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# *The Chromosomal Theory of Heredity and the Problem of Gender Equality in the Work of Theodor and Marcella Boveri*[1]

*Helga Satzinger*

In the early years of the twentieth century Theodor Boveri (1862—1915) and Walter Sutton (1877—1916) proposed the chromosomal theory of heredity. In his paper 'Ergebnisse über die Konstitution der chromatischen Substanz des Zellkerns', published in 1904, Theodor Boveri summarised the results of two independent fields of research: experimental cytology on the one hand, which was his field of expertise, and Mendelian hybridisation experiments on the other. At the end of his 130-page paper he came to the conclusion: 'The probability becomes extraordinarily high that the characters traced in Mendelian experiments are actually bound to specific chromosomes'.[2] Working independently, Sutton and Boveri correlated the behaviour of chromosomes during cell cleavage, germ cell development, and cell fusion in fertilisation to the recently rediscovered laws of Gregor Mendel.[3] In doing so, they laid a cornerstone of modern genetics, as our textbooks on the history of biology tell us. The localisation of the hereditary material in the chromosomes became the precondition of all gene-mapping projects of the twentieth century, the first one starting in 1911 with the famous fruit fly *Drosophila melanogaster* and a recent one being the HGP with humans.[4]

Yet, upon a closer examination of how Boveri established the chromosomal theory of heredity, things do appear confusing. First of all, Boveri did not call his theory the 'chromosomal theory of heredity', he gave no name for his combination of two fields of research. In 1904 he was proposing the 'theory of chromosomal individuality', attributing to each chromosome a specific relevance

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1 This paper is part of an extended work on the history of genetics from the perspective of science and gender studies. I want to thank Staffan Müller-Wille, Karin Hausen, Christiane Eifert and my colleagues at the Wellcome Trust Centre for the History of Medicine at UCL for critical and supportive comments.

2 Boveri (1904), p. 117: '... so wird die Wahrscheinlichkeit, daß die in den Mendelschen Versuchen verfolgten Merkmale wirklich an bestimmte Chromosomen gebunden sind, ganz außerordentlich hoch.' [Translation: H.S.] Translating Boveri's texts into English is difficult, both because the meaning of certain terms changed over the years, and because some German forms of conceptualisation escape an appropriate one-to-one translation. The terminology of genetics was developed in the first decade of the twentieth century, but Boveri did not use it: he used his terms derived from cytology and from early Mendelian work in Germany. Especially for the mathematically defined entities, which were called Mendelian 'genes' after 1909, a translation is not possible without changing the meaning in an a-historic way. Boveri most frequently used the term 'Anlagen', which I do as well in this paper, adding the English expression 'disposition' as an indicatory term in brackets. The only contemporary, but still very late translation of a text of Theodor Boveri was done by his widow Marcella Boveri in 1929: Boveri, Theodor: The Origins of Malignant Tumors. London, Baillière, Tindall & Cox, 1929, German: 1914. Here the term 'inheritance factors' is used for the German 'Erbfaktoren, über die wir durch die Mendelforschung unterrichtet sind', thus linking this hereditary unit directly to the experimental approach of the Mendelians. Marcella Boveri's translation, not using the term 'gene' but 'inheritance factors', indicates a conceptual difference between the 'heredity', she and her husband were investigating and the transmission of 'genes', the Mendelian geneticists were after. This will become clearer, as I hope, at the end of this paper.

3 The terms 'mitosis' for cell fission and 'meiosis' for the cell divisions during germ cell development were coined in 1905. See: Churchill (1970), esp. p. 445.

4 Rheinberger and Gaudillière (2004); Gaudillière and Rheinberger (2004).

for the inheritance of certain characters. This difference in the theory's name signifies an important difference in the understanding of heredity that Boveri had in mind, compared to that of his contemporaries and even that of recent genetics. Second, well equipped with new experimental results, Boveri called his own theory into question shortly before his untimely death in 1915. Since 1902 he had claimed that the chromosomes imprinted parental properties onto the next generation's cell or organism, as the substrate of the hereditary material.[5] In 1915 he expressed his doubts: 'Experience does not teach us what the substrate that contains the paternal [!] 'Anlagen' ['dispositions'] might be.'[6] Thus, the cell nucleus probably no longer could be seen as the carrier of the 'Anlagen', but as a factor enabling development only ['Entwicklungsfaktor']. Boveri came to the surprising conclusion — and he did it explicitly in the face of the rapidly growing science of genetics — that 'Our knowledge of heredity itself ... amounts to nearly nothing.'[7]

These doubts of Theodor Boveri reflect a very complicated process in the generation of knowledge in cytological research, which aimed at an understanding of heredity. This research used very sophisticated experimental approaches and microscopic techniques to illuminate the interplay of the cell's plasma and its elements on the one hand and the chromosomes in the cell's nucleus on the other. Both plasma and chromosomes took part in the process of heredity — the question was how they interplayed.

