VERSUCHE ÜBER PFLANZEN-HYBRIDEN EXPERIMENTS ON PLANT HYBRIDS (NEW TRANSLATION WITH COMMENTARY)

GREGOR MENDEL

EDITED BY STAFFAN MÜLLER-WILLE, KERSTEN HALL AND ONDŘEJ DOSTÁL

MASARYK UNIVERSITY PRESS

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BRN0 2020

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ISBN 978-80-210-9555-7 ISBN 978-80-210-9554-0 (paperback)

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GREGOR MENDEL'S MULTIPLE PLACES IN HISTORY

Patricia Fara • President of the British Society for the History of Science

This splendid volume is the culmination of a long-standing collaborative venture between the Mendel Museum in Brno, the Royal Society in London, and the British Society for the History of Science (BSHS). Although many people have been involved, it results in particular from the linguistic and historical expertise of Staffan Müller-Wille and Kersten Hall, and the enthusiastic commitment of Ondřej Dostál and Gregory Radick to ensuring the project's completion. Thanks to this unique international cooperation, scientists as well as historians will gain new insight into their shared heritage, and I am absolutely delighted that it is appearing during my two-year tenure as BSHS President.

As an initial step, the interactive on-line translation was launched in January 2017, when I had the great – if personally undeserved – pleasure of receiving many tributes to its excellence. As just one example of these unsolicited accolades, this arrived from an eminent Mendelian specialist: 'The BSHS translation was incredibly useful and informative. The on-line format works really well, the level of detail in the commentary is awe-inspiring, and the whole really helps the English reader to get *much* closer to the text than was possible previously. It's a genuine scholarly triumph, and something the BSHS should be very proud of.' The BSHS is indeed extremely proud of this achievement, and I am looking forward to similarly enthusiastic appreciations from the readers of this present expanded print-format publication.

Annotated translations of key texts are crucial not only for facilitating international access, but also for enabling scholars to question previous accounts and hence to provide fresh interpretations. For me, the most exciting aspect of being a historian is that there are no definitive versions of the past: there are always new perspectives to adopt, new stories to tell, new insights to gain. Historians have woven Gregor Mendel into several different narratives, so that although I am certainly not myself an expert, I have encountered him in several different contexts.

Most obviously, Mendel's pea experiments in the monastery garden at Brno are often presented as the vital mechanism that was missing from Charles Darwin's original formulation of evolution by natural selection. That is, of course, a vastly over-simplified explanation, and many academics have provided more nuanced accounts of the relationships between genetics and modern evolutionary theory. But he also features in other types of historical revisionism. For instance, students of Soviet history may not have a scientific background, but they still need to understand why and how Mendel featured in the agricultural, educational and penal policies of Stalinist Russia; moreover, the anti-genetics research projects instigated by Trofim Lysenko affected not only life in Russia, but also the behaviour of Marxist scientists in Britain and other countries, including Czechoslovakia. As a very different type of example, scientific historians interested in the relationships between theory and observation have used Mendel as a casestudy, debating whether or not his results were suspiciously close to prior expectations of round numbers; others are interested in the apparent coincidence of three claims in 1900 by scientists interested in plant hybridization that they had independently rediscovered Mendel's original results.

Perhaps surprisingly, this Moravian friar also appears in the work of gender historians. For scholars interested in tracing the experiences of female scientists, William Bateson – who promoted Mendel's paper and coined the words 'genetics' – offers a striking example of a male catalyst who enabled women to enjoy success in the face of widespread prejudice. During the first decade of the twentieth century, he gathered around him a group of researchers at the University of Cambridge, more than half of whom were women. Working at a time when Mendel's ideas and also Darwin's were often regarded sceptically, Bateson was struggling for recognition at the margins of scientific endeavour. He recruited a series of female graduates to his team: regarded with contempt (or perhaps apprehension?) by many male academics, these women were not in a position to be too picky about their topic or their leader. The advantage for Bateson lay in gaining some exceptionally intelligent, determined and resilient researchers who could be employed more cheaply than men for carrying out the same work.

