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ORIGINAL PAPER

‘Further Development’ of Mendel’s legacy? Erich von Tschermak-Seysenegg in the context of Mendelian–biometry controversy, 1901–1906

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Abstract The contribution of Erich von Tschermak-Seysenegg (1871–1962) to the beginning of classical genetics is a matter of dispute. The aim of this study is to analyse, based on newly accessible archive materials, the relevance of his positions and theoretical views in a debate between advocates of early Mendelian explanation of heredity and proponents of biometry, which took place in England around 1901–1906. We challenge not only his role of an ‘external consultant’, which at the time de facto confirmed his status of ‘rediscoverer’ of Mendel’s work but also analyse his ambivalent positions which are to be seen as a part of ‘further development’ (Weiterführung), a development of Mendel’s legacy as he understood it. Second, there is an interesting aspect of establishing connections within an ‘experimental culture’ along the Mendel’s lines of thought that was parallel to the first step of institutionalizing the new discipline of Genetics after 1905/06. Part of the study is also the analysis of contribution of his older brother Armin von Tschermak-Seysenegg (1870–1952) who—much like in the case of ‘rediscovery’ of 1900–1901—was for his younger brother an important source of theoretical knowledge. In this particular case, it regarded Bateson’s ‘Defence’ of Mendel from 1902.

Keywords Mendel’s Laws · ‘Rediscovery’ · Biometry · Mendelism · v. Erich and Armin v. Tschermak-Seysenegg · William Bateson

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Introduction

> “*Their* [H. de Vries’s, E. Tschermak’s] *groups of papers, if their work is all reliable, carries things on a long way.*”
> William Bateson to Sir Francis Galton, August 9, 1901

The ‘great controversy’ (Mayr 1973), which most intensively took place in England around 1901–1906, represents one of the key theoretical disputes in twentieth-century biology (MacKenzie 2000; Punnett 1950). It highlighted substantive differences in understanding of Mendel’s theory, and underscored the need to relate Mendel’s findings to evolution in general, and Darwin’s theory of continual variations in particular (Farrall 1975; MacKenzie and Barnes 1975; Provine 1971; Allen 1979; Roll-Hansen 1980). It is seen not only as a testing ground of a new paradigm but also as a “case study in the role of controversy and conflict in science” (Farrall 1975, p. 270), where the competing camps established themselves as opposing schools. Chronologically, this controversy overlapped with the reception and experimental verification of Mendel’s rules of heredity but it occurred in a different institutional and intellectual context (Kevles 1981; MacKenzie and Barnes 1975). It took place during a crucial period of ‘conceptual and terminological clarifications’ (Mayr 1973), which became the starting point of classical genetics before WWI. Nonetheless, it remains a current question whether this discussion in effect “delayed progress in Britain in various areas related to genetics”, that is, whether it did or did not delay the incorporation of Mendel’s analysis of heredity in the theory of continual variations (Richmond 2008; Olby 1988; MacKenzie and Barnes 1975; Provine 1971; Cock 1973; Wright 1967).

The main persons involved in this debate were two former collaborators and colleagues, the botanist William Bateson (1861–1926) and the zoologist Walter F. R. Weldon (1860–1906). They not only "differed in the scientific problems which they confronted and the alternative programmes they adopted" (MacKenzie and Barnes 1975, pp. 166–167) but also came from different backgrounds, and took not similar views on issues such as the influence of the environment, etc. (Kevles 1981; Provine 1971). One should also take into account the link with Bateson's own experimental research in hybridisation, which started already in 1897 and helped to create his status as one of the contributors to the 'rediscovery' (Richmond 2008; Darden 1977; Cock 1973; Provine 1971; Sturtevant 1965). This put the botanist in a position well-suited to appreciate Mendel's work, and "…once Mendel's work was brought to his notice, he was peculiarly well fitted to recognize its importance and far-reaching implications" (Cock 1973, p. 7). Weldon, on the other hand, originally worked on evolution of marine fauna, and in 1890–1900, focused on research of evolution in quantifiable terms (Olby 1988). Karl Pearson (1857–1936), Weldon's student and later leading biometrician also played an important role in this discussion.

The origins of the controversy, in fact, predate the 'rediscovery' of Mendel's work in 1900–1901. Already in 1894, when Bateson published his 'Materials for the Study of Variation', Weldon replied with a criticism. Similarly, tense was the relationship between Bateson and Pearson after they clashed in 1900 about the issue of homotyposis (Pearson 1901; Farrall 1975; Provine 1971). In general, the 'phase of virulent dispute' can be said to have taken place in 1902–1906, ending in the year of Weldon's premature death (Cock 1973: 9). It should be noted that the debate also concerned the issue of academic positions and sources as well (Pearson 1910; Kevles 1981; Provine 1971). The main journal Weldon and Pearson used during the controversy was the 'Biometrika', which first appeared in October 1901.