The creation in 1902/1904 of the scientific fact that bound hereditary 'Anlagen' to chromosomes was a decision taken in favour of the chromosomes as the decisive entity in the cell. In the same move the cell's plasma became the supportive element, active only in the ontogenetic realisation of an organism. This decision had far-reaching consequences for the science of heredity and the understanding of the functions of the cell. It helped to create a split into two disciplines, genetics dealing with the chromosomes, and embryology investigating the plasma and development. It was reinforced in further developments in genetics, social and experimental, which centred the experimental approach on the chromosomes, the genes in the chromosomes, and the DNA as their basic structural unit. Needless to say, the belief in an identifiable, stable, Mendelian hereditary unit was crucial for the belief in the feasibility of eugenics and plant and animal breeding, and it is still alive in the current understanding in medicine of a 'gene for' a certain disease.

By using the word 'decision' I am implying that there were other options available around 1900. Because the chromosomal theory of heredity was not accepted immediately by Boveri's

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5 'In diesen väterlichen und mütterlichen Kernelementen [i.e. den Chromosomen] müssen wohl die dirigierenden Kräfte liegen, welche dem neuen Organismus neben den Merkmalen der Species [sic] die individuellen Eigenschaften der beiden Eltern kombiniert aufprägen.' Boveri (1902), p. 35.

6 'Welches das Substrat ist, das die väterlichen Anlagen enthält, darüber lehrt die Erfahrung nichts. Den Kern läßt sie nur als Entwicklungsfaktor, nicht als Träger der erblichen Anlagen erkennen.' Boveri † (1918), here p. 467. Published posthumously and in an unfinished state by his widow, Marcella Boveri. The manuscript reached the publishing journal on 10 April 1917; p. 417. - The word 'Anlage' in embryology refers to an undifferentiated cellular structure out of which a certain organ or limb may develop. In this sense it also can mean a potential of a given structure, whereas the 'Entwicklungsfaktor' refers to a function only, enabling the development. Both notions have their difficulties, as it was not known how at the microscopic and submicroscopic level the development — not growth — of an organism took place.

7 'Über die Vererbung selbst ... wissen wir so gut wie nichts.' Ibid., p. 417.

contemporaries due to various scientific and some idiosyncratic reasons, we can say that options existed.[8] The impression of a certain fragility of the theory is underlined by the fact that, in the years 1914/1915, Boveri himself found it difficult to stick to his own theory, which he had developed ten years earlier and still praised in 1913, a fact overlooked by current historiographers and biologists. Evidence for the importance and activity of cell plasma had been provided by Boveri himself in the years before and after 1902/1904, when he was studying heredity in cell fission and embryonic development in the flatworm *Ascaris* and in sea urchin embryos. Thus, data on the plasma's importance were available at the time of the chromosomes being made the site of the 'Anlagen'; they were there at the beginning of 'the century of the gene'. The cytoplasm and its activities were not discovered by geneticists at the end of the twentieth century in the form of '"postgenomic" metabolic pathways' or 'multiple systems of inheritance'.[9] It was there in the founding years of genetics and it is currently rediscovered by developmental geneticists praising Boveri as their long forgotten founding father.[10]

In this paper I shall argue that the problem of gender equality was one important cultural and social factor in the making and stabilisation of the chromosomal theory of heredity. This social problem was a factor that supported the decision in favour of the chromosomes as the hereditary material and hampered the possibilities to formulate the interaction of cell plasma and chromosomes as a kind of co-operation, most likely non-hierarchical, by using the experimental evidence available in 1915.

Historians of biology have shown for the 1920s and later that the relations of cell nucleus/chromosomes and cell plasma were understood according to highly contested political concepts, such as the monopoly of power exercised by the nucleus upon the plasma, the 'Kernmonopol'.[11] According to recent science and gender studies, the chromosomal theory of heredity is an example of how the order of the cell's elements follows a gendered hierarchy. Analysis of the scientific language and the metaphors used reveals the familiar Aristotelian, hierarchical dichotomy between male form and female matter: on the one hand, the (male) active, controlling, imprinting chromosomes or genes, represented by the sperm; on the other, the female, passive, obedient cell plasma, the egg.[12]

