Theory Biosci. (2017) 136:59–67
DOI 10.1007/s12064-016-0236-8

ORIGINAL PAPER

Armin von Tschermak-Seysenegg (1870–1952): Physiologist and Co-'Rediscoverer' of Mendel's laws

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Received: 5 September 2016 / Accepted: 29 September 2016 / Published online: 13 October 2016

Abstract The 'rediscovery' of Mendel's laws in 1900 was a turning point in modern research of heredity/genetics. According to the traditional view, adopted and fostered by many textbooks of genetics, Mendel's principles were presented in the first half of 1900 simultaneously and independently by three biologists (H. de Vries, C. Correns, E. v. Tschermak-Seysenegg). Having thus laid the foundations of further development, the 'rediscovery' continues to attract considerable interest. Since the 1950s, however, serious questions arose concerning both the chronology and specific conceptual achievement of the scientists involved. Not only the independence but also parallelism was analysed in the context of individual research programmes of these three scholars. The youngest of them, Erich v. Tschermak-Seysenegg, was even excluded from the list of 'rediscoverers'. The aim of this paper is to use new archival evidence and approximate the contribution of the physiologist and ophthalmologist Armin von Tschermak-Seysenegg (1870–1952) to the events of 1900 and 1901.

Keywords Mendel's Laws · 'Mendelism' · 'Rediscovery' · Tschermak-Seysenegg v. Armin & Erich

This article is dedicated to the memory of Olaf Breidbach—inspiring thinker, tireless researcher, and colleague.

This article forms part of a special issue of *Theory in Biosciences* in commemoration of Olaf Breidbach.

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Introduction: in the shadow of Mendel

The term 'rediscovery' is frequently used for the events of 1900, when the experimental verifications of some of Mendel's conclusions were announced publicly by three European botanists: Hugo de Vries (1848–1935), The Netherlands; Carl Correns (1864–1933), Germany; and Erich von Tschermak-Seysenegg (1871–1962), Austria-Hungary (Johannsen 1923; Iltis 1924; Roberts 1929; Grant 1956; Dunn 1965; Stubbe 1965; Johansson 1979; Keller 2000). The 'rediscovery' of Mendel's laws resulted in the growth of 'Mendelism', which was seen by contemporaries as a subfield of genetics (e.g. Plate 1932; more about Ludwig Plate in Levit and Hossfeld 2006).

For each protagonist, two principle questions arise: First—whether they discovered the principles on their own or used Mendel's papers to interpret previously obtained results. Second—whether each of those scholars made the discovery independently from each other. Especially the latter question touches upon the parallelism of the discovery, and, eo ipso, also later claims of priority and glory. Depending on the answers and the level of analysis, events of

1900 might be seen not as a 'rediscovery' but rather as a 'new discovery' (Jahn 1957), 'delayed discovery' (Zirkle 1964), or even a complex of 'multiple discoveries' (Brannigan et al. 1981). Issues pertaining to independence, originality, and parallelism are thus reflected in various interpretations of the 'rediscovery' (Roberts 1929; Stomps 1954; Jahn 1957; Dunn 1965; Stubbe 1965; Sturtevant 2001; Zirkle 1968; Olby 1985; Bowler 1989). Furthermore, given the evolving nature of experimental research programmes of the protagonists, it remains unclear what should be the extent of the period covered by the term 'rediscoverery' (Jahn 1957).

For a long time, Erich v. Tschermak-Seysenegg (hereinafter E.T.S.) had been seen as one of the 'rediscoverers' (Johannsen 1923; Nilsson-Ehle 1924; Roemer 1941; Stubbe 1941; Reinöhl 1950; Gasking 1959; Heinisch and Rudorf 1961; Simunek et al. 2009). Some contemporaries even called him "*… the very first Austrian scientist after Mendel who understood the rules of heredity*" (Hänsel 1962: 13). It is also relevant that E.T.S. lived until the early 1960s. He supported the position of a triple parallel (simultaneous) rediscovery already in his first papers (Tschermak-Seysenegg 1900a: 239; Tschermak-Seysenegg 1900b: 555), and consistently promoted his view also in later publications (Tschermak-Seysenegg 1901b: 642; Tschermak-Seysenegg 1901d: 1029, 1908, 1928, 1956, 1958). Implying the identity of discoveries in 1865 and 1900, he even mentioned "(…) *a 35 years long interval*" when comparing in 1931 the original publication of Mendel's paper and the events of 1900 (Tschermak-Seysenegg 1931: 1). Last but not least, he saw himself as a leading contributor in applying the Mendelian knowledge in the field of plant breeding (Wunderlich 1951; Harwood 1997, 2000). However, in the mid-1960s, concerns were raised, highlighting that his original understanding of Mendel's explanations in the context of 1900 had a limited validity both in conceptual and terminological terms (Dunn 1965: 76). He was dropped from the list of the 'rediscoverers' (Stern and Sherwood 1956, 1978; Bowler 1989). Recently (e.g. Moore 2001), it has been argued that he failed because (1) he was not able to draw any generalizations from the data he obtained, and (2) he did not attempt to explain the results he obtained by discovery within an appropriate theoretical framework.