The controversy was largely seen as a 'British affair', closely connected with the introduction of Mendelism to England in general, and with the 'process of Bateson's conversion to Mendelian heredity' in particular (Olby 1987, 1988, p. 300; Provine 1971, p. 89). Even so, in their different ways, various foreign researchers have also entered the debate. Of the contemporary 'rediscoverers', this was the case mainly of Dutch botanist Hugo de Vries (1848–1935)[1] and Austrian botanist and agronomist Erich von Tschermak-Seysenegg (1871–1962) (Olby 1988).

[1] Unfortunately, the inventory of H. de Vries' correspondence does not include the letters of W. Bateson, or/and W.F.R. Weldon and K. Pearson (Zevenhuizen (1996), pp. 88–96).

The meanders of 'rediscovery'

After 1900, E.T.S. was seen, according to the 'traditional view' (Corcos and Monaghan 1990), as one of the three 'rediscoverers' for a longtime (Johannsen 1923; Nilsson-Ehle 1924; Stubbe 1941; Barthelmess 1952). He supported the position of a triple parallel (simultaneous) 'rediscovery' already in his first papers (von Tschermak-Seysenegg 1900), and consistently promoted this view also in his later writings. 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 events of 1900 (von Tschermak-Seysenegg 1931). Very important in this context was also his involvement in the commemoration and celebration of Mendel's personality and his work, which started immediately after 1900, and took the form of, for example, re-publication of Mendel's paper in 1901 (von Tschermak-Seysenegg 1901d). He saw himself as a leading advocate of application of the Mendelian theory in the fields of plant breeding and botany, and interpreted this contribution regarding the new 'rational' basis (von Tschermak-Seysenegg 1958; Wunderlich 1951; Harwood 1997, 2000; Roll-Hansen 1997; Müller-Wille 2005; Wieland 2004, 2006). And last but not least, it may also be relevant that E.T.S. lived until the early 1960s. Some of his fellow countrymen even viewed him as "… the very first Austrian scientist after Mendel who understood the rules of heredity" (Hänsel 1962, p. 113; Kříženecký 1965; Scheibe 1970; Ruckenbauer 2000).

Doubts regarding the general claims of E.T.S., in 1900, the youngest of the three 'rediscoverers', appeared in 1950s (Platt 1959). In the next decade, he was even dropped from the list of 'rediscoverers' (Stern and Sherwood 1966, 1978; Corcos and Monaghan 1986a, b, 1987, 1990). In the mid-1960s, it was argued that his original understanding of Mendel's explanations in the context of 1900 had limited validity both in conceptual and in terminological terms. He was seen as a scientist whose views were shaped by '… preceding generations of the older hybridizers rather than the direct influence of Mendel himself' (Roberts 1924, p. 356), and 'an example of a biologist who interpreted what we now regard as Mendelian phenomena within a pre-Mendelian concept of heredity' (Olby 1985, p. 114). Lately (Moore 2001), it has been argued that he failed because he was not able to draw any generalisations from the data he obtained experimentally (Corcos and Monaghan 1990). Despite the 'universal rejection' of E.T.S.' role in the 'rediscovery' (Bowler 1989), some contemporary authors, however, see him as a 'key player' among the first generation of Mendelians (Carlson 2004). Another line of argumentation tries to make clear difference between his activities in the area of academic and practical breeding on one and theoretical genetics on the other side (Harwood 2000).

To a large extent, existing interpretations have been based on contemporary statements and/or memoirs. Recently published new archival sources, however, justify a correction of former interpretations (Simunek et al. 2011). Firstly, they shed a new light on E.T.S.' reading of Mendel's papers; secondly, they provide new information about his collaboration with his older brother, the prominent physiologist Armin von Tschermak-Seysenegg (1870–1952; hereinafter A.T.S.).[2] Although Armin supported his younger brother in promoting the story of the triple, simultaneous, and independent '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 lately published views (von Tschermak-Seysenegg 1901a). On a theoretical level, Armin's contribution concerned both special issues of plant cytology and a general interpretation of experimentally obtained results (Simunek et al. 2011). His help 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 E.T.S. later in the unpublished version of his memoires (Ibid.: 25). It is quite plausible that it was Armin's insistence on a highly critical approach, which shaped his brother published interpretations.