But, in considering the making of the gendered order of the cell before World War I, something else becomes apparent. The decision in favour of the chromosomes as the carriers or place of the 'Anlagen' reflects an uneasiness. Cytologists based their understanding of hereditary processes on the investigation of cell fusion in fertilisation and subsequent cell fissions. Since 1875 fertilisation was understood within the paradigm of cell theory, thus entailing a highly alarming connotation. Former theories of fertilisation saw a male force active on female matter, thus providing a hierarchical order of unsurpassable eternal and cosmic dimensions.[13] At the new

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8 Thomas H. Morgan, Hans Driesch, and Oskar Hertwig, just to mention three important contemporary scientists, did not immediately accept the chromosomal theory of heredity in the decade before World War I. Cremer (1985); Gilbert (1978).

9 Keller (2000), p. 9.

10 Moritz (1993); Moritz (1996).

11 Harwood (1993), pp. 315—350; Sapp (1987).

12 The Biology and Gender Study Group (1989); Keller (1995). Keller extends the argument to the 'gene action talk', in which the gene even became the only representative of life itself.

13 See Lesky (1951), pp. 125-159, on the canonisation.

material level of cells only, the male tended to be much smaller than the female, if not irrelevant. In this situation the chromosomes defined as the hereditary substance helped to rescue gender equality for the male. It was in no way a feminist move to claim gender equality at the level of cells and chromosomes; it was a move to regain at least some male influence in the realm of generativity and heredity in a situation in which matter mattered.

Contemporaries noticed that a negotiation of the social gender order was taking place in cytology. In 1909 the Prague scientist and historian of biology Emanuel Rádl saw the 'philosophy of gender' [die Philosophie des Geschlechts], 'the subject of deepest thoughts throughout the ages, culminating in the science of the chromosomes'.[14] Rádl criticised Boveri, Hertwig and other cytologists for their claim that there was equality and no fundamental difference between men and women. The situation appeared to be even worse: Rádl uttered the fear that man himself was in danger. The research of Jacques Loeb had shown that fertilisation and egg development could be initiated by chemicals only. In Rádl's words, 'Some potassium chlorate or everyday salt taken from the kitchen may substitute the male of the Echinide, of the worms, the starfish and other animals, if not the human male himself.'[15]

Before looking more closely into Boveri's formulation of the chromosomal theory of heredity, some remarks on his social background are relevant.[16] His work is the work of a creative couple in the sciences.[17] Theodor Boveri was born the son of a medical doctor in 1862 in a small town of northern Bavaria. He studied in Munich, where he got his doctorate title, beginning with ancient history and philosophy, then changing to anatomy. Again he changed to the Institute for Zoology under the directorship of Richard Hertwig, and continued his cytological work on the cell in fertilisation and development. In 1893 he became professor for zoology and comparative anatomy at the University of Würzburg, primarily teaching medical students. The institute became an internationally renowned place to do the latest research in cytology, and several female scientists of the first generation worked here and completed their doctoral dissertations. Theodor Boveri gained such a high reputation in the German scientific community that he was assigned to become the director of the newly founded Kaiser Wilhelm Institute for Biology in Berlin-Dahlem in 1911/1913. The institute and the composition of its staff was planned by Boveri, but in the end he did not take up its directorship. Since 1897 he had been married to the U.S.-American Marcella O'Grady (1863—1950). After their marriage they co-operated scientifically all his life, with Marcella Boveri remaining in the shadows of her husband. The daughter of a Boston architect, she was the first 'woman to graduate with a concentration in biology' at the Massachusetts Institute for Technology. She studied comparative zoology and embryology at Bryn Mawr College, carried out research at the Marine Biological Laboratory (MBL) Woods Hole and received an appointment as a teacher of biology at Vassar Women's College in 1889. Here she became a full professor in 1893 and developed a new curriculum. In 1896 she left for a sabbatical year with

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[14] Rádl (1909), p. 498. 'Die Philosophie des Geschlechts, welche zu allen Zeiten den Gegenstand tiefsten Nachdenkens bildete, kulminiert heute in der Lehre von den Chromosomen.'

[15] Ibid., p. 501. 'Ein wenig Chlorkali oder Küchensalz ersetzt, wenn nicht geradewegs den Mann, so doch das Männchen der Echinide, der Würmer, der Seesterne u.a. Tiere.'

[16] Baltzer (1962); Neumann (1998).

[17] Wright (1997). See, for comparison, the case studies of several marital co-operations in: Pycior, Slack, and Pnina (1996).