In the summer of 2009, a personal collection of E.T.S. held by the *Archives of the Austrian Academy of Sciences* in Vienna was catalogued and opened for historical research. At the same time, a significant part of personal possessions of Armin v. Tschermak-Seysenegg (hereinafter A.T.S.), his older brother and a prominent physiologist, was identified.[1] Both collections contain correspondence between the two brothers, comprising as a whole 87 items of letters, correspondence cards, postcards, and telegrams. They cover the period from 1898 until 1951 (the year before the death of A.T.S.). The vast majority of the extant correspondence was written and sent from A.T.S. to E.T.S. (83 items): only four items conversely. There are 14 pieces of correspondence sent by A.T.S. to E.T.S. in the period from March 13th, 1898, until November 19th, 1901 that were transcribed and published recently (Simunek et al. 2011a, b; Simunek and Hossfeld 2011, 2012).

Although the mutual correspondence is clearly incomplete, the information contained can help to provide more detailed answers to questions pertaining to their degrees of success in interpreting Mendel's principles in the crucial period of 1899–1901.

An until recently unknown fact is the involvement of A.T.S. in the events of the rediscovery of the Mendelian laws. Despite some very clear statements of E.T.S. and the assumption that the two brothers were very close (Harwood 2000: 1062), the extent, quality, and significance of their relationship for the early Mendelian studies remained unknown. However, it is certain that A.T.S. supported his brother in promoting the narrative of the triple simultaneous 'rediscovery' from the very beginning and though he always excluded himself from the group of Mendel's 'rediscoverers', his interpretations and comments may have played a crucial role in shaping Erich's published views (Tschermak-Seysenegg 1901a, 1923).

On a theoretical level, Armin's contribution concerned both special issues of plant cytology (Simunek et al. 2011a, p. 49–50) and a general interpretation of experimentally obtained results. His support of the younger brother was especially important when it came to mathematical solutions: "*… our numerous discussions concerned primarily my work and various issues of heredity. When it came to mathematical problems, I was quite dependent on his* [Armin's] *guidance, since that was a field where I invariably failed since my earliest youth*", stated for example by E.T.S. later in the unpublished version of his memoires.[2] In another part of his unpublished memoires, E.T.S. even specified: "*He read, improved, and completed almost everything I wrote since the age of 28 until the age of 79, and always insisted on reading with me the proof sheets.*"

With few exceptions, the existing historiography of genetics contains very limited information about this important representative of continental physiology and medicine in early and mid-20th century. A scientist, who was especially during his stay in Prague from 1913 until 1945, deeply connected to a prominent tradition in continental European life sciences, established in the Bohemian

[1] The collection was part of the family archives of A.T.S.'s grandson Dr. Armin Tschermak von Seysenegg Jr. The only two persons who went through the correspondence in the 1980s and 1990s were Armin von Tschermak-Seysenegg's son, Wolfgang Tschermak von Seysenegg, and his son, Dr. Armin Tschermak von Seysenegg Jr.

[2] Collection of A.T.S. Stuttgart, transcription of E.T.S.'s manuscript 'Mein Bruder Armin' [My Brother Armin], p. 25.

capital already by Jan (Körting 1968, 120–1; Maaß 1971, 60, 81).

Life and professional career

Armin (Eduard Gustav) was born in Vienna on September 21, 1870, as the second child of Gustav Tschermak (1836–1927), professor of mineralogy, and his wife Hermine, born Fenzl. She was a daughter of Eduard Fenzl (1808–1879), an Austrian botanist and examinator of G. J. Mendel in Vienna.