Before long, Bateson's wife Beatrice had become enlisted at home, helping to record breeding data and to coordinate the project. He was an inspiring teacher who regularly invited students to spend Sunday afternoons at his own farmyard garden, examining poultry and discussing questions of inheritance. Bateson's female researchers studied a great variety of organisms – one specialised in guinea pigs, another in oats, a third in mice – although few of them achieved lasting fame. One who did was Edith Saunders; already established as an independent researcher in plant hybridization, she later became president of Britain's Genetics Society. Like many female scientists of the period who lacked appropriate role models, she adopted austere masculine clothing, but her students adored her. More and more women were attracted to the Bateson-Saunders duo, and as the experimental results began to look increasingly impressive, men asked to join as well.

This new volume will prompt still further investigation into Mendel's original paper. For the first time, non-German speakers can access this seminal scientific text in the vocabulary used by his contemporaries, but complemented by notes designed for twenty-first century scholars. It will become an indispensable tool for researchers – and they will have great cause for gratitude to the dedicated experts who put so much effort into its production.

MENDEL'S IMPACT ON SCIENCE

Paul Nurse • director of the executive comittee, Francis Crick Institute

Mendel was a biological scientist who carried out experiments into plant breeding and invented genetics. He had humble origins, born to peasant Silesian farmers in 1822. He entered Augustinian Brno Monastery as a novice and became a supply teacher at the local gymnasium school whilst preparing for examinations in the natural sciences at the University of Vienna. However, he never passed his examinations and never obtained a permanent teacher appointment. He was a student of maths and physics, and when he subsequently carried out his experiments into plant breeding he used the approach of a physicist as well as that of a biologist. Mendel began experimenting seriously in 1856 but had to stop his work in 1871 by which time he had been elected life-long Abbot of the Monastery. He then became embroiled in controversy with the local authorities over payment of an ecclesiastical tax, which distressed and saddened him, and he died in 1884. He seemed to have been popular as can be read in his obituary in the local Brno newspaper:

"His death deprives the poor of a benefactor, and mankind at large, of a man of the noblest character, one who was a warm friend, a promotor of the natural sciences, and an exemplary priest".

So what did Mendel do that had such an impact on the future of biology? The problem he was interested in was plant hybridisation, that is understanding how characteristics were produced in hybrid offspring when two plants with differing characteristics were crossed together. This was a problem of considerable interest to scientists of the time. The German Joseph Koelruter working in the late eighteenth century had carried out crosses with tobacco, pinks and carnation varieties, and had demonstrated that the first hybrids generated from differing parents often exhibited rather uniform phenotypes intermediate in character between the two parents, whilst the second generation was much more varied, and more like one or other of the originating parents. Later Carl Friedrich von Gaertner who worked with both peas and maize, reported the dominance of certain characters of one of the parents over those of the other parent in the first hybrids, and the subsequent reappearance of both the original parental characteristics in the second generation hybrids. Just before Mendel's work began Charles Naudin in France carried out systematic hybridisation experiments in many plant species and from his work proposed that a hybrid of two parental types formed different types of germ cells. Germ cells are the pollen and ovules which fuse together to form plants of the next generation. He suggested that the germ calls can form three possible combinations in the subsequent hybrids. Two

were like the original parents, and the third was like the first generation hybrid. However, the work of these earlier scientists had not led to a coherent unifying idea explaining plant hybridisation, although all were important for Mendel's subsequent work.

When Mendel started his experiments he used a different approach which meant that he was successful when his predecessors had not been. Firstly, he was very careful with his choice of experimental material. He carried out preliminary experiments with a number of plant species before settling on the pea, eventually choosing 22 pea varieties which had clearly differing characteristics which could be used for his experimental crosses. Examples of the characteristics he studied were differences in the seeds, whether round or wrinkled, green or yellow. This focus on plants with clear characteristics was important, because biological material is often very variable, and the reproducibility of results is improved if unambiguous classification of plants with differing characteristics is possible. Secondly he was quantitative, accurately counting the numbers of different types of offspring that were generated in his crosses. The traditional approach in natural history research was to be more qualitative, describing the different types observed but not carefully counting how many of them there were. His quantitative approach probably reflected his training as a physicist. Thirdly, his way of working involved first generating an explanatory hypothesis, and then carrying out experiments to confirm or refute that hypothesis.