Theodor Boveri at the Würzburg Institute in order to do a PhD dissertation, which she published in 1903. She stayed, raised one daughter and returned to the United States in 1927 to work as a biologist, teaching at the Albertus Magnus Women's College in New Haven.[18] In the life of the Boveris the woman was not restricted to a purely female domain: she took part in his professional work, understood what he was doing, and co-operated in the experiments and other scientific activities. In addition, she was responsible for the running of the house, with a child and servants.[19] Marcella and Theodor Boveri lived at a time when women in Germany were struggling hard for regular access to academic training and independent income and for an improved legal standing. Women in Germany faced a severe step back as in the years around 1900 a new German Civil Code was passed, which made the situation for women much worse than before. It gave husbands control over their wives: they had the final decision in any respect, they controlled women's means and property, they decided on all matters concerning the children, on her professional activities and so on. The women's campaign for suffrage ended in 1919, with the new Weimar constitution giving women the right to vote.[20] The women's movement was an important social force in the time of the Boveris, and its repercussions can be seen in their professional life. The scientific work of Theodor Boveri has to be regarded as the work of a married couple, thus creating some problems for the historiographer. How to talk of a work that is authored by one person only, but created by two from a certain time, from 1897, onwards? The publications bear his name only. How to escape 'the ~~Mathew~~ Matilda Effect in Science', which attributes to the known male scientist the contributions of his collaborator?[21] I would like to pay tribute to Marcella Boveri's contribution to the shared work. She was active in the performance of the experiments, but she did not publish under her own name, with one exception only.[22] Marcella Boveri even did not finish her late husband's last and incomplete paper, she cannot be viewed as his invisible co-author, and it does not seem legitimate to attribute every sentence that Theodor Boveri authored to her as well.[23] For lack of a better solution, I refer to Theodor Boveri when I am discussing the papers he put his name on, thus risking a continuation of her 'silencing by his pen'.[24] I use the phrase 'the Boveris' when I am referring to their common work and not explicitly to him as the author of a specific statement in a paper.

All the usual elements that take part in the creation of a scientific fact can be found in the making of the chromosomal theory of heredity. There was a good deal of experimental and observational material involved, women's work, inductive and deductive modes of reasoning, several hypotheses carefully combined, with the most important ones left to be tested further in complicated experiments. Scientific enemies had to be fought in the development of the new theory [e.g. Oskar Hertwig], and scientific authority had to be accumulated by building bridges to promising new fields of research, such as the Mendelian hybridisation experiments.

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18 Wright (1997), pp. 629-636.
19 Ibid. pp. 638-643; Boveri (1982), pp. 10-50.
20 See, e.g., Bleker (1998); Hausen (1986); Special Issue 'Universität — Frauen — Universitäten', Feministische Studien 20/1, 2002; Gerhard (1990), here pp. 137-324.
21 Rossiter (1993).
22 Boveri (1903).
23 Boveri † (1918).
24 Pycior, Slack, and Abir-Am (1996), p. 6.

The above-mentioned paper of 1904, 'Ergebnisse über die Konstitution der chromatischen Substanz des Zellkerns', presents a combination of the Boveris' own observations and experimental results and the results of twenty years of cytological research, undertaken by an international group of male and female cytologists and zoologists. Most of them came from Germany, the United States and Belgium. Nearly all of them also had worked for some time at marine laboratories, like the Stazione Zoologica in Naples; they used insects, sea urchins, frogs, *Ascaris* and other species as animal models.[25]

The paper starts with the interpretation that the number of chromosomes was a characteristic one for each species and that the chromosomes appeared in a reliable and constant way in every cell division. This 'persistence of chromosomes' was a hotly debated issue of the time and not at all agreed upon by all cytologists.[26] This finding was combined with the results of two of the sea urchin experiments Theodor Boveri had begun in 1889 and continued with Marcella Boveri.[27] In the so-called Merogonie experiment, egg cells were deprived of their nucleus and fertilised with one or two sperm of another sea urchin species. In the early experiments made before 1902, the resulting larvae did not show maternal properties, thus proving relevance of the sperm's nucleus. The second experiment used sea urchin eggs that had been fertilised simultaneously by two sperms; it showed abnormal developments due to the wrong number of chromosomes in the various cell lineages derived from the fertilised egg. Both experiments used the variation of the number and quality of chromosomes in fertilised eggs and its effects on the developing embryo. The experimental results allowed the conclusion that each chromosome had its own relevance for the development of the new organism. This interpretation was called the 'theory of chromosomal individuality'. Attributing a specific quality to each chromosome and describing the regular reduction of chromosomes during germ cell development, it was possible to see a parallel between the behaviour of chromosomes and the Mendelian 'Anlagen'. Most of the experiments stabilising the 'theory of chromosomal individuality' were performed in a sophisticated way in the years to come until the final ones led to some destabilisation.[28]