Armin had an older sister, Silvia (1868–1923), and the already mentioned younger brother Erich. Silvia (married Hillebrand) was a bacteriologist and an active scientist in her own right. For example, in 1918–19, she shortly worked as a laboratory assistant under Karl Landsteiner (1868–1943), the discoverer of the blood groups A, B, AB, and 0 from 1909.

The relationship between the brothers remained very close throughout their lives. When their father retired (1906), he was knighted and chose the aristocratic predicate 'Edler von Seysenegg'. In 1881–98, A.T.S. attended the Catholic gymnasium in Kremsmünster, Upper Austria. In October 1889, he started his medical studies at the Viennese university. In the summer term of 1893 and winter term of 1893–94, he stayed in Heidelberg, Germany. A.T.S. eventually graduated from the university in Vienna on July 1, 1895, whereby he became a doctor of general medicine. Later, he also qualified as a general practitioner.

Already early on, A.T.S. decided to aim at an academic career. He started by working for a few months as a demonstrator at the Institute for General and Experimental Pathology under Salomon Stricker (1834–1898). Then, he transferred as a volunteer to the Institute of Physiology of the Royal Saxonian United Friedrich University in Halle-Wittenberg under the supervision of the famous physiologist Ewald K. K. Hering (1834–1918). On January 23, 1899, based on his work 'Colour Sense in Indirect Vision' he was named *Privatdozent*. In 1900–06, he worked as assistant of Julius Bernstein (1839–1917). In 1902, he undertook a short study trip to Sankt Petersburg, Russia, where he collaborated with Ivan P. Pavlov (1849–1936). Later on, he also stayed at marine station for zoology of Anton Dohrn (1840–1909) in Naples, Italy. On August 1st, 1903, A.T.S. was named extraordinary professor. In early 1906, he accepted a chair at the Veterinary University (Hochschule) in Vienna. Though his primary interest was in human physiology, he there worked as a full professor of physiology and veterinary physics. In 1908, he served as the managing pro-rector of the school, and in the following year, he became its first elected rector. On November 5th, 1911, he was at the age of forty-four appointed a court counsellor (Hofrat), thus becoming the youngest person in the whole Habsburg monarchy who at that time held this title. In the meantime, he married in Berlin on June 6th, 1911, Ilse Charlotte Penck (1886–1951), daughter of (Friedrich) Albrecht K. Penck (1858–1945), well-known professor of geography and geology in Berlin. Armin and Ilse had four children (one daughter died prematurely) (Fig. 1).

On May 28, 1913, A.T.S. was appointed here a full professor of physiology effective as of June 1, 1913, where he followed in the footsteps of Ewald Hering. In the end, he stayed in Prague until 1945. Tschermak's strongly pro-German feelings surfaced during the WWI, when in 1915 he volunteered for military service in the Austro-Hungarian army in the rank of assistant physician. First, he served in the 2nd army, later in the Emperor Franz Joseph I Guards. He was also deployed with the group of the Knights of Malta, 1st surgical unit in Vielgereut and Malga Belem, Tyrolia, and later in Dolina, Galicia. During his military service, he distinguished himself mainly as a capable surgeon but also played an important role in advocating a reform of Austrian military healthcare. After the end of

Fig. 1 The siblings Tschermaks, app. 1880s (Photo Archive Michal Simunek, Prague)

WWI and creation of Czechoslovakia, he returned to Prague, where he opposed the new development and demanded the establishment of a German University in Prague and was a *spiritus movens* of several incidents of the radical German circles (Hoensch et al. 1999: 120–122; Osterloh 2006: 110–111). Nevertheless, he remained in Prague and went on to establish his own school (among his colleagues or students we find, e.g. Richard Kahn, Eugen Steinach, Steffan Jellinek, and Viktor F. Hess, the winner of Nobel Prize in physics). He was an important member of the local German scientific community. In 1920–21 and then again in 1925–26, he served as Dean of the German medical faculty in Prague. In 1929, he became the chairman of the newly founded society, which later became known as "Deutscher Verein für Familienkunde und Eugenik in der Tschechoslowakischen Republik", in which he published together with several of the main representatives of the early Sudeten German eugenics movement such as Bernhard Brandt, Friedrich Breinl and Otto Grosser in a yearbook on genealogy, genetics and eugenics (Simunek 2015) (Fig. 2).