In this context, it is crucial to see that 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 in the next future (Simunek et al. 2011; von Tschermak-Seysenegg 1901c). It means 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. Later on, Erich described his original approach as '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, p. 123). In the words of Tschermak's contemporaries he dealt primarily with the 'outer art of heredity' (äußere Vererbungsweise) (Roemer-Bromberg 1914, p. 4). This was especially the case of understanding of the theories of purity of gametes, factors [Faktorenlehre/Elementenlehre]. For example, the theory of factors was attributed by both Tschermak-Seysenegg brothers to C. Correns, W. Bateson, R. Punnett and L. Cuènot (Roemer-Bromberg 1914, pp. 4–37; von Tschermak-Seysenegg 1912, 1913; Olby 1979).

What were the main conclusions of E.T.S. regarding his studies on crossbreeding and heredity in 1900 and 1901? Having started his research early, at the age of just 28 years, he focused primarily on traits in hybrids, in particular on data he obtained in F_1 and F_2 generation by heteromorphic xenogamy (von Tschermak-Seysenegg 1901a, p. 37). In Mendel's work, he appreciated the analysis of traits (Merkmalsanalyse), or 'decomposition of the whole habitus into individual traits' (von Tschermak-Seysenegg 1901c, p. 1030). E.T.S. 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 alternative (alternierend) form. He saw this as a proof of 'different values' of the traits. Based on this observation, E.T.S. introduced his own terms for recessive ('undervalued'/unterwertig) and dominant ('over valued'/überwertig) traits. The 'valuation of a trait' was thus 'comportment of a trait' (von Tschermak-Seysenegg 1906, p. 882). He did not, however, see this valuation as something generally valid but rather as something limited to vegetative traits (von Tschermak-Seysenegg 1901a, p. 51, 1901c, p. 1032). In relation to both the breeding praxis and a 'racial history', E.T.S. was especially interested, most probably from the practical reasons, in the 'age of a trait' (Tschermak-Seysenegg 1901c, p. 1058). He implied that dominant traits may be older then the recessive ones. 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 (von Tschermak-Seysenegg 1906, p. 887).

[2] Armin (Eduard Gustav) von Tschermak-Seysenegg (September 21, 1870 in Vienna, Austria to October 9, 1952 in Bad Wiessee, Germany) studied medicine at the Universities of Vienna, Austria, and Heidelberg, Germany. After completing his studies in Vienna in 1895, he moved to Leipzig. From 1899 until 1906, he worked at the University of Halle, where he was appointed adjunct professor in 1902. He counted himself to the school of E. Hering. After 1906, he returned to Vienna where he temporarily received full professorship in physiology and medical physics at the Veterinary College (Hochschule für Tiermedizin), a school he helped to establish. In 1909–1911, he served as its Rector. In 1913, he came to Prague, Bohemia, to fill a vacancy at the Institute of Physiology, a venerable institution founded in the nineteenth century by J. E. Purkinje. After receiving full professorship, he was appointed director of this Institute. He continued to lecture in Prague at the German (Charles) University until the end of WWII in 1945. His research focused mainly at general and special physiology (physiology of sight), anatomy, and neurology. He co-edited the *Zeitschrift für Physiologie*, the *Zeitschrift für Sinnesphysiologie*, and the *Archiv für Augenheilkunde*. He was a member of several scientific societies and academies across Europe. In 1936, together with Th. H. Morgan he became member of the Academy of Sciences of the Holy See (Pontificia Academia Scientiarum) in the Vatican. He died on October 9, 1952 in Bad Wiessee in Bavaria.

Interestingly, hereditary 'factors' or 'elements' did not play explicitly significant role in his 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 him 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 1901c, p. 1030). In several places, the so-called 'trait carriers' (Träger der Merkmale) were used in connection with the ratio of 3:1 (von Tschermak-Seysenegg 1901a, pp. 37, 39, 1901b, p. 644). On May 16, 1900 Armin, for example, admonished Erich: "The entire theory of heredity requires critical examination. So far, it has offered no proof that a hereditary transfer of traits of, for example, a species or of 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 the fact is just a 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. 2011, p. 22). Trying to explain the different valuation of traits, he also allowed for further 'factors' such as, for example, the sex of the transmitter (von Tschermak-Seysenegg 1901a, p. 47), and of special influence was the 'race' or a 'combination of the races'(von Tschermak-Seysenegg 1901a, p. 48, von Tschermak-Seysenegg 1901c, pp. 1059, 1428, 1903, pp. 3–45). Following an older tradition, he even mentioned a strengthening (or weakening) of paternal traits in the hybrids (von Tschermak-Seysenegg 1901a, pp. 49–50), which he suggested could be used in 'valuation tables' (Wertigkeitstabellen) for individual traits.