The gender problem lay in the apparent size difference of the germ cells, the maternal ones contributing much more material to the offspring than the paternal ones. As parthenogenesis showed, the egg cell made a different and a much greater contribution to heredity than the spermatozoon did.[29] Theodor Boveri had elaborated on that explicitly in a short paper of roughly 40 pages, 'Das Problem der Befruchtung' [The Problem of Fertilisation].[30] The paper had been published in 1902 and made the first step to the chromosomal theory of heredity, linking chromosomes to the Mendelian 'Anlagen' as the parental properties [Eigenschaften] were situated in the chromosomes.

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25 Some names should be mentioned: Edmund B. Wilson, Thomas H. Morgan and his wife Lillian Morgan, C. E. McClung, Nettie Maria Stevens, Kristine Bonnevie, Oskar Hertwig, Yves Delage, Eduard van Beneden.

26 See, Cremer (1985).

27 The first paper on a series of experiments of 25 years is: Boveri (1889).

28 Boveri (1910); Boveri (1908).

29 Boveri (1904), p. 112. '... und es hat ... die Eizelle ... eine andere und ungleich viel größere Bedeutung bei der Vererbung als die Samenzelle.'

30 Boveri (1902). The paper derived from a talk at the Versammlung Deutscher Naturforscher und Ärzte in 1902. All of the following quotations are from this paper.

The understanding of fertilisation was the starting point for the understanding of heredity in cytology. The Boveris' research can be characterised as the 'investigation into processes, which cause the generation of a new individual with specific properties from the parental procreative substances.'[31] Hence, research into heredity had to begin with the germ cells. The paper on the problem of fertilisation began with the proud declaration that the untranslatable 'uralte menschheitsgeschichtliche Problem' finally was solved. Everywhere in organic nature, even at the level of protozoons, two sexes co-operated in the creation of their offspring. This, according to Theodor Boveri, was new.[32] In his eyes the co-operation occurred in a reciprocal way, as both germ cells were dependent on each other. Both germ cells had a potential for cell cleavage and development, but they were inhibited. Through co-operation they could overcome this inhibition, through co-operation they supplemented each other in their intrinsic urge to procreate and combine different properties, through co-operation they had enough plasmatic and nutritive substances necessary for the building of the embryo.[33]

This order of the germ cells resembles quite clearly the ideal of a German middle-class/ bourgeois couple around 1900, practising the model of the 'Arbeitspaar' [working couple] in a gendered division of labour, like the Boveris themselves. The unquestioned purpose was the raising of children and the common production of its economic basis, enhanced by the dowry of the woman. At the level of biological reasoning, Theodor Boveri derived his concept of the reciprocity of the male and female germ cells from evolutionary thinking. Boveri was no Darwinist in the sense of seeing selection as one important force of evolution. According to Boveri, the evolution of the organisms was a progressive process driven by intrinsic forces, the 'bildnerische Elementargesetzlichkeit', leading from the primitive 'Urzustand' [primordial state] to utmost complexity.[34] Attempting to find a reason for the existence of male and female germ cells, Boveri described a line of development starting with single cells procreating via cell fission. Then copulation developed between two equal cells. At the evolutionary state of colonies of 16 cells, a differentiation of copulating cells developed — and in the case of the flagellate *Eudorina elegans*, the first egg and sperm cells were to be found, characterised by their difference in size.

The 'Urzustand' was the self-sufficient cell, procreating through growth and subsequent fission. Bees and other insects procreating partially by parthenogenesis exhibited this property of the egg cell. The egg cell in higher animals still had this self-sufficiency, albeit a bit hampered by inhibition. Boveri compared the egg cell to a perfect clock that was missing the spring. In 1902 he had to give up his earlier idea that the centrosom of the sperm caused the cell cleavage of the (fertilised) egg cell, as this process was not found to be a general one in all organisms. Thus, Boveri abandoned the concept of a male induction of embryonic development, which he saw as being in perfect line with the Aristotelian notion of the female providing the matter and the male giving the activating stimulus for the movement of the matter.[35] Having lost this possibility of explaining a

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31 Es ging um die 'Erforschung jener Vorgänge, ... durch die aus den elterlichen Zeugungsstoffen ein neues Individuum mit bestimmten Eigenschaften hervorgeht.' Baltzer (1962), p. 81.

32 The long tradition of not seeing two sexes or more existing in the plant kingdom had been overcome in the 16th century; now the protozoons had it as well.