The major hypothesis Mendel generated, which underpinned much of what he achieved. concerned the behaviour of what he called character elements during the various crosses he carried out. For example, if a plant making round seeds was crossed with one making wrinkled seeds, then the hybrid formed would have two character elements, one for round seeds and one for wrinkled ones. He hypothesised that the germ cells produced by that hybrid, would either have the round or the wrinkled character element, and after fertilisation of a pollen germ cell with an ovule germ cell, the newly formed hybrid would either have only round or wrinkled character elements and so would make round or wrinkled seeds, or would have both a round and a wrinkled character element. He made simple combinatorial calculations to predict what proportions of the three types of hybrid plants are generated, and it came out as a ratio with one plant containing two round seed character elements, one plant containing two wrinkled seed character elements, and two plants containing both a round and a wrinkled seed character element. If the round character element is dominant over the wrinkled one, then plants with both the round and the wrinkled character elements would be round, and so the overall ratio of plants making round seeds to ones making wrinkled seeds would be 3 to 1. It was this hypothesis that Mendel tested and he showed in his experiments that 5,474 round to 1,850 wrinkled plants were formed, a ratio of 2.96. Mendel carried out many other crosses to test his hypotheses, but the central observation was this 3 to 1 ratio.

Although these experiments were simple, the implications of these results were profound. They demonstrated that the basis of heredity is particulate, based on character elements which we now call genes. The characteristics of most living organisms are determined by the actions of pairs of genes passed on as essentially unchanging discrete entities or particles within the germ cells, one from each parent to the hybrid offspring. Mendel's experiments and abstract reasoning were brilliant and awesome, and laid down the foundation of genetics.

However, his magnificent discovery was not recognised in his life-time, and it took over 30 years before similar results obtained by others, particularly the Dutch scientist Hugo de Vries, led to the rediscovery of Mendel's work. The world was more receptive to Mendelism by this time, perhaps because of the discovery of chromosomes in cells. These were thought to be responsible for heredity, and their behaviour precisely matched that proposed by Mendel. Chro-

mosomes split in two every time a cell reproduces, and during germ cell formation only one of each pair of chromosomes is passed on to each germ cell. When two germ cells then go on to fuse and form an organism of the next generation, the chromosome pair is reformed. So Mendel's law could be seen to be no longer abstract, but based on the observed concrete behaviour of chromosomes.

Also implicit in Mendel's work was that the gene is a unit of information, and unravelling how that information is encoded and transmitted is probably the most outstanding contribution to biology of the last century. We now know that the gene is made of deoxyribonucleic acid consisting of a linear sequence of nucleotide bases. Pairing rules for these bases explains how genes are precisely copied during cell reproduction, and the sequence of the bases acts as a digital information storage device. Modern biology is built on all of this, and without the advances due to Mendel it is difficult to imagine molecular genetics and all that has produced for the benefit of humankind, including the human genome project and the present and future revolutions in health care and agriculture. And all this came from a modest monk from a poor background, working in a small town of the Austrian-Hungarian Empire, studying crosses of the humble pea plant. We need to remember today that discovery research into unlikely topics sometimes by unlikely researchers working in unlikely places, can bring about discoveries which change the world.

And Gregor Mendel did indeed change the world forever. His name should be celebrated throughout the world, on a par with the greatest scientists of all time. His genius can be seen in the paper that revolutionised biological science, and is freshly translated in these two new translations into English.

LEGUMES AND LINGUISTICS:

TRANSLATING MENDEL FOR THE TWENTY-FIRST CENTURY

Staffan Müller-Wille • University of Exeter / Kersten Hall • University of Leeds

INTRODUCTION

In this book, we present a new English translation of Gregor Mendel's seminal publication, "Versuche über Pflanzen-Hybriden" (Experiments on Plant Hybrids), which appeared a little more than 150 years ago, in 1866, and is regarded as one of the founding documents of genetics. We present our translation along with the original German text, and detailed glosses on almost each and every sentence.