In 1900, and even more in 1901, he resumed his research of 'theory of regular differential valuation of traits in heredity' (Lehre von der gesetzmässigen Verschiedenwertigkeit der Merkmale für die Vererbung) (von Tschermak-Seysenegg 1901a, pp. 643–647, 1901b, pp. 37–38).[3] It was seen as consisting of three basic postulates: (1) the principle of a regular dimensional valuation (Satz von der gesetzmässigen Maasswertigkeit) related to an 'absolute dimension' (das absolute Ausmass) or a '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 valuation (Satz von der gesetzmässigen Mengenwertigkeit), which concerned the number of 'carriers' of one particular trait in comparison with other corresponding traits; (3) the principle of regular hereditary valuation (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 (von Tschermak-Seysenegg 1901a, p. 38, von Tschermak-Seysenegg 1901b, pp. 645–646).

He saw the notion of 'regular differential valuation of traits in heredity' as especially important for the practical plant breeding since it offered a "point of departure and instrument of a rational creation of hybrids and mongrels, or breeding of new races by the means of crossing of other, already existing races" (von Tschermak-Seysenegg 1901a, pp. 38, 1428; 1901b, p. 647). This was also reflected by a group of Austrian and German plant breeders and agronomists with whom E.T.S. stayed in touch immediately after the publication of his well known paper on *Pisum.* These were Franz F. Schindler (1854–1937), Emanuel von Proskowetz (1849–1944), and Carl Fruwirth (1862–1930).[4]

Between the quarrelled parties

In late October 1901, W.F.R. Weldon asked E.T.S. to provide information on his experiments with *Pisum*. The timing coincided with the first phase of the controversy in England (Provine 1971, pp. 70–71). We find no mention in extant correspondence of any similar request being made by Weldon of Hugo de Vries or Carl Correns. It is likely that Weldon's intention in this case—like in his later experiments with mice—was to carry out own hybridisation experiments (Ibid.: 73). Weldon's letter of October 26, 1901, thus introduced a period of several years when E.T.S. occupied a position of 'foreign consultant' in the 'British affair'.

He knew he was involved in the debate from the outset, because Weldon explained the purpose of his request with these words: "I am preparing an account all work bearing upon Mendel's Laws for the new statistical journal Biometrika".[5] This writing was based on E.T.S.' works heretofore published in Zeitschrift für landwirthschaftliche

[3] There is a problem with the English translation of 'Werthigkeit' dating back to 1906 and Bateson's corrections of Tschermak's paper on 'The Importance of Hybridisation in the Study of Descent', in: Wilks, W. (1907), $$$Report of the third international conference 1906 on genetics, London: Royal Horticultural Society, p. 279. We assume that more accurate is the 'valuation' since the German expression for 'valency' is 'Valenz', and Tschermak used it some of his German-published papers in different context (Olby 1985, pp. 121, 129). For understanding as 'capacity to prevail, or its ability to breed in subsequent generations' see Harwood 2000, p. 1064.

[4] Immediately in 1900 and 1901, E.T.S. corresponded with F. Schindler (May 22, 1900, May 14, 1901, January 11, 1901, and November 14, 1901), E. von Proskowetz (June 4, 1900), C. Fruwirth (May 23, 1901), C. Fruwirth (May 23, 1901), and J. v. Wiesner (October 27, 1901).

[5] Weldon to E.T.S., October 26, 1901, Archiv der Österreichischen Akademie der Wissenschaften (hereinafter A ÖAW) Wien, C1, 1–27.

Versuchswesen in Oesterreich, that is, on all of his basic writings immediately related to the 'rediscovery'. Weldon phrased the main objective of his request rather diplomatically: "I feel that I could better appreciate your work, if I knew more accurately the characters of the varieties of *Pisum* which you used in your experiments".[6] That was also why he asked about the name and address of the gardener in Ghent, Belgium, from whom E.T.S. received the plant material he used in his experiments. Weldon wanted to "… get from him samples which will show, both to me and my pupils, the exact characters you describe".[7] He was particularly interested in the 'shades of colour' which were 'hard to follow from (E.T.S.') verbal description'. He openly admitted he wanted "to be sure that I fully understand [E.T.S.'s] results". Less than a month later, on November 21, 1901, Weldon reacted to E.T.S.' response, in which the sending of samples of plant materials ('seeds of hybrids') was only promised. At this point, E.T.S. only sent his abstracts.[8] Weldon also clearly stated: "I am especially interested to find that you now think Mendel's laws [are] only special cases of something much wider and more general…"[9] This point interested him also for the purpose of researching 'similar cases of dominance among animals'. The reasons behind Weldon's questions are also revealed in his assessment of E.T.S.' works from 1902 (Weldon 1902a, b): "It is not quite to follow Tschermak's account, because he does not describe all his very numerous and careful experiments in such a way that one can be sure how many hybrid peas he observed" (Ibid.: 238). On the other hand, E.T.S.' experiments played a key role in Weldon's argumentation, because he clearly saw the Mendelian explanation, which he aimed to show, as not generally valid, writing that "…in special cases, other formulae expressing segregation have been offered … but these seem as little likely to prove generally valid as Mendel's formula itself" (Ibid.: 251–2). Yet it seems that some doubts Weldon entertained were not removed by correspondence with E.T.S. In February 1902, he sent his 'little paper … on Mendel's Laws' to E.T.S., and asked him for remarks and criticism.[10] He also encouraged E.T.S. to publish his studies in the 'Biometrika', wherein speaking of the editing policy he stated: "Our guiding principle is the great importance of numerical statements in matters of this kind." At that point, he also once again asked E.T.S. to send the promised specimen of pea seeds, complaining of "… the difficulties which the present condition of certain hybrid peas, which are grown commercially, seem to me to place in the way of a full acceptance of Mendel's work."