33 Theodor Boveri followed August Weismann's line of argument that amphimixis, the combination of different parental properties in the offspring, was the purpose [Zweck] of fertilisation. Boveri (1902), p. 36.

34 Ibid. p. 38.

universal biological difference between the male and the female, he tried to create a full reciprocity of male and female germ cells: 'One could say the spermatozoon is fertilising the egg, one could also say that the spermatozoon is being fertilised by the egg.'[36] Both cells needed each other to get procreation started. However, Boveri had to concede that it was always the egg cell that started development: there was parthenogenesis only and no androgenesis. No development of an embryo started from the sperm. Having to admit a generative difference in germ cells, Boveri posed the question: 'How does it come that the properties of the sperm are not suppressed within the egg? How do they cope with the properties of the egg, which exceeds the sperm in size by the thousands and millions?'[37] Boveri sought rescue in the mere statement that the sperm could cope with the egg, though he did not know how. He referred to the experience that 'generally the father's influence on the constitution of the child equalled that of the mother's'.[38] This equal influence was guaranteed by equality at the level of chromosomes. Boveri saw his work in the tradition of others, starting with Carl Naegeli's postulate of an 'Idioplasma'. Naegeli had claimed that a substance was present in every cell in a very small quantity, which derived from equivalent substances in the egg and the sperm cell. This substance provided an equal force of heredity ['gleiche Vererbungskraft'] of both parents, despite the enormous differences in their material contributions for the gestation of a child.[39] After 1900 the Mendelian laws provided an experimental approach to prove parental equality in heredity. This claim of equality, however, entailed a specific definition of heredity. In a rather circular reasoning, heredity now only dealt with properties characterised by their binary difference in both parents. In other words, only the inheritable differences between members of a species could be dealt with and localised in the chromosomes. All the general properties of an individual, like the inheritable features of the mammalians, the properties of the genus and higher classificatory groups, were not included in this definition.[40]

For Boveri, the chromosomes of the sperm incorporated the sperm's equal influence on the offspring's properties in this narrow sense of inheritable properties. Describing the behaviour of chromosomes after the sperm's integration into the egg, he rhapsodised in a pseudo-religious language: 'Indiscernible the grown nucleus of the sperm stands face to face with the nucleus of the egg; in fullest equality in size, form and number ['Gleichheit nach Größe, Form und Zahl'] the paternal and maternal nuclear elements ['Kernelemente'] lie close to each other. They are passed on in the same combination to the daughter cells and, as we may suppose, to all the cells of the new individual. All this happens with unsurpassable, painstaking care. In these paternal and maternal nuclear elements lie the directing forces, which in combination imprint onto the new organism not only the properties of the species but the individual characters of the parents.'[41]

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35 Ibid. p. 23.
36 Ibid. p. 34.
37 Ibid. p. 35.
38 'Zahllose Erfahrungen ... lehren, daß der Vater auf die Konstitution des Kindes im allgemeinen ebenso viel Einfluß hat, wie die Mutter.' Boveri (1902), p. 35.
39 Boveri (1904), pp. 102-103.
40 The paradigmatic example for the species-specific properties lying in the chromosomes was derived from the crossbreeding of a horse and a donkey. It made a considerable difference in the offspring if the maternal animal was the horse or the donkey, thus showing the influence of the maternal cell plasma.

Boveri was so fascinated by the notion of two equal sets of chromosomes in the fertilised egg that it took him some time in the following years to accept the findings of Nettie Maria Stevens (1861-1912) on chromosomal sex determination. According to this theory, two types of male germ cells existed, which differed in the number of chromosomes, thus determining the sex of the offspring.[42] Stevens had worked with Boveri in his institute in Würzburg in 1903, and she was the one who immediately saw the applicability of Boveri's chromosomal theory of heredity to the problem of sex determination. Boveri did not — he was trapped in the creation of gender equality at the level of chromosomes. As late as 1908 he revised his interpretation that there always were two completely equal nuclei in the germ cells.[43]