This is clearly not the first English translation, as we will set out in more detail below, and another one by Scott Abbott and Daniel J. Fairbanks appeared three years ago in the journal *Genetics* (Mendel 2016). We do not think that any of the existing translations are particularly problematic, nor do we consider ours as the definitive one that should replace earlier ones. What we want to offer instead is a window onto the original German text for those who know little or no German at all. Our translation thus serves as a resource for making up one's own mind about how best to translate Mendel. In this introduction, we want to set out our rationale for producing such a translation in more detail.¹

MENDEL AND THE HISTORY OF GENETICS

Ask a biologist to name the three publications which have defined the intellectual landscape of their subject and the chances are that, alongside Darwin's *On the Origin of Species* (1859) and James Watson and Francis Crick's publication of the structure of DNA in *Nature* in April 1953, will be a paper published in 1866 by the Augustinian monk Gregor Johann Mendel (1822–1884) about "Experiments on Plant Hybrids" (Mendel 1866). The British evolutionary biologist Sir Gavin de Beer went so far as to say, "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 Johann Mendel" (De Beer 1966, p. 154). Certainly a cursory glance through most A-level and undergraduate biology textbooks will find photographs of Mendel accompanied by figure legends revering him as the founding father of genetics (Kampourakis 2013). Further drama is often added by portrayals of Mendel as being a lone, neglected genius whose work was

1 An earlier version of our translation appeared on the website of the British Society for the History of Science (see http://www.bshs.org.uk/bshs-translations/mendel).

way ahead of its time and who, pottering around in a garden in a remote corner of the Austro-Hungarian empire, was consigned to scientific oblivion until the rediscovery of his work around 1900 (cf. Kampourakis 2015).

What then did Mendel do to justify the accolades heaped upon him by biology textbooks? Working in his garden at the monastery in Brno, in what is now the Czech Republic, Mendel crossed varieties of the species *Pisum sativum* (the common garden pea) exhibiting differences with regard to particular traits. By meticulously recording the numerical ratios in which these traits appeared in each generation of progeny, Mendel derived conclusions that later became known as Mendel's two laws. The first of these laws (the Law of Segregation) states that when a sex cell, or gamete, is formed, only the disposition for one form of the trait can enter the newly formed gamete. The second law, or Mendel's Law of Independent Assortment, maintains that this process occurs independently of other traits. So, for example, whether a newly formed sex cell receives a disposition for a particular flower colour occurs completely independently of the disposition it receives for seed shape.

The significance of Mendel's work is that the precise numerical ratios he observed have subsequently been interpreted as providing the basis for our contemporary understanding of genes as small pieces of DNA determining inheritance. But how much of what we today call "Mendelian genetics" can actually be found in Mendel's original paper? This was a question raised in a paper entitled "Mendel — no Mendelian?" published in 1979 by the historian of science Robert Olby. In his paper, Olby argued that far from anticipating general laws of heredity, Mendel was actually working in a long established tradition of naturalists interested in the formation of new species through hybridisation of pre-existing species. Olby went even further and claimed that Mendel never actually believed that the traits he observed were controlled by pairs of discrete particulate entities within the cell — what in our contemporary parlance we would call genes or alleles (Olby 1979).

Olby's argument did not go unchallenged (Orel and Hartl 1994), but it provides a good example to show how, far from being set in stone, Mendel's work is subject to interpretation, and has been so, in fact, since his paper's so-called re-discovery in 1900 (Müller-Wille 2018). The paper itself was immediately reprinted by one of its re-discoverers, the Austrian agriculturalist Erich von Tschermak-Seysenegg, in a prestigious series of classics in the history of the "exact" sciences, which had been founded in 1889 by the famous Baltic-German chemist Wilhelm Ostwald (1853–1932). Unlike today, most academics back then were able to read German (and usually a couple of other languages). And so, within a year of having caught the attention of a few highly specialized botanists, Mendel's paper was widely available to an international, educated audience and found itself in the company of publications by the likes of Galileo Galilei, Isaac Newton and John Dalton (Mendel 1901a).

OTHER TRANSLATIONS

The first English translation followed soon after Tschermak produced his edition. It was commissioned by the English naturalist William Bateson (1861–1926) for the Royal Horticultural Society, and appeared in the Society's Journal in 1901, next to an advertisement for "Carters Grass Seeds as used at Lords and The Oval and other Leading County Cricket Grounds" (Mendel 1901b). The translation had been prepared by Charles T. Druery (1843–1917), a one-time poet and expert on British ferns, and we are referring to it as Druery's translation in our comments. It was provided with an introductory note by Bateson, in which he perceptively remarked that "the whole paper abounds with matters for comment and criticism", but also that it can be "doubted whether in his own day, [Mendel's] conclusions could have been extended". In 1902, Bateson included Druery's translation "with corrections and modifications" in his polemic *Mendel's Principles of Heredity: A Defence* (Mendel 1902). This version we will refer to as Bateson's translation in our comments.

