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8 Concepts of Gender Difference in Genetics

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Genetics is a quantitative subject. It deals with ratios, with measurements, and with the geometrical relationships of chromosomes.

—Alfred Sturtevant and George Beadle (1939)[1]

Alfred Sturtevant (1891–1970) and George Beadle (1903–1989), two prominent representatives of Thomas Hunt Morgan's school of *Drosophila* genetics, started their textbook, *An Introduction to Genetics* (1939), with the claim that genetics was "a mathematically formulated subject that is logically complete and self-contained."[2] The first chapter is entitled "Sex Chromosomes." It begins with the observation that "[t]he existence of diversity among organisms is one of the most familiar of natural phenomena. Every child recognizes not only the differences between dogs, cats, and men, but also those between different individuals of each of these species." Sturtevant and Beadle presented genetics as "the science that deals with the underlying causes of these resemblances and differences." Focusing on "the cases of discontinuous variation [which] are most easily dealt with," they went right to the heart of the matter and declared: "[t]he most widespread and generally recognized discontinuous character is that of sex."[3] In their view "sex differences" provided the paradigm for Mendelian genetics in 1939. Consequently, a founding couple in genetics is depicted on the frontispiece of Sturtevant and Beadle's introduction. A very detailed drawing by Edith Wallace, personal assistant of Thomas Hunt Morgan (1866–1945), shows two fruit flies followed by the caption "Wild-type Drosophila melanogaster. Male at left, female at right."[4]

"We have attempted to treat the subject […] as a logical development in which each step depends on the preceding ones," claimed Sturtevant and Beadle.[5] One might argue, however, that the creation of an origin narrative, commencing with Adam and Eve, is not necessarily a logical procedure. In times of evolutionary thought, a different origin could have been seen as more "logical." The primary case for inheritance could have been seen in the invention of cell division in the primordial cell, and following that, the spontaneous creation of differences in the offspring. According to this "logic," processes of cell fusion producing a new generation of organisms would be a later

innovation in evolution. Starting the science of genetics with a binary, discontinuous sex difference is not a logical step; it rather prioritizes, whether deliberately or not, a distinction derived from the social conventions of a society which conceptualizes its own origin from the normative difference between man and woman as a binary, discontinuous one. What is new about modern genetics, compared to classic and other natural philosophical theories on procreation, is the attempt to answer this question: what are the maternal and especially the paternal material contributions to the offspring?[6] Does genetics finally provide a new approach to the old Roman and purely social definition of paternity—"The status as husband makes the father" (*pater est quem nuptiae demonstrant*)—by introducing a material proof?[7]

Without referring to the nebulous realm of paternity, but staying strictly within the historiographical framework of scientific practice, Sturtevant and Beadle's logic simply derives from that of their experiments with *Drosophila melanogaster* in the second decade of the twentieth century. The resulting genes, localized as discrete units on chromosomes, were made by mating.[8] The experiments were designed to trace the transmission of binary and discontinuous differences of members of one species, or its laboratory-bred strains, to the next generation. For this purpose male and female specimens had to copulate and procreate. Consequently, these experiments reduced the meaning of inheritance and excluded from its gaze the transmission of other characteristic, but nevertheless inheritable, morphological features of these organisms, which defined their taxonomical status. Sturtevant and Beadle's type of genetic investigation did not deal with all inheritable features. In the words of the geneticist Edwin G. Conklin (1863–1952) in 1915, the scope of Mendelian genetics was rather narrow as it excluded the role of the cytoplasm in the transmission of bodily features: "We are vertebrates because our mothers were vertebrates and produced eggs of the vertebrate pattern; but the colour of our skin and hair and eyes, our sex, stature and mental peculiarities were determined by [Mendelian factors in the chromosomes of; H. S.] the sperm as well as by the egg from which we came."[9] In addition, Mendelian genetics could not investigate the transmission of hereditary traits from one cell to another during ontogenesis.[10]