In the following years, Theodor Boveri argued as a convinced Mendelian geneticist. In 1913 he praised the results of the latest research, which enabled the localisation of certain characters onto the sex chromosome: 'sex and colour blindness — what could be more different? Nonetheless, there is nearly no doubt that the 'Anlagen' for both characters are located in the same chromosoma.'[44] He thus was on the same track as his scientific enemy Thomas H. Morgan, who, with his group of PhD students had started mapping *Drosophila* genes onto sex chromosomes.[45] The Boveris, however, favoured a different experimental approach: heredity was to be investigated in embryonic development. The qualities of the germ cell's nucleus were to be analysed here. This approach was called in analogy to the spectral analysis of light in physics: 'Embryonalanalyse des Zellkerns' ['Embryonic analysis of the cell nucleus']. Heredity was to be investigated in fertilisation and ontogenesis; the methods used were a combination of cytological analysis and hybridisation experiments, including interspecific crossbreeding of sea urchins. In co-operation with his wife, Marcella O'Grady, Theodor Boveri designed experiments to change the chromosomal constitution of the egg cell and fertilised egg to observe and interpret their abnormal development. He planned to use a device that was to remove single chromosomes from a cell, and various other techniques were applied to influence a cell such that the relation of plasma and chromosomes was changed. These experiments aimed at the understanding of the interplay of chromosomes and cytoplasm at various stages of embryonic development.

The last Merogonie experiments did not provide the desired result that the chromosome was the site of the 'Anlagen'. Marcella Boveri published her husband's last paper in its unfinished form in 1918 under the very unpromising title: 'Zwei Fehlerquellen bei Merogonieversuchen und die Entwicklungsfähigkeit merogonischer, partiell-merogonischer Seeigelbastarde'.[46] If this paper contained at least some dynamite to shake the chromosomal theory of heredity, then most probably nobody took notice — with one exception perhaps: Richard Goldschmidt (1878-1958).[47] For the geneticists after World War I, there was no longer a need to take notice of the

[41] 'In diesen väterlichen und mütterlichen Kernelementen müssen wohl die dirigierenden Kräfte liegen, welche dem neuen Organismus neben den Merkmalen der Species die individuellen Eigenschaften der beiden Eltern kombiniert aufprägen.' Boveri (1902), p. 35.

[42] Brush (1978).

[43] Boveri (1909).

[44] 'Geschlecht und Farbenblindheit, was könnte verschiedener sein. Und doch können wir ... kaum zweifeln, daß die Anlagen für beide Eigenschaften in dem gleichen Chromsoma lokalisiert sind.' Boveri (1913), p. 16.

[45] See, Kohler (1994); Gilbert (1978).

[46] 'Two sources of artefacts in merogonic experiments and the potential for development of merogonic, partially merogonic sea urchin bastards.'

results of a paper that promised to deal with methodological problems in a very complicated experimental system using sea urchin development, as it no longer was in use in the research into heredity.

The main and unexpected results of Boveri's last paper are that embryonic development is divided into two phases. In the first phase, the plasma alone is active; the chromosomes step in at a later stage. In addition, chromosomes and plasma need to be compatible with each other in order to enable proper development. As mentioned, the results were such that Boveri doubted his own proposal of 1904, that the chromosomes might be the material substrate of heredity. But this last, unfinished paper shows as well that these new and severe doubts were outweighed by the desire to believe, in disregard of the new findings, that the substance within the cell nucleus actually was the hereditary substance [die 'Vererbungssubstanz'].[48] Boveri did not reformulate the interaction of plasma and chromosomes in heredity according to his and his wife's new findings. It makes no sense to speculate what Boveri might have done had he lived longer. He ended with drawing a line between the 'exakte Vererbungslehre', the newly developed genetics, on the one hand and the research into the processes of ontogenesis on the other. The one approach used hybridisation experiments, the breeding of pure lines, it applied Mendel's laws and the notion of a gene; the latter asked how the constellation in the zygote leads to the 'Erbeffekt' [Charakter] that the geneticists ['Vererbungsforscher'] deal with. For Boveri, only the latter equalled 'heredity itself', the 'Vererbung selbst'.

In the work of the Boveris the interaction of plasma and chromosomes in the fertilised egg and the developing organism was conceptualised in various ways. In the same move in which gender equality at the level of the chromosomes was introduced, a gendered hierarchy between the chromosomes and the plasma was established. In the years 1902 and 1904, Theodor Boveri appreciated the Aristotelian notion of fertilisation as female matter set in motion by a male activating impulse, but he had to concede that this solution was not a general one and dropped it. The Aristotelian hierarchical dichotomy between form and matter could, however, be applied to the chromosome-plasma relation by interpreting the chromosomes as entities that contained 'conducting forces to imprint paternal properties onto the egg cell and the organism of the next generation'. Theodor Boveri was criticised by colleagues who saw him as advocating the autocracy of the nucleus within the cell.[49] Boveri replied that the cell plasma and the nucleus were dependent on each other and that neither could exist alone; he used his opponents' metaphor: the huge crowd of workers necessary for the autocrat's existence was present in the cell plasma and inherited by the plasma.[50] His own analogy was that of the brain and the body to exemplify the mutual dependency of chromosomes and plasma, or of the plan of an architect and the construction workers building the house.[51] Obviously, mutual dependency was not an equal dependency. It entailed a clear hierarchy following the Aristotelian model, which ensured a gender hierarchy as

47 Goldschmidt who followed his own track in conceptualising the genes and the chromosomes became the head of one department at the Kaiser-Wilhelm-Institute in Berlin in 1914. He appreciated Boveri's work until the end of his own life.