A.T.S. retired at the end of February 1939 with various honours. Nonetheless, after the German occupation of Bohemia and Moravia and transfer of the Prague German University under the competence of the Reich Ministry of Science, Education etc. (Reichsministerium für Wissenschaft, Erziehung und Volksbildung), A.T.S. returned from retirement and headed the institute *de facto* until the end of the WWII in May 1945. His continuing academic career in the Third Reich was doubtless aided by his political conformity. In summer 1942, at the age of 72 years he volunteered and joined the German Navy (Kriegsmarine). He served first as chief staff surgeon, later as squadron physician and advisor for optics of *Kriegsmarine* in Kiel, Saßnitz, and Swinemünde, where he took part in the research on night vision. In 1946, however, he decided to officially move to Straubing, Bavaria. Despite his advanced age, he tried to get involved in Bavarian academic life, and advocated the establishment of another university in Regensburg. In consequence of very stressful negotiations, he suffered a brain haemorrhage on February 9, 1950. He died two years later, during a regular walk on October 9th, 1952, after suffering another stroke.

He was interested in the physiology of muscles and nerves (e.g. the so-called Tschermaksche Druckversuch, that is, Tschermak's pressure test), bio-electrics and physiology of the brain, but also in general physiology, in particular in physiological optics (physiology of the eye and sight), and even in issues of physics and chemistry as well as cellular physiology and biochemistry (digestion enzymes and fermentation, generation of heat during enzymatic splitting, etc.) (Maaß 1971, 62–5). Tschermak's first teacher, Julius Bernstein, attracted him especially to

Fig. 2 Armin von Tschermak-Seysenegg as an extraordinary professor in Halle, 1901 (Photo Archive Michal Simunek, Prague)

issues of electric phenomena in living organisms, questions of pre-existence of electric charge in body organs, including intact ones, issues of relation between the size of a muscle and the magnitude of the electric process, but also for example the thermodynamics of electric discharge in the particular case of electric ray (Maaß 1971, 62–5). Another large area of A.T.S.'s interest was connected with psycho-physiology, a scientific discipline whose foremost representative was another important teacher of him, Ewald Hering. Continuing in his footsteps, A.T.S. focused mainly on the notion of a living substance surviving under conditions of two balanced contrasting phenomena (so-called assimilation and dissimilation), which led to his work on tonic innervation of autonomous organs. In somewhat related line of research, A.T.S. also studied the general physiology of senses and ophthalmic physiology. In these areas, he focused on sight and colour vision—where he was inspired by the Purkinje phenomenon —but also on the stereoscopy of colours, colour blindness, mutual interference of colours, photosensitivity, night vision, etc. (Maaß 1971: 81). A central place among several hundreds of original papers belongs doubtless to his synthetic work 'General Physiology' (Tschermak-Seysenegg 1916–24) (Fig. 3).

During his long and uncommonly prolific scientific career, A.T.S. won numerous awards and distinctions. In 1911, he received the Japanese Meiji Imperial Cross of Merit together with the badge of 2nd class of the Order of the Rising Sun (Commander), he was named Grand Officer of the Order of the Crown of Italy with a star, Knight Commander of the Order pro Merito Melitensi with a cross, Grand Officer of the Yugoslav Order of St. Sava with a star, and received various Austrian distinctions. He was a member of many scientific societies, such as the German Academy of Natural Scientists (Leopoldina) in Halle an der Saale or the Section for Mathematics and Natural sciences of the German Society for Science and Art for the Czechoslovak Republic in Prague. As a devout Catholic, he was especially honoured when, as one of just a handful of German scientists (e.g. M. Planck, C. Delouge, E. Abderhalden, E. Schrödinger, and E. F. Petritsch), he was in 1936 offered membership in the Vatican academy *Academia Pontificia de las Ciencias*.