Bateson's translation has been the basis of several reprints. The US-American geneticist William E. Castle included it in his *Genetics and Eugenics*, which became a very popular textbook (Mendel 1916). The publisher, Harvard University Press, subsequently decided to re-issue the translation as an inconspicuous brochure, obviously for study and working purposes. This version came out in fourteen editions between 1916 to 1965, the last edition still being in print (Mendel 1965a). Also in 1965, the year which marked the 100th anniversary of Mendel's paper, Bateson's translation was reprinted with a detailed "commentary and assessment" by the statistician and population geneticist R. A. Fisher (Mendel 1965b), who had sparked a major controversy in 1936 by demonstrating that some of Mendel's results were "too good to be true" (Fisher 1936). The MendelWeb provides ready online access to this translation today, with useful notes and a glossary produced by Roger B. Blumberg.² As Blumberg explains in his notes: "Although this translation may strike readers of German as painfully inaccurate in places, its significance in the history of genetics is beyond dispute; when English and American biologists and students of biology read Mendel in the first decades of the 20th century, they most often read the Druery-Bateson translation".

The inaccuracies mentioned by Blumberg had not gone unnoticed. A new translation was made by the Drosophila-geneticist Eva R. Sherwood (Mendel 1966), which was included in a collection of Mendeliana entitled The Origin of Genetics: A Mendel Source Book that she and Curt Stern (1902–1981) edited in 1966 — that is, one-hundred years after the correct year of publication of Mendel's paper, but of course coming a year late to really beat the Fisher edition. As Curt Stern recalled in his foreword to the collection, his colleagues Leslie Clarence Dunn (1893–1974), retired from Columbia University, and Alan Robertson (1920–1989) from the Institute of Animal Genetics in Edinburgh, had drawn his attention to errors in Bateson's translation. Subsequent "careful comparison with the original German text showed not only a number of mistakes which fundamentally changed the meaning of Mendel's sentences but in addition so many other inaccuracies that Eva Sherwood undertook a completely new translation" (Stern 1966, p. vii). Not much is known about the author of this translation, apparently a gifted student of Stern's who died shortly after the translation came out. More faithful to the original style and wording of Mendel, Sherwood's translation has served as the basis for the interesting "guided study" of Mendel's paper that was published by Alain F. Corcos and Floyd V. Monaghan in 1993. Overall, however, it has never matched Bateson's translation in popularity. We refer to this translation as Sherwood's in our comments.

Finally, just as we were putting the final touches on our translation, a third translation came out as an open-access article in the journal *Genetics* (Mendel 2016). Its authors — Scott Abbott, Professor of Integrated Studies, Philosophy and Humanities at Utah Valley University, and Daniel J. Fairbanks, Professor of Biology at the same institution and a renowned Mendel scholar, — stress in an accompanying article that their translation was motivated by two objectives (Fairbanks and Abbott 2016). First, "to be more accurate than the Druery-Bateson translation and more accessible than the Sherwood–Stern translation". And second, "given that a German translation of *Origin of Species* was probably the only source originally written in English

that influenced Mendel" to make "an exhaustive effort to employ Darwin's phraseology ... when choosing English words in the translation". They achieved the second objective of "Darwinizing" Mendel, as they put it, by "cross-comparing German words and phrases in Mendel's paper" with those in H. G. Bronn's German translation of Darwin's *Origin* (1863), a copy of which Mendel possessed and annotated, and then "identifying the corresponding words or phrases in Darwin's original English". This provides their translation "with a decidedly 19th century Darwinian tone, which, of course, is consistent with the time when Mendel presented and published his paper" (Fairbanks and Abbott 2016, p. 403).

WHY THIS TRANSLATION?