Karl Pearson, who already in the autumn of 1901 expressed his doubts regarding the general applicability of Mendelian approach to heredity, joined the correspondence with E.T.S. in June 1902, and E.T.S. forwarded his articles to him as well. Regarding his views on the results of Mendel's experiments, however, Pearson expressed himself rather clearly: "They [Mendel's Laws] seem to me personally very obscure, but I should be still more your debtor, if you would notice these experiments too".[11] Pearson then asked E.T.S. for an updated overview of his work, and promised him a mediation of possible further publication in Europe and in the US. After E.T.S.' reply, Pearson wrote back less than a month later, on July 11, 1902, suggesting that he, should review the works of William Bateson and Edith R. Saunders, mentioning in this connection the Reports to Evolution Committee I (Bateson and Saunders 1902), and in particular 'Defence', which Bateson wrote in March 1902 (Bateson 1902). E.T.S.' contribution was planned for publication in *Biometrika* in September 1902.[12] At the beginning of September 1902, however, E.T.S. wrote a letter, most likely to Pearson,[13] informing him that he would finish his contribution by September 13 and send it by September 16–17. He also informed Pearson that he would pay less attention to Bateson's work Mendel's Principles of Heredity, stating Bateson's book to be 'purely polemical'. In an undated letter addressed probably again to Pearson, which must have been sent still during September 1902, E.T.S. explicitly mentioned "… the manuscript of my reviews of both of Bateson's publications for your journal *Biometrika*".[14] At the same time, he expressed his thanks for "… being invited to write these reviews… I hope my reviews are not too lengthy and similar in content; I took the liberty of introducing a few new observations"[15] At the end, however, E.T.S.' reviews were not published in the 'Biometrika', which probably seems to confirm Pearson's reluctance to provide space for pro-Mendelian or neutral views. One can suppose the reviews were used in E.T.S.' later published studies (von Tschermak-Seysenegg 1902,

[6] Ibid.

[7] Ibid. This articulated aim is important in connection with Bateson's statement from 1902 that "Professors Weldon refers to no experiments of his own and presumably has made none", see Bateson 1902, p. 129.

[8] Weldon to E.T.S., November 21, 1901, AÖAW Wien, C1, 1–27.

[9] *Ibid*.

[10] Weldon to E.T.S., February 18, 1902, AÖAW Wien, C1, 1–27.

[11] Pearson to E.T.S., June 23, 1902, Wien, AÖAW Wien, C1, 1–27.

[12] Pearson to E.T.S., July 11, 1902, AÖAW Wien, C1, 3–66.

[13] E.T.S. to Weldon, September 1, 1902, University College (hereinafter UC) London, Pearson Papers, Nr. 804/7. Unfortunately the addressee is not clearly stated.

[14] E.T.S. to Pearson, s.d., UC London, Pearson Papers, Nr. 804/7. In the original: "… das Manuscript meiner Besprechung der beiden Publicationen von Bateson für Ihre geschätzte Zeitschrift Biometrika".

[15] E.T.S. to Pearson, s.d., UC London, Pearson Papers, Nr. 804/7.

1905, 1906). The last letter sent by E.T.S. to Karl Pearson, which was written in early March 1904, then deals with the exchange of works published in the 'Zeitschrift für das landwirtschaftliche Versuchswesen in Österreich' on the one side and articles from 'Biometrika' on the other.[16] E.T.S. here also mentioned that he would like to meet Pearson during his visit of Great Britain at the occasion of a meeting of the British Association.