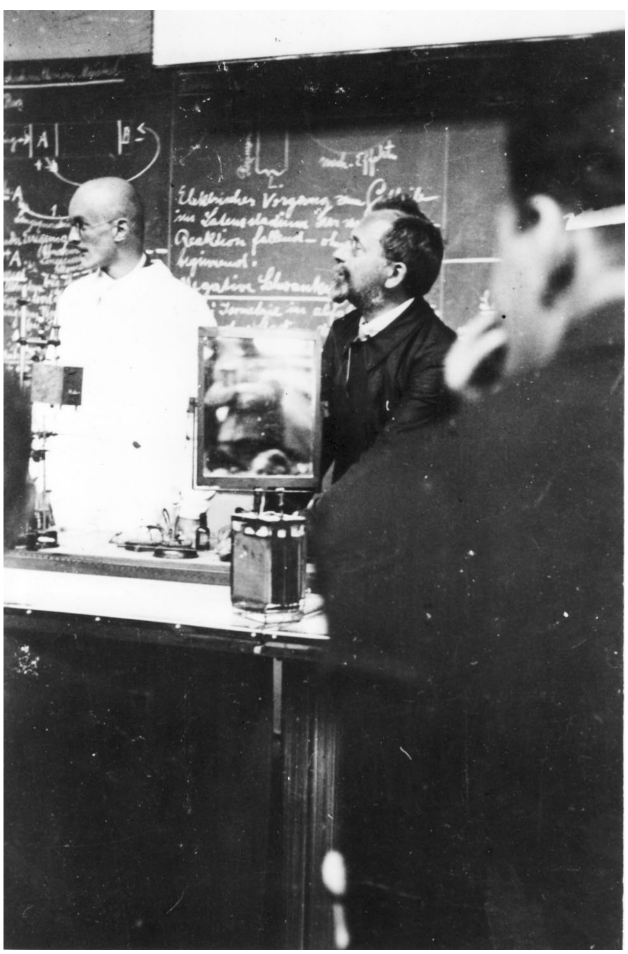

Fig. 3 Armin von Tschermak-Seysenegg giving his lecture at the Institute of Physiology of the Faculty of Medicine of the German University in Prague, 1920s (Photo Archive Michal Simunek, Prague)

Hereditary/genetic issues

In the area of hereditary studies, A.T.S. was among the pioneers of a line of research that was inspired by Gregor J. Mendel's studies from 1850s and 1860s, which after 1900 became known as 'Mendelism' (Simunek et al. 2012; Hossfeld et al. 2015a, b, 2016).

The mutual collaboration with his brother started already before 1900. In March 1898, A.T.S. encouraged his younger brother to write his second thesis (Habilitation) in botany with the clear goal of pursuing an academic career (Simunek et al. 2011a: 39–40). As a research topic, he suggested the phenomenon of doubleflowered varieties and the study of natural and artificial processes such as the use of irritant liquids (organic acids) that may be used to stimulate this phenomenon. At that time, there already existed a large number of both original papers and reviews on this topic (Masters 1886; Penzig 1890–1994). Interestingly, A.T.S. also brought to his brother's attention the possibility of appearance of double-flowered varieties due to the influence of parasites such as nematodes. This research direction was quite unique at that time because reasons behind the phenomenon were still unknown (Korschinsky 1901). A.T.S. advised his brother on the methodology of research, offered help with preparation techniques, and suggested the assistance of Adolf von Liebenberg. During the following year, 1899, he encouraged his brother to focus primarily on his habilitation (2nd degree in Germany, Dr. sc.), and suggested they would meet in the city of Halle, Germany, where he stayed, to discuss further details (Simunek et al. 2011a: 41).