The reasons for, and consequences of, Sturtevant and Beadle's choice of sex difference as the paradigm of genetics were hidden behind the claim of providing a purely mathematical approach. Their case is just one example of the centrality, but invisibility, of gendered concepts in the history of genetics.[11] Several gender concepts were prevalent at different times; they differed considerably and were sometimes articulated, sometimes not. They all played their part in contemporary debates on the social gender order; in the 1920s and 1930s these debates were also, at least in Germany, part of the anti-Semitic debate on racial purity and superiority.[12]

Despite the centrality of gender concepts for genetics, they are generally not considered relevant to configurations of biological thought, neither by the scientists

themselves, nor by a considerable number of historians. Outlined below are some examples of the variety of gendered concepts present in genetics in the early twentieth century. These can be seen in the research into fertilization processes and sex difference in Germany before 1933, in the establishment of the chromosomal theory of heredity and chromosomal sex difference in the first decade of the twentieth century, in the genetics of sex difference in the 1920s, and finally in the problem of sex difference in molecular genetics in the 1950s and 1960s. The scientists dealing with these issues to be discussed here were Theodor (1862–1915) and Marcella Boveri (1863–1950), Nettie M. Stevens (1861–1912), Richard Goldschmidt (1878–1958), Felix Mainx (1900–1983), and François Jacob (1920–2013).

8.1 De-gendering Sexuality—Sex without Differences

In the early 1930s, and in a way that still seems astonishing, apparently clear assumptions about sex differences were questioned by scientists themselves. This development, had it happened today, would be seen as an effect of postmodern feminist or even queer scholarship: biologists questioned the binary sex difference exactly at the main site of its usual incarnation within the paradigm of cell theory: the female egg and the male sperm.[13]

In the German-speaking scientific community of the early decades of the twentieth century, "sexuality" was seen as "a problem of genetics."[14] Sexuality meant all the processes involved in the development and fusion of different germ cells to generate a new organism. Shortly before Sturtevant and Beadle started their "introduction to genetics" with the unquestioned assumption of a binary, discontinuous sex difference, a c. 90-page monograph by the Prague botanist Felix Mainx entitled "Sexuality as a Problem of Genetics" gave a very different picture.[15] The booklet was published by the respected Gustav Fischer Verlag in Jena. Mainx based his considerations on at least two decades of research of zoologists, botanists, and specialists on unicellular organisms called "protists." These scientists had combined the search for the mechanisms of inheritance at the level of genes, chromosomes, and cytoplasm with the investigation of various fertilization processes. They sought to elucidate the question of how sex differences were transmitted from one generation to the next and how they unfolded during ontogenesis. A prominent center for this research was the Kaiser Wilhelm Institute for Biology in Berlin-Dahlem from its inauguration in 1914. Here Carl Correns (1864–1933) studied sex determination in plants, Richard Goldschmidt (1878–1958) explored the question for animals (insects and vertebrae), and Max Hartmann (1876–1962) investigated processes in unicellular eukaryotes, which he identified as mating. Based on this work he provided a general theory of "sexuality."[16]

In 1933 Mainx discussed the main current theories of the inheritance and determination of sex difference and came to a surprising conclusion. Even today the process of

fertilization, understood as the fusion of two germ cells after meiosis, is usually conceptualized in the framework of a veritable classic romance between female egg cell and male spermatozoon by evoking the full repertoire of a gender order invented in nineteenth-century European bourgeois society.[17] Furthermore, the mere name "egg" for the "female" procreative cell identifies the female as the caring, nourishing element, which does not have the same procreative potency as the sperm.[18] Minority voices today go beyond the egg–sperm romance and claim that the egg also is active and energetic, thereby adjusting the model to late-twentieth-century feminist agendas.[19] In a comparably more dramatic move, Felix Mainx in 1933 proposed abandoning all notions of femininity and masculinity in the conceptualization of germ cells and fertilization. "Sexuality," understood as processes of fertilization, should be defined only by the fusion of two cell nuclei resulting in a nucleus with a double set of chromosomes, followed by reduction and division during the production of germ cells to create the procreative cells with one set of chromosomes each. These cells had to fuse to create the next generation.[20] Sex difference was not necessary for processes involving sexuality. According to Mainx, sex difference did not come first:

> The bipolar differentiations of gametes, […], genitals, and "individuals characterized by a particular sex" [*"Geschlechtsindividuen"*], which are generally connected with the process of copulation, should be regarded as secondary. They have to be seen as adaptations to the function of sexual procreation [*geschlechtliche Fortpflanzung*]. The increase in the copulation probability and the need to supply the zygote with metabolic resources [*Reservestoffversorgung*] are most likely the prominent elements of an advantage in the selection process during the phylogenetic evolution of these differentiations.[21]

In short, Mainx concluded that there was no universal bipolar sex difference to start evolution with, let alone genetics. Thus, the prevalent "comprehensive style"[22] in German biology, with its characteristic inclusion of the problems of evolution, development, and sex difference into genetics, had led to a more complex picture than the one the Morgan school could provide.

One reviewer of Mainx's publication was very outspoken in this respect. The botanist E. G. Pringsheim commented,

> [s]ince we discovered the processes of fertilization in algae and unraveled the very complicated situation in most of the fungi, our knowledge of sexuality in organisms of the lower taxa has increased considerably. A variety of phenomena could be shown which dramatically exceeds everything we might imagine.[23]

Pringsheim conceded that the assumption of a binary difference between man and woman as the model for all sexual difference used to be the unquestioned basis of all considerations. The new scientific results showed, however, that the generalization of this sex difference was inadequate. According to Pringsheim, even Max Hartmann's notion of "relative sexuality" was inappropriate. Using the processes of conjugation of

unicellular organisms, Hartmann had developed the concept of a scale between male and female, along which individual cells could be situated. On this scale, the behavior of one and the same cell could be described as "female" if a more "male" cell was around, and "male," if a more "female" cell showed up. According to Pringsheim and Mainx, sexuality—the various processes of cell fusion to start a new organism—could not be ordered in a bipolar mode, as was shown very strikingly by the "multipolar sexuality" of fungi.[24] There was either a variety of differences or no "sex difference" at all in the fusing cells. Procreation was not bound to the existence of a binary, discontinuous sex difference.

Further evidence of the evolution of a multiplicity of "sexualities," was provided by the seemingly innocent strawberry plant (*Fragaria*). This plant could display the most diverse types of sexual identity. In 1931 the Berlin geneticist Elisabeth Schiemann (1881–1972) had shown that the plant could be hermaphroditic; it could be male or female, and there were cases where a genotypic sex change took place in the flowers of one and the same plant.[25] The plant, during its lifetime, could change its chromosomal constitution, generating at a particular point in time either "male" or "female" organs, and sometime later the opposite.

Using "male" or "female" to characterize organisms and their behavior in procreation and inheritance obviously led to a rather inconsistent and confusing picture. Mainx and others tried to get rid of these categories for the sake of clarity and openness in their biological observations. In a way, they tried to "undo gender" in exactly the area usually seen as the unassailable refuge of "natural" masculinity and femininity: sex difference in the realm of procreation.[26] But there was a catch: with the identification of chromosomes as the decisive components in inheritance, a new gendering within cells and their elements took place. This happened simultaneously with the development in which the gendering of full germ cells was fundamentally questioned. This parallel development will be revisited later in this chapter.