Less than 3 months after starting a correspondence with Karl Pearson, E.T.S. started exchanging letters with William Bateson, who contacted him on September 2, 1902, with a request almost identical to one made less than a year earlier by W.F.R. Weldon. That is, Bateson asked E.T.S. for samples of plant material, this time in particular beans.[17] Dating Bateson's first contact with E.T.S. is somewhat complicated by an obvious confusion in Bateson's published paper 'Problems of Heredity as a Subject for Horticultural Investigation' (Bateson 1901).[18] It seems therefore that his very first information about E.T.S.' experiments came from a review in the 'Botanisches Zentralblatt' as he noted in his letter to Francis Galton from August 9, 1900. Still, Bateson concluded that E.T.S.' work from 1900 and 1901 were a 'definite confirmation in the case of *Pisum*', from which it followed that "…there can be no doubt that Mendel's law is a substantial reality" (Bateson 1901, pp. 59, 60).

At the very beginning of the new year, on January 1, 1903, Bateson thanked E.T.S. for 'an account of [his] work'. This referred probably to an article mentioned at the end of the previous year to K. Pearson. Regarding the biometricians, Bateson wrote: "Of late years they have used every means in their power to suffocate truth and it was time someone spoke out freely. They have never learned the facts of variation and are lost when they try to deal with them," adding: "… as witness Weldon's article, which contains some ten flagrant misinterpretations of easily accessible facts."[19] In the same latter, Bateson informed E.T.S. about the meeting of the British Association, that is, he addressed him as one of those 'who have taken part in such work' alongside de Vries, Correns, Cuénot, Castle, and Darbishire, noting that at that meeting, the issue of heredity was supposed to be 'a prominent subject of our discussion'. Bateson's next letter, of December 19, 1903, also dealt with this meeting.[20]

We can understand this invitation as clearly confirming E.T.S.' status as one the sympathisers of Bateson's camp. Their relations developed further the following year, when Bateson travelled to Vienna, Austria, and Brno/Brünn, Moravia, and planned a visit to Mendel's birthplace of Heizendorf/Hynčice. A month later, on February 15, 1905, Bateson sent to E.T.S. some maple seeds, and commented on Weldon's lecture: "We had another absurd lecture from Weldon yesterday. He finds great happiness in the exceptions!"[21] In an undated letter from that year, they then discussed *Telephone* characters, especially those which 'do not segregate properly'. In early February 1904, they dealt with the issue of de Vries's *Antirrhinum*, and Bateson also touched upon a recently published edited correspondence between G. J. Mendel and C. von Nägeli, asking E.T.S.: "Have you read the Mendel letters (Correns)? They are delightful."[22] It seems that Bateson played something of a role of a catalyst in the inimical relationship between E.T.S. and Correns. We can detect a hint of such attitude for example from his remark in a letter of January 4, 1906: "All the trouble with Correns must be an annoyance to you, but my experience is that such things are inevitable." Once we come to the year of 1906, we find nothing in the extant correspondence that would have a bearing on the controversy. The reason for that might be that both of them met in London at the International Conference on Hybridisation and Plant Breeding that took place between July 30 and August 8, 1906. E.T.S. was introduced by Bateson as "… one who took a part in the original discovery of this [Mendel's] principle" (Bateson 1907). He hold his lecture concerning *The Importance of Hybridisation in the Study of Descent* on August 1, 1906 (Ibid.: 279–283). In October 1906, Bateson and E.T.S. debated mainly technical issues pertaining to corrections of the English translation of E.T.S.' contribution at the hybridisation conference, and the financing of a planned Mendel memorial in Brno. E.T.S. chaired the international preparatory committee.[23]

Ambivalent positions

In 1902–1906, E.T.S. presented his views in three larger studies dealing with issues closely related to debates that were at that time taking place in Great Britain.

The first of these papers appeared in 1902 under the name 'The Current Situation of Mendel's Teaching and the

[16] E.T.S. to Weldon, March 9, 1904, UC London, Pearson Karl, Nr. 874/7 (see Pearson 1904).

[17] Bateson to E.T.S., September 2, 1902, AÖAdW Wien, C1, 1–27.

[18] The reason is that Tschermak's first article was delivered to the editors on June 2, 1900. Moreover, Bateson himself mentions on p. 61 de Vries's letter of October 31, 1900.

[19] Bateson to E.T.S., January 1, 1903, AÖAW Wien, C1, 1–27.

[20] Bateson to E.T.S., December 19, 1903, AÖAW Wien, C1, 1–27.

[21] Bateson to E.T.S., February 15, 1905, AÖAW Wien, C1, 1–27.

[22] Bateson to E.T.S., February 4, 1904, AÖAW Wien, C1, 1–27.