The first extant letter on hybridisation was written on April 4th, 1900, after the brothers spent the Christmas season of 1899/1900 together in Vienna (Simunek et al. 2011a: 42–5). At this time, A.T.S. translated and reviewed for his brother de Vries's notes *Sur la fécondation hybride de l'albumen* [On the Hybrid Fertilisation of the Albumen] published in the end of 1899 in the Parisian journal *Comptes Rendus de l'Académie des Sciences* (De Vries 1899). He also recommended to Erich's two further papers authored by Hugo de Vries and Carl Correns (Correns 1899; De Vries 1900). Although he focused primarily on Sergej Nawaschin's and Jean-Luis Guignard's theories of fertilisation, the connection to hybridization experiments was apparent. Last but not least, A.T.S. explicitly discussed de Vries's knowledge (or ignorance) of 'Mendel's teaching'. Commenting on de Vries's experiments with xenia in *Zea Mais,* A.T.S. wrote at the beginning of April 1900: "*But he* [de Vries] *doesn't know the teaching of Mendel! Ha! Ha!! But please don't offend him: He will need to learn it from you!*" (Simunek et al. 2011a: 42–5). More than ten days later, on May 16th, 1900, A.T.S. first commented on the corrections of Erich's thesis (Simunek et al. 2011a: 46–8). At that time, Armin suggested that Erich should publish a short report (Autoreferat) on his results in the *Biologisches Centralblatt*. This idea, in the end, did materialise in a further early 're-discovery' paper (Tschermak-Seysenegg 1900c), which has been often overlooked (Mielewczik et al. 2016). Using some of Mendel's terminology, A.T.S. returned to his study of de Vries's work (in particular, to the hybridization of *Chierathus*). He expressed his views on current research of variation and especially heredity as follows: "*The entire theory of heredity needs critical examination. So far* [underlined in the original], *it offered no proof that a hereditary transfer of traits of, for example, a species or an individual from a parent organism to the offspring takes place in such a way that the differentiation of the former causally determines that of the latter. What is a fact is just the conformity, the sharing of certain traits: one part involves the living substance (the personal part) immediately, the other (germinal) only later, usually only after some infusion of foreign plasmas, after a 'fertilisation'. This conformity may be for the main part related to some particular difference between the cytoplasm and the nucleus…*" (Simunek et al. 2011a: 46–8). In this context, he called Mendel '*blessed*' [Segen bringend]. Congratulating Erich on June 23rd, 1900, A.T.S. answered his question about the origin of the fabric of the *Pisum* corns (Simunek et al. 2011a: 49–51). He recommended to his brother to notify Hugo de Vries of certain corrections in his, that is, Erich's larger paper (Tschermak-Seysenegg 1900b) by a postcard, and added explicitly that Carl Correns should not be included. Referring to Correns, he wrote: "*… that squabbler will be eventually proven wrong by a (later) correction*" (Simunek et al. 2011a: 49–51). He also strongly discouraged the adoption of de Vries's segregation [Spaltung] hypothesis. He advised his brother: "*The segregation of traits is a schematic speculation of de Vries: I emphatically warn against believing it!*" (Simunek et al. 2011a: 49–51). On October 15th, 1900, A.T.S. told E.T.S. that he should finish the second paper on heredity of peas and beans (Tschermak-Seysenegg 1901b), and discussed de Vries's theory of mutation (Simunek et al. 2011a: 52). In the first half of 1901, A.T.S. was apparently very actively working on interpreting the results of Erich's hybridization experiments. Correcting their crucial misunderstanding of Mendel's original notion of a '*first generation of hybrids*', he wrote on February 18th, 1901, about the collaboration with his brother, and mentioned explicitly that some corrections Erich adopted had the effect of "*… saving us from disgrace in front of that vicious Correns*" (Simunek et al. 2011a: 53–57). On March 10th, 1901, A.T.S. welcomed the reprint of Mendel's original papers (Mendel G. J./Tschermak E. 1901), which he perceived unambiguously as offensive to Correns (Simunek et al. 2011a: 56–8). On May 18th, 1901, he helped Erich with the question of whether endosperm fertilisation has the same validity as a real fertilisation (Simunek et al. 2011a 58–9). On May 19th, 1901, he commented on his experiments with *Primula*, and informed his brother of his intention to work on cotyledon formation (Cotyledonenkeimungsplan), a subject Erich which also touched previously (Tschermak-Seysenegg 1901b) (Simunek et al. 2011a: 60–1). On October 19, 1901, A.T.S. recommended that Erich should present his 1901 *Zeitschrift für das landwirthschaftliche Versuchswesen in Österreich* article as an '*important correction of the views of Mendel and Rimpau*', that is, not as their pure repetition (Simunek et al. 2011a: 62–3). He also instructed Erich on the presentation of Mendel's laws in Vienna. When congratulating him on his birthday on November 13th, 1901, A.T.S. expressed his view that Erich's chances for a successful academic career were at that stage promising (Simunek et al. 2011a: 66–7). He also mentioned some further unspecified metaphorical '*preparation*' (Präparation) of Hugo de Vries' person, and commented in this context that "*Correns will keep his peace now*" (Simunek et al. 2011a: 66–7). A week later, he thanked Erich for a paper on cereals (Tschermak-Seysenegg 1901c); he ranked this paper very high (Simunek et al. 2011a: 68). Later, both A.T.S. and E.T.S. supported the interpretation line of simultaneous and triple 're-discovery' (Simunek et al. 2016).