So, do we really need yet another translation of Mendel's paper? We thought so while working on it for five years, and we still think so now that it is out. Our translation combines the approaches of Sherwood and Abbott and Fairbanks. On the one hand, it is quite literal, adhering closely to the syntax and terminology of the German original in order to make it easier for users to compare the translated text with the original. What we thereby gained in transparency, we certainly often lost in elegance of the resulting translation. On the other hand — using similar strategies as Abbott and Fairbanks, but based on a broader range of sources, — we have also been careful to preserve the distinctly nineteenth-century tone of Mendel's paper and avoid any anachronisms in our translation. We would also like to emphasize that we have not tried to reinvent the wheel. Our first "raw" translation was done without recourse to earlier translations, but we have happily followed Bateson or Sherwood in cases where we thought their translation was particularly ingenious.

While we, like most translators, believe that there are ways to be more or less accurate in translation, we are also aware that semantic relations between different languages are not one-to-one but many-to-many. Other translations therefore retain their value, which is why we have included alternative readings from earlier translations in our comments. While Bateson's translation was indeed inaccurate in places (beginning with the title, as we shall see below), it also was in many ways far more sensitive to the context of nineteenth-century biology than Sherwood's. And while Sherwood was guilty of a few anachronisms, she often found ingenious solutions to problems posed by Mendel's syntax. It was too late to consider Abbott and Fairbank's new translation of our project. What neither of the previous translators did at any length, however, is discuss alternative readings or provide explicit reasons for their choices. This is where our translation differs. It is accompanied by detailed notes, furnishing a critical apparatus with details on the German original, including Mendel's manuscript and possible sources he drew upon, how earlier translators rendered certain words and phrases, and the reasons that made us choose a different translation.

Such an exercise can reveal many subtle points that tell us a lot about Mendel's reasoning and its reception by later geneticists. Already the title of Mendel's paper offers a good example. Druery and Bateson rendered the German original — "Versuche über Pflanzen-Hybriden" — as "Experiments in plant hybridisation", insinuating that Mendel's experiments should be understood as an exercise illuminating a much more general phenomenon. Sherwood gave us a much more literal translation with "Experiments on Plant-Hybrids". Even this translation, however, does not capture the sense of the German unambiguously. The German *über* can be translated by "on", but not in the sense that plant-hybrids were the objects of Mendel's experiments, but rather in the sense that they were the very subject of his experiments, the topic he wanted to scrutinize by way of experiment. The most literal, but rather awkward translation would therefore render the title as "Experiments about Plant-Hybrids." Since "Experiments on Plant-Hybrids" has become widely accepted as the correct translation in the English-speaking world — Abbott and Fairbanks use it as well — we decided to retain it. The difference may seem subtle, but preposition choice here can give an important steer to how one understands Mendel's aims, particularly given Olby's view that Mendel's real interest was in hybridization as a process that gives rise to new species.

Mendel's precise understanding of the term "species" is itself another important concern. Here, Druery and Bateson were more consequential in almost always choosing "species" when Mendel used the German term *Art*. By contrast, Sherwood renders *Art* as 'variety' or 'form' or 'stock' most of the time. The explanation of her more varied vocabulary lies in changing understandings of the species concept. Bateson was still familiar with a nineteenth-century meaning of the term, according to which plant forms differing by a few heritable traits, or even only one, belonged to different species; in the case of *Pisum* such varieties were even referred to by different Linnaean binomials by Mendel and his contemporaries. This understanding of species vanished in the aftermath of the evolutionary synthesis in the late 1930s. For the translator, the issue gets even more complicated by the fact that Mendel occasionally used the Latin expression *Species* (capitalized according to German orthographic rules) in order to single out taxonomic units that were distinguished by many traits; and he used this word interchangeably with *gute Art* or "good species" — an expression that Darwin also used in the *Origin*.

Many commentators have remarked on the fact that Mendel never used the German counterpart for heredity or inheritance, *Vererbung*. Only twice in his published and unpublished writings did he use the verb *vererben*, and in these instances in order to emphasize that a certain trait was *not* inherited. This does not mean, as our translation effort has revealed, that transmission talk was completely absent. Occasionally, Mendel uses a typically German verb construction — *übergehen* ... *auf* — that previous translators have rendered as "are transmitted to". *Übergehen* is a peculiar expression, however. Since it is an intransitive verb, it does not suffer the passive voice, nor can it have a direct object. There is no straightforward equivalent for this in English. In German, *übergehen* is often used in the context of inheritance of landed property or titles, and hence for the inheritance of indivisible and inalienable goods. This may serve to provide further evidence that Mendel's understanding of hereditary mechanisms was not the same as that of later geneticists.