[23] Beteson to E.T.S., October 11 and October 30, 1906, AÖAW Wien, C1, 1–27. Tschermark's contribution was parallely in German and English. It, first, occured in German (von Tschermak-Seysenegg 1906), and secondly in English in 1907.

Works of W. Bateson' (von Tschermak-Seysenegg 1902). One can assume it was originally intended for publication in the *Biometrika* journal. In the article, E.T.S. with reference to Bateson focused on 'defences of the principles of heredity according to Mendel' and analysed Weldon's work 'Mendel's Laws of Alternative Inheritance in Peas'. Referring to Bateson, he emphasised that he 'has a tendency to adopt his positions on substantial issues in numerous cases' (von Tschermak-Seysenegg 1902, p. 1391). He not only highlighted the importance of his study of variations but also claimed that it is Hugo de Vries and somewhat surprisingly—but in full accordance with his brother's Armin view—the Austrian botanist Richard von Wettstein (1863–1931) who showed a real 'genius' in this line of research. E.T.S. mentioned Bateson in connection with endogenous and spontaneous variations. Referring to Bateson's 'Reports to the Evolution Committee', he appreciated his effort "…to unify comprehensive botanical experiments with zoological ones" (Ibid.: 1365). He welcomed Bateson's special contribution as the new terminology, which introduced terms such as 'allelomorph' and 'homozygote' (von Tschermak-Seysenegg 1902, p. 1387). Yet it seems that it was his brother's Armin's input that played a key role in E.T.S.' analysis of Bateson's 'Defence' from 1902 (von Tschermak-Seysenegg 1902, pp. 1387–1392). Thanks to an extant copy from E.T.S.' personal library—currently kept in Bateson's collection at John Innes Centre in Norwich, England—we know that Armin played an active role in forming E.T.S.' views in reading of Bateson's early key work. In a copy of the first edition of 1902, we see that, in fact, only Armin's handwritten remarks are preserved while Erich's notes are illegible or erased altogether. Most of their attention focused on two parts, namely passages 'The problems of Heredity and Their Solution' (pp. 1–39), and 'A Defence of Mendel's Principles of Heredity' (pp. 104–208), which dealt with the question of crypto-hybridism in relation to Galton's theory. Crypto-hybridism was by A.T.S. related, for example, to Bateson's statement that "dominance, as we have seen, is merely a phenomenon incidental to specific cases… It may perfectly well be that we shall be compelled to recognize that in many cases there is no such purity" (Bateson 1902, p. 32). This was contrasted with the claim that 'this principle declares that the cross-breeding of parents need not diminish the purity of their germ-cells or consequently the purity of their offspring' (Ibid.: 114). Armin fundamentally disagreed with Bateson's hypothesis that 'ancestry does not touch these facts in the least' (Ibid.: 193). At this point, a hand-written A.T.S.' note unambiguously says: "? Na! Na!". It is also interesting that in general, A.T.S. did not share Bateson's often quoted view that "had Mendel's work come into the hands of Darwin, it is not too much to say that the history of the development of evolutionary philosophy would have been very different from that which we have witnessed" (Bateson 1902:39). On that point, A.T.S. remarked: "I do not believe: nemo agreditur e quelle sua". With reference to W. F. R. Weldon, E.T.S. emphasises his 'undeniable contribution' in carrying out precise observations of variability of paternal forms used in hybridisation, his focus on the creation of non-intermediate traits in hybrids, and last but not least, the foresight he had shown in fully appreciating the importance of origins and ancestry in the 'value' of traits (Werthigkeit der Merkmale) (von Tschermak-Seysenegg 1902, p. 1392). He was critical of the style in which the discussions in Britain were conducted. That referred mainly to Bateson, of whom he said: "I cannot help it but I find the form of discussion Bateson chose in some cases unhelpful, and I can but hope that in the newest phase of development of the evolution issues signs of personal polemic that marked the previous phase to its disadvantage would not return" (von Tschermak-Seysenegg 1902, p. 1391).