This rough overview rises the following question: Which version of early 'Mendelism' E.T.S. presented in around 1900? He focused primarily on traits in hybrids, in particular on data he obtained in F_1 and F_2 generation by heteromorphic xenogamy (Xenogamy means the transfer of pollen grains from the anther to the stigma of a different plant) (Tschermak-Seysenegg 1901b). In Mendel's original work, he appreciated the analysis of traits (Merkmalsanalyse), or '*decomposition of the whole habitus into individual traits*' (Tschermak-Seysenegg 1901d: 1030). He also analysed the expression of various traits including the so-called vegetative traits (vegetative Merkmale), and concluded that some traits are realised in hybrids only in an alternating (alternierende) form. He saw this as a proof of 'different valuation' of the traits. Based on this observation, he introduced his own terms for recessive ('undervalued'/unterwertig) and dominant ('over valued'/überwertig) traits. The 'valence of a trait' was thus 'behaviour/comportment of a trait' (Tschermak-Seysenegg

1906: 882). He did not, however, see these characteristics as generally valid but rather limited to vegetative traits. In relation to both breeding practice and a 'racial history', he was especially interested, most probably for very practical reasons, in the historically understood 'age of a trait' (Tschermak-Seysenegg 1901d, 1906: 882). He implied that dominant traits might be older than recessive ones, however clearly stating himself, that there are certainly many exceptions (Tschermak-Seysenegg 1906: 882). This would not support his inclination to hereditary factors as 'atoms of heredity' in the mechanistic materialistic sense at this time (Allen 2002). Even later, he distinguished between 'racial or mendeling traits' and 'special traits' in accordance with H. de Vries (Tschermak-Seysenegg 1906). Later on, E.T.S. described his original approach as purely 'descriptive' and 'phenomenological' "*… in order not at once to anchor the newly-beginning experimental phase of the doctrine of heredity—as had happened inexpediently with Darwinism—to definite theoretical terms*"(Olby 1985: 123). In the words of Tschermak's contemporaries, he dealt primarily with the 'external mode of heredity' [äußere Vererbungsweise] (Roemer-Bromberg 1914) (Fig. 4).

In 1900, and even more in 1901, E.T.S. resumed his views into 'theory of regular differential valence of traits in heredity' (Lehre von der gesetzmässigen Verschiedenwertigkeit der Merkmale für die Vererbung) (Tschermak-Seysenegg 1901b: 37–8, 1901c: 643–47). It was seen as consisting of three basic postulates: (1) The principle of a regular dimensional valence (Satz von der gesetzmässigen Masswertigkeit), related to an 'absolute dimension' (das absolute Ausmass) or a proportional 'relative dimension' (das relative Ausmass) with a clear 'prevalence' (Prävalenz) or 'undervaluation' of one or almost of both traits; (2) the principle of a regular quantitative valence (Satz von der gesetzmässigen Mengenwertigkeit), which concerned the number of 'carriers' of one particular trait in comparison with other corresponding traits; and (3) the principle of regular hereditary valence (Satz von der gesetzmässigen Vererbungswertigkeit) or 'segregation of traits' (Spaltung der Merkmale), which could be derived from regular quantitative valuation in a chain of generations.

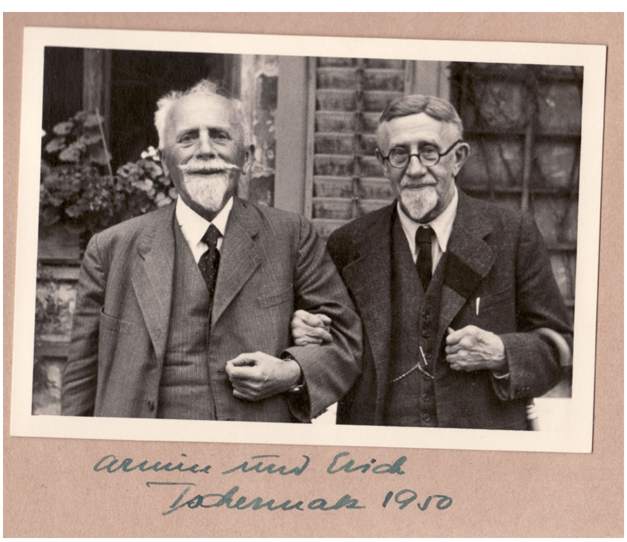

Fig. 4 Last known common photo of the brothers A. T. S. And E. T. S., 1950 (Photo Archive Michal Simunek, Prague)

Hereditary 'factors' or 'elements' as well as the theory of a 'purity of gametes' did not play an explicitly significant role in his/their early analysis, i.e. in association with a pair of determiners which segregate to individual reproductive cells as they are formed. In papers published by E.T.S. in 1900 and 1901, there is only one detailed remark on Mendel's view, namely, that he '*… even deduced some elements to be in the special organs of the cell or parts of the plasm*' (Tschermak-Seysenegg 1901d: 1030). Especially the theory of factors was later attributed by both Tschermak-Seysenegg brothers to C. Correns, W. Bateson, R. Punnett and L. Cuénot. In several places, the so-called 'trait carriers' (Träger der Merkmale) were used in connection with the ratio of 3:1. As a part of 'further development of Mendel's legacy' A.T.S. further added the theory of cryptomery, which was, for example, understood by both as a parallel line of genetical thinking to the theory of cumulative and simultaneously acting factors (Herman Nilsson-Ehle) (Tschermak-Seysenegg 1923: 704, 1942: 228).