48 Boveri (1918), p. 468.

49 Boveri (1904), p. 103.

50 'Vor allem wird eben im Protoplasma das ganze Heer des Arbeitsvolks vererbt, ohne welches selbst ein Alleinherrscher, wenn wir einmal dieses Bild gebrauchen wollen, nicht existiert.' Ibid, p. 113.

51 Ibid, p. 103.

well. The order of cell nucleus and plasma followed this double hierarchy. At the level of gender, it parallels the legal situation of a married couple according to the civil code of the time. The man had the legal power to make all decisions, he was the head of the household, and all the negotiations and co-operations made to keep the family going were left invisible between husband and wife.

In 1914/15 there was no new conceptualising of the nucleus-plasma relation possible, albeit the possibility had to be considered that the chromosomes were not the decisive forces but enabling the specific 'Gestaltung' of the developing organs of an organism only. The cause for its concurrence with the specific 'Gestalt' of the parents could lie in other parts of the cell.[52] It is even much more remarkable that the Boveris did not re-conceptualise the plasma-chromosome relationship as Theodor and Marcella Boveri provided important findings on the interplay of the plasma and the cell nucleus, findings Theodor Boveri is praised for nowadays by developmental geneticists.[53]

1. The centrosoms and spindles organised the distribution of chromosomes during cell cleavage. They organised the positioning of the hereditary material/chromosomes within the cell and thus 'decided' on their fate during development.
2. Substances and processes in the plasma were important for the first phase of embryonic development before gastrulation.
3. Even more dramatic: the plasma was able to reorganise the chromosomes; it could change their size and composition. This process, called 'Chromosomendiminution — chromatin diminution', was observed for the first time by Boveri in 1887 in *Ascaris*, and examined in extensive cell lineage studies later on. Boveri showed in 1899 that only the germ cells did not undergo chromatin diminution. For him, this was a necessary finding to support Weismann's germ line theory and his own theory of chromosomal individuality. The reorganisation of the chromosomes by the plasma during ontogenesis was crucial, as a process was needed which could explain an unequal distribution of hereditary material during ontogenesis so that cell differentiation could occur. It was a process of circular reasoning due to which chromosomal diminution could not happen in the germ line.

Let me end with a kind of a-historic thought experiment using a bricolage of the Boveris' findings of the plasma's own activities. It would have been a very radical move to claim that the plasma could rearrange the chromosomes of the germ line as well.[54] Boveri had postulated that chromatin diminution happened in species other than *Ascaris*, even if it was not visible under the microscope — so why not in the germ line, where one could not see it as well? Obviously, there was no way of conceptualising an interaction between plasma and chromosomes in heredity which was a co-

[52] The nucleus (Kern) was only to be recognized 'als ein Organ ..., welches dazu da ist, die Ausbildung des Larvendarms, des Skeletts usw. zu ermöglichen' while 'die *spezifische* Gestaltung dieser Prozesse, d.h. die Übereinstimmung mit der spezifischen *Gestalt* der Eltern, in anderen Teilen der Gameten ihre Bedingungen haben werden.' [emphasis by Boveri]. Boveri (1918), p. 467.

[53] Moritz (1993).

[54] See for comparison the fate of the contemporary experimental system in hereditary research using the worm *Planaria*. *Planaria* did not have a visible germ line thus providing reasons for a completely different understanding of heredity as a process of metabolism, not linking it to a specific structure in the cell. The scientists using *Planaria* did not gain the social authority to efficiently compete with the Morgan group in the US. Mitman and Fausto-Sterling (1992).

operative, non-hierarchical one, which would have made the egg cell much more powerful than the chromosomes of the sperm, and which would have resulted in a completely new understanding of 'heredity' and its science.

For the social gender order there was obvious progress attached to the knowledge of genetics. In 1934 the Norwegian geneticist Otto Mohr enthusiastically praised it, claiming that the times of pure male genealogy were over: 'one of the most far-reaching achievements of modern biology is the definite establishment of the fact, that men and women are genetically equivalent'.[55] For genetics, however, it might not be seen as a success story.

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[55] Mohr (1934), p. 207.

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