The second work, 'Mendel's Teaching and Galton's Theory of Ancestral Heritage', appeared 3 years later (von Tschermak-Seysenegg 1905). Here, we once again see E.T.S.' ambiguous and ambivalent involvement in the controversy. Regarding further theoretical elaboration of 'Mendelism', he was interested mainly in the relation between the theory of hereditary factors (which he linked to Bateson, Cuénot, and others) and his own theory of cryptomery (Von Tschermak-Seysenegg 1903, 1904a, b, 1905, 1906), to the formulation of which his older brother importantly contributed. He defined it using, among other things, "fully consistent observations of Bateson and Saunders…that certain races…, which remain constant in inbreeding, when hybridised with an often arbitrarily distant races, still show the rise of new traits" (von Tschermak-Seysenegg 1906, p. 885). In this theory, E.T.S. focused mainly on explaining the basic principles of recessivity in hybrids. He also analysed the preconditions of purity of gametes, regarding which he admitted only in 1905 that it was one of the cornerstones (Kernpunkte) of Mendel's teaching (von Tschermak-Seysenegg 1905, p. 664, 1906, pp. 885–886), on par with the possibility of unequal hereditary contribution of the parents (von Tschermak-Seysenegg 1906, p. 885). Later, especially when formulating Johannsen's theory of genotype/phenotype and criticising Ludwig Plate for assuming a redundancy of this theory, he defined cryptomery in the sense of "…possession of factors, which in a changed constellation of factors—especially in entering into concordant relations (adding foreign factors or merely 'associating' the already existing ones—see below) or in dissolving discordant relations (splitting or mere dissociation)—may be enabled in a special, new way. Cryptomery in the most general sense also denotes the presence of factors that do not have a

non-creative effect" (E.T.S.:185). Further, he wrote that "A manifestation of a cryptomeric character or inactive factors is in elementary forms of cryptomers possible only after the addition of the missing factors. In the case of other elementary forms of cryptomers, it is possible only after the splitting of contrary (inhibiting, suppressing, disguising) factors" (Ibid.). E.T.S. explicitly admitted the relevance of 'Erscheinung der Regression nach Galton' again a year later, in 1906, in his overview of main factors determining evolutionary forms of the organic world in the case of endogenous and continuous changes (Abänderungen) (Von Tschermak-Seysenegg 1903). He understood variation to be above all the source of the appearance of races (Rassenbildung), and placed Galton's and Bateson's work alongside theories advocated by Wigand and Eimer. Fully in agreement with his older brother's views, he saw them as scholars who added a degree of order to Darwin's 'versatile' (allseitig) and 'unplanned' (planlos) theory, a law-like structure (Gesetzmäßigkeit] (Ibid.: 30). He also praised the work of Hugo de Vries and Richard von Wettstein, and it was in this context, that E.T.S. touched upon the relation between Mendel's teaching and Galton's theory of the hereditary contribution of ancestors. In accordance with his previous works he highlighted mainly the 'substantial difference between the two theories on the issue of value' (von Tschermak-Seysenegg 1905, p. 663). While Galton's approach in his view was characterised by a 'purely genealogical value of some traits…in a regularly decreasing progression'(Ibid.), in Mendel's case, one could discern '…an independent, and fully regular value of traits, which is in principle independent of the characteristics of parents and grandparents as well as of the sex of so-called carriers' (Ibid.) He admitted some link with Galton's theory in the case of hybrid atavisms (Hybrid-Atavismen) and crypto-hybrids (Ibid.: 664). Already since 1903, he had been attempting to find in a systematic fashion these so-called crypto-hybrids, which he viewed as retaining—through the mediation of activating regression in crossbreeding—certain specific traits in a latent manner (Ibid.: 666, 669). In such cases, he stated explicitly that '…a reduction to a simple Mendelian scheme cannot be done, at least for the moment being' (Ibid.: 670). He justified his view as follows: "No gametes would be produced, and moreover, if, so to say, a trace of a now antagonistic trait of another parent form crossed over, a latent crypto-hybrid disposition could quickly become manifest due to hybridisation with certain foreign races….According to the other view—as Mendel found out—manifest traits of a mixed offspring could be observed only in virtue of their own, independent value of a trait that was observed in a parent, but in case of latent traits, it may be the other parent or an ancestors ('Stammeltern' in the original). With this notion, one could undoubtedly re-establish a certain relation to Galton's theory of heredity without necessarily adopting a purely genealogically supported notion of value of traits according to Galton's and Pearson's formula" (E.T.S.: 670–671).

Finally, the third work published at the end of the controversy was the article 'On the Significance of Hybridism for the Theory of Descent' from the following year (von Tschermak-Seysenegg 1906). It was originally a lecture presented at the international conference on hybridisation and plant breeding RHS in London. In this paper, in contrast with the previous view, he highlighted the immediately productive role of hybridism in the appearance of new forms and combinations, as well as 'rise of progressive mutations' (Eintritt progressiver Mutationen) (von Tschermak-Seysenegg 1906, p. 885). With reference to his experiments with different varieties of barley, E.T.S. distinguished between varieties continuous or discontinuous with respect to 'purely Mendelian relations' (rein Mendelsches Verhalten). And last but not least, he summarised the importance of hybridism in that it '…not infrequently permits experimental proof of the ancestors/ancestral heredity', von Tschermak-Seysenegg 1906, p. 888).

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