The mutual collaboration of Tschermak-brothers on hereditary/genetic issues clearly did not end in 1901. In the already quoted manuscript of his memoirs, E.T.S. acknowledges that "(…) *he* [A.T.S.] *was from the beginning to the end of my scientific career my collaborator and advisor*".[3] And added that for example, they commented together on W. Johannsen pure-line theory (Tschermak-Seysenegg and Tschermak-Seysenegg 1927). A.T.S.'s probably most important single contribution was his 'theory of weakening of traits through hybridisation', also known as a 'theory of hybridogenous genasthenia' (Tschermak-Seysenegg 1918). It was based on his own experimental research with the crossbreeding of poultry (Tschermak-Seysenegg 1918). At his physiological institute in Prague, A.T.S. carried out hybridisation experiments, including reciprocal ones, using 5 species of poultry and 161 hybrids, until winter 1916–17. In three/four generations, he followed and correlated 32 traits. This theory was closely related both to the theory of cryptomery—best known in E.T.S.'s formulation—and described a precursor of a true disappearance of a hereditary trait, that is, of genophthisis (Tschermak-Seysenegg 1935: 192). Last but not least, A.T.S. referred the results of hybridisation

[3] Collection of A.T.S. Stuttgart, transcription of E.T.S.'s manuscript 'Mein Bruder Armin' [My Brother Armin], p. 1.

experiments also to the area of eugenics, or ‘Familienkunde’, as part of which it was then called in German. In the 1920s, it was in his view both already possible and desirable to develop a systematic study of heredity in humans (Tschermak-Seysenegg 1931). From a medical point of view, he emphasised especially the hereditary character of blood diseases, but was interested also in the heritability of diseases of the eye (such as colour blindness for greed and red colours or albinism of the eye), which he found particularly relevant. He spoke explicitly of ‘pathological hereditary units’ and ‘abnormal properties and diseases’ (Tschermak-Seysenegg 1931: 18–20).

Conclusion

At the time of ‘rediscovery’, a particular line of thought was developed out of the brothers Armin and Erich von Tschermak-Seysenegg mutual collaboration, and the themes that originated then were about to influence interpretation of ‘Mendelism’ later on.

On a theoretical level, A.T.S.’s contribution at that time concerned general interpretation of experimentally obtained results and some specific issues, e.g. of plant cytology. Reasons behind A.T.S.’s involvement, which went far beyond merely helping his brother, may offer some clues: especially his interest in the ‘anatomy of hybrids’ seems significant. On a practical level of ‘doing science’, including personal ties and tensions, his role was clearly even more significant: he helped design his brother’s research schedule, suggested methodical improvements, reviewed and commented on his brother’s manuscripts and papers and, if necessary, gained support for their positions within the scientific community.

Both brothers repeatedly and explicitly mentioned not only a ‘rediscovery’ (Wiederentdeckung) as an initiating act, but also a need of ‘further development’ (Weiterführung), ‘extension’ (Erweiterung), and even a ‘new build-up’ (neuer Ausbau) of Mendel’s teaching as a further process. This clarifies that they understood the potential benefits of incorporating further theoretical frameworks into their understanding of Mendel’s legacy as it was publicly articulated by E.T.S and A.T.S. several times. On the other hand, it strongly limits their original understanding of Mendel’s explanations presented publicly by E.T.S. in 1900 and 1901.

Considering the role A.T.S. played in moderating the events of 1900 and 1901, known as ‘rediscovery’ of Mendel’s laws, the parallelism aspect of the ‘rediscovery’ story becomes even more tangled than previously thought. Based on existing evidence, it also seems to be confirmed that the degree of independence between the ‘rediscoverers’ and original Mendel’s conclusions was substantially smaller than it has been generally assumed previously.

Acknowledgments This paper was published as part of a research project HO–2143/8–1, 8-2 supported by the German Research Foundation (DFG). GL‘s work is supported by the *Russian Foundation for the Humanities*, project 16-03-00555.

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