A final example may suffice to show what details a reflective translation exercise can reveal. Of particular interest to anyone trying to locate the current concept of genetics in Mendel's paper of 1866 are the different ways in which he talked about the relationship between the traits (*Merkmale*) that he observed and the dispositions for these traits within the germ cells. While the first half of Mendel's paper exclusively concerned itself with visible traits, the second half, from section 9 onwards, also contains speculations as to the state of affairs within reproductive cells. The two main terms that he used in these discussions referred to fertilised cells possessing some kind of generative capacity or dispositions (*Anlagen*), or being composed of elements (*Elemente*), that were responsible for the production of a trait. At one point Mendel surmises that in hybrids, these elements fail to reach a "compromise between the conflicting elements" (*Ausgleichung ... der widerstrebenden Elemente*). *Widerstrebend* conjures images of struggle and active resistance, while *Ausgleichung* connotes a settlement of conflict by negotiation — in short, Mendel ascribes agency to the elements that unite in a newly fertilized cell. Sherwood has "balance between the antagonistic elements" where Druery and Bateson speak of an "arrangement between the conflicting elements". To contemporary readers, both translations hide much of Mendel's vitalist language, which is more reminiscent of the language of German *Naturphilosphie* than of twentieth-century genetics. They also hide the distinct political undertones these terms must have had for Mendel's contemporaries who witnessed the negotiations that came to be known as the "Austro-Hungarian Compromise" in 1867.

TRANSLATION BASIS

Mendel's paper first appeared in volume IV of the journal *Verhandlungen des naturforschenden Vereins zu Brünn*, which covered papers that had been read at the monthly gatherings of the Brno naturalists' association in 1865, but was printed in 1866. Mendel presented his paper, in two parts, at meetings on February 8 and March 8, 1865, respectively.³ Reports in the daily press on Mendel's two presentations reveal that in the first session Mendel covered the first eight sections of his paper, while in the second session the remaining three sections were read, in which Mendel proposed theoretical interpretations of his results (Olby and Gautrey 1968, pp. 7–9). A manuscript in Mendel's hand has been preserved, which is very close to the printed version, some orthographic differences and printer's errors notwithstanding. It is likely, though not proven, that this is the manuscript that Mendel actually read at the Brno naturalist association's meeting. A facsimile of the original manuscript was reproduced in the journal *Der Züchter* (now *Theoretical and Applied Genetics*) in 1941 (Mendel 1941), and a full transcription was published as a "revised edition of Mendel's classic paper" in Kříženecký (1965a, pp. 57–92).

As a basis for our translation, we have neither used the original manuscript, nor the version that was published in the journal, but an offprint. A note on the original manuscript reveals that Mendel ordered 40 offprints, of which six have been tracked down. For our translation, we used a pdf-file of an offprint that is available online from the Virtual Laboratory and has some corrections in Mendel's hand.⁴ These corrections are included in our transcription within square brackets. We decided to use an off-print for our translation because it was offprints that at least two of Mendel's re-discoverers, Hugo de Vries and Carl Correns, relied on, and because the corrections Mendel entered manually in some of the offprints demonstrate that this can be considered his final, "authorized" version. On the original manuscript and publication history, see Kříženecký (1965b), Weiling (1970) and Orel (1996, pp. 273–276). Czihak (1984) contains a facsimile of another offprint that has the same corrections by Mendel as the one we used for our translation.

HOW TO USE THIS TRANSLATION

As with our online edition of Mendel's paper, this print version places a transcription of the German original text against the English translation on the facing page. This will make it easy for the reader to compare the original with the translation, and identify the German expressions Mendel used. Both transcription and translation contain superscript numbers in blue-green,

3 A full pdf of the journal volume is available from the Biodiversity Heritage Library (http://biodiversitylibrary.org/item/188027).

4 See http://vlp.mpiwg-berlin.mpg.de/library/data/lit26745.