. 3: "published in 1865 (sic!) these laws had been ignored partly because Mendel had written in an obscure local journal and partly because the excitement generated by Darwin's theory had kept attention on outdated models."

22. Howard, J.C., Why didn't Darwin discover Mendel's laws? J. Biol. 8 (2), 2009, 15.

23. For discussion of the translation of "Die Entwicklung" see Gliboff, S., Gregor Mendel and the Laws of Evolution, *Hist. Sci. XXXVII* (1999), 217-235.

24. Compare for example with F. Unger: *Botanische Briefe*, Wien, Verlag von Carl Gerold & Sohn, 1852, which does not contain a single formula in all of its 156 pages and the whole treatment is a good example of the (advanced) Naturphilosophie tradition. Similar comments can be made for other sources from Mendel's time, e.g. Gärtner, C. F., *Versuche und Beobachtungen über die Bastarderzeugung im Planzenreich*, Stuttgart 1849, K.F.Hering & Comp. Mendel himself points this out in his first letter to Nägeli.

25. See Matoušek, J., Nešetřil, J., *Invitation to Discrete Mathematics*, Oxford University Press 1998, 2nd printing 2008, for the history and striking variety of (6!) proofs of Cayley formula for trees.

26. Wichura, M., *Die Bastardbefruchtung im Pflanzenreich, erläutert an den Bastarden der Weiden.* Breslau, Verlag von E. Morgenstern (1865). This short book (94 pp. + 2 pages of illustrations) is a dense and clear treatment which could have influenced Mendel's style.

27. Wichura, M., Über künstlich erzeugte Weidenbastarde, Jahresbericht der Schlessischen Gessellschaft Vaterlicher Kultur 31 (1853), 160-164. Reprinted in Flora 12, 1 (1854), 1-8.

28. Note that the first paper of Wichura appeared twice. Flora was an established journal which Mendel *could have seen* prior to the start of his experiment. Before delivering his lecture he could have certainly seen Wichura's book op. cit. [27] as it was published in 1865. Mendel refers to Wichura with admiration. Thus the mere experimental side, the courage to design the experiment, and to investigate the hybridisation process in its combinatorial complexity could have been encouraged by Wichura more than by any other predecessor.

In active science a short discussion over coffee can play a fundamental role. Possibly this is what happened in 1854-5 to Mendel if he had seen Wichura's paper. Just a few hints which ten years later materialised in a giant experiment and a seminal discovery. Compare also P. Lorenzo, Max Wichura, Gregor Mendel y los híbridos de sauce, *Epistemologia de la Cienca,* vol. 8, no. 8 (2002), 210-217 or Olby, R., Mendel's Vorläufer: Köhlreuter, Wichura and Gärtner, *Folia Mendeliana 21 (1986), 49-67.*

29. Only Wichura[26] uses the letters a, b, c, … to denote plants in his experiment. But these are never individual (isolated) traits. Wichura's own words on his contribution are as follows: "Durch diese komplizierten Bastardformen, bei deren Entstehung mehr als zwei Species mitgewirkt haben, glaube ich einen neuen Beitrag zur Lehre von der Bastardbefruchtung geliefert zu haben" (*Flora* (1854), p.7).

30. Semiotics and semiology (as a science dealing with signs) of the Locke-Peirce-Saussure tradition.

31. Boyer, Carl B.: *A History of Mathematics*. New York, Chichester, Brisbane, Toronto, Singapore 1991, ISBN 0-471-54397-7, p. 205.

32. Ettingshausen, Andreas, *Die combinatorische Analysis als Vorbereitungslehre zum Studium der theoretischen höheren Mathematik,* J. B. Wallishausser, Wien 1826. Surely one of the first books devoted solely to combinatorics.

33. A. von Ettingshausen is often mentioned but his book on combinatorics[32] is often absent from the main Mendelian sources (see e.g. op. cit. [1, 2]). It is quoted briefly e.g. in J. Jindra, A possible derivation of the Mendelian series, *Folia Mendeliana(1967)*, 71 – 74; W. George, Gregor Mendel and Andreas von Ettingshausen, *Folia Mendeliana* 17 (1982), 213- 215; V. Krůta, V. Orel, Mendel, Johann Gregor. In: *Dictionary of Scient. Biogr. 9*, (1074), 277-283. However the contents (and innovative aspects of the notation) of Ettingshausen's book[31] are not mentioned.

34. The symbol $\binom{n}{k}$ is now fully accepted, see Knuth, D.E., *The Art of Computer Programming,* Vol. 1: Fundamental Algorithms, Addison-Wesley 1997 (3rd ed.), Higman N.J., *Handbook of writing for mathematical sciences*, SIAM, 1998, p. 25. One has the feeling that Ettingshausen himself was fond of this symbol — certainly he does not spare its use in the book. The symbol $\binom{n}{k}$ is also relevant to recent research, it has been generalized to $\binom{X}{k}$ to denote the *set* of all *k*-element subjects of X and to $\binom{B}{A}$ to denote the set of all substructures of B which are isomorphic to A. This then led to *Pascal theory* introduced by K. Leeb in the context of Ramsey theory, see e.g. J. Nešetřil, Ramsey theory. In: *Handbook of Combinatorics.* (eds. Graham, R.L., Grötchel, M., Lovász, L., North Holland (1996), 1331-1403). Ettingshausen was less lucky with the other symbols that he suggested. For example, he denoted the product of an arithmetical progression $a(a+d)\ldots(a+n{-}1d$ by $a,dn.$

35. Mendel could have met the name of Ettingshausen already in his Olomouc years (1841-1843). The story goes as follows. Mendel's future examiner Andreas von Baumgartner wrote a book *Die Naturlehre nach ihrem gegenwärtigen Zustande mit Rücksicht auf mathematische Begründung,* Wien 1825. This became a standard textbook for teaching physics and ran through eight editions to 1845. The sixth and seventh editions in 1839 and 1842 were revised by Ettingshausen (see W. George op. cit.[32] and P. Weiling, Die Meteorologie als die wahrscheinliche Quelle der statistischen Kentnisse J.G.Mendels, *Folia Mendeliana 5* (1969), 73-85). The world of higher learning was small in Austria.

36. See e.g. Olby[2], Gliboff [23] .

37. We do not claim that the MAX algebra (per se) was anywhere close to Mendel's thinking. But it is interesting to note that around 1850 new algebraic structures were being disscussed and studied, e.g. by Hamilton, Cayley and Kirkman; see Nešetřilová, H., Nešetřil, J., Poznámka ke Kirkmanovu problému školních dívek, *Dějiny věd a techniky 72* (1972) 171-173 (in Czech, English summary), Nešetřilová, H., Philosophical Magazine and English Mathematics 1800-1850, *Dějiny věd a techniky 74* (1974), 83-100 (in Czech, English summary).

38. Wigner, E., The unreasonable Effectiveness of Mathematics in the Natural Sciences. In: *Communications in Pure and Applied Mathematics,* vol.13 (1960), 1-14. I.M.Gelfand added to it: "There is only one thing which is more unreasonable than the unreasonable effectiveness of mathematics in physics, and this is the unreasonable ineffectiveness of mathematics in biology." Well, Mendel seems to be an early counter-example to this.

39. Etherington, I.M.H., Non associative algebra and the symbolism of genetics, *Proc. Royal Soc. Edinburgh B 61* (1941), 24-42.

Reed, M.L., Algebraic structure of genetic inheritance, *Bull. of AMS 34 (2),* 1997, 107-130.

It seems that such a setting is based on the analysis of multiplication tables. This is true and our examples are not exhaustive. There are also ("evolution") algebras which relate to non-Mendelian situations, see e.g. J.P.Tiam, P.Vojtěchovský, Mathematrical concepts of evolution algebras in non-Mendelian genetics, *Quasigroups and related systems 14,1* (2006), 111-122.. This kind of mathematics was also nicknamed by G.H.Hardy (in the context of the Hardy–Weinberg law) as the mathematics of multiplication tables (see G.H. Hardy, Mendelian proportions in a mixed population, *Science 28 (1908),* 49-50).

40. Gromov, M., Mendelian Dynamics and Sturtevant's Paradigm. In: *Geometric and Probabilistic Structures in Dynamics* (K. Burns, D. Dolgopyat, Y. Pesin, eds.), Contemporary Math. Series 469, AMS, 2008, 227-242.

41. We thank Magdaléna Šustová from Národní pedagogické muzeum a knihovna J. A. Komenského v Praze (J. A. Komensky Pedagogical Muzeum in Prague) for her help.

42. Mendel's examining committee included Baumgartner, Doppler, Fenzl, and Kner; Ettinghausen, Baumgartner , Fenzl and Unger were members of the Section of Mathematics and Physics at Vienna Academy of Sciences. Again, in those days the world of mathematics and physics was small in Austria, and Mendel was part of it.

43. As explicit examples we mention the work of Cayley and Hamilton on "generalised" complex numbers, of Boole on "*Laws of Thought*", and of Bolzano on "*Paradoxes of Infinity*".

44. Littrow, J.J., *Die Wahrscheinlichkeitsrechnung in ihrer Anwendung auf das wissenschaftliche und praktische Leben,* Wien, F. Becks Universitätsbuchhandlung 1833.

45. Ettingshausen, A., Forlesungen über höhere Mathematik, 2 vol., 1827, Wien.

46. Doppler, Ch., *Arithmetik und Algebra mit besonderer Rücksicht auf die Bedürfnisse des practischen Lebens und der technischen Wissenschaften*, Prag 1844. On p. 95 begins a section "About application of combinatorics on the first elements of probability. On p. 103 begins a section "About powers of monomials and polynomial numerical values" and here on p. 110 as a Remark (!) we read: "Because many calculations involve the binomial formula, it is desirable to have a simple notation for binomial coefficients as we know them today." No reference to Ettingshausen is given.

47. Štoll, I., Christian Doppler – Man, work and message. In: *Phenomenon of Doppler,* (Prague), 1992, 13 - 29.

48. Seidlerová, I., Christian Doppler and Prague Polytechnic. In: *Phenomenon of Doppler,* (Prague), 1992, 30 –4

49. It is interesting to note that, apart from discussion with Petzval, the Doppler effect was also tested when A. Ettingshausen asked his student young Ernst Mach to decide in favour of or against it. In 1860 Mach constructed a "simple apparatus" which answered the

question positively and later (1888) in Prague arranged a public demonstration with students and colleagues. (J. Mehra, H. Rechenberger, The historical development of quantum theory, Part I. Springer 1987, p. 43.). It is perhaps fitting to add that a son of A. von Ettingshausen was Constantin von Ettingshausen (1826 – 1897), a botanist known for his paleobotanical studies of flora.