8.2 Gendering Cell Components and Inheritance

As Pringsheim pointed out in 1933, the categories "male" and "female" had been convenient at the beginning of cell-based investigation of inheritance in late nineteenth century. They were uncontested when in 1903 Theodor Boveri, in cooperation with his wife Marcella, identified chromosomes in the cell nuclei as the crucial physical structures harboring the Mendelian "Anlagen" or "Erbfaktoren."[27] These chromosomes and their transmission through germ cells and the germ line behaved the same way the Mendelian "Anlagen" (later called "genes") were supposed to do, according to the newly rediscovered Mendelian laws.[28] The correlation between chromosomes and Mendelian "genes" was established around 1903 and was only later, and with some changes, referred to as the chromosomal theory of heredity.[29] It was based on a

considerable amount of experimental and observational work on the processes of cell division, germ cell maturation, fertilization, and ontogenetic development. From the late 1880s, and after 1897 in cooperation with his wife Marcella, Theodor Boveri had used sea urchins and the parasitic worm *Ascaris megalocephala* to investigate the interplay between cell plasma and chromosomes in cell fusion during fertilization, and in cell division and differentiation during embryonic development, in an effort to understand what they called "Vererbung" (inheritance or heredity).

Starting points in the work of the Boveris were provided by the assumptions of August Weismann (1834–1914) and Carl Nägeli (1817–1891). Weismann had postulated a division between a germ line and the line of somatic cells, which allowed for a transmission of inheritable material from one generation to the next via the germ cells, and an unequal distribution of the inheritable material during the development of differentiated, somatic, cells of an organism. Nägeli had postulated a minute substance within the cells, which originated in equal quantity from the paternal and maternal organisms. The axiomatic setting of a paternal and maternal equality in the contribution to the offspring guided the search for the responsible substance of inheritance.[30]

Theodor Boveri began in the 1880s with fertilization experiments using sea urchins. He manipulated the larger, cytoplasm-containing "female" cells so that their chromosomes were no longer visible and could be regarded as being lost.[31] Fertilization of these cells with sperm of different sea urchin species in his view resulted in sea urchin larvae showing paternal features only—thus indicating the central role of the chromosomes as the transmitters of the hereditary "Anlagen." Further work elaborated on the mechanisms of cell division and identified the centrosomes and spindle apparatus as cellular "organs" which provided—normally—an exact distribution of chromosomes into the "daughter" cells.[32]

Based on the conviction that a precise mechanism was at work, the analysis of abnormal distributions of chromosomes during embryonic development became possible. This resulted in the conclusion that each chromosome had a specific importance for the organism, equal to the Mendelian "Anlagen."[33] The establishment of the chromosomal theory of heredity needed a careful consideration of the role of the cytoplasm in heredity. This role proved absolutely critical: the chromosomes were indeed subject to active intervention by the cytoplasm.

In the years before the establishment of the chromosomal theory of heredity, Boveri had shown in microscopic studies that during ontogenesis the chromosomes of the somatic cells become reorganized or even dissolved. This process, called "chromosome" or "chromatin diminution" was necessary to explain cell differentiation, as it created the different genetic constitution of different somatic cells.[34] In 1910 Boveri published the results of experiments which he, his wife, and female PhD students and postdocs had performed to show that it was indeed the cytoplasm and the spatial and temporal distribution of its components that reorganized the chromosomes during ontogenesis

to make cell differentiation possible.[35] This activity of the cytoplasm was more or less axiomatically excluded from being present in the germ line, despite the fact that some observations could not be explained.[36]

Shortly before Theodor Boveri's untimely death in 1915, he and Marcella Boveri had reinvestigated his earlier findings based on the chromosome-deficient sea urchin egg cells. He identified these experiments as having been flawed by a methodological error, as he could not be positive that the egg cells' chromosomal material had definitely disappeared. The new experimental findings of these "merogonic experiments," however, clearly demonstrated a strong influence of the cytoplasm in early embryonic development, which even exceeded that of the chromosomes.[37] For the Boveris the interaction of chromosomes and cytoplasm was the crucial process for inheritance and development. Their experimental approach—based, as it was, on the fertilization of germ cells of sea urchin and the nematode worm *Ascaris*, on systematic manipulations of these cells to change the interplay between chromosomes and cytoplasm, and on the subsequent interpretation of embryonic development—could not establish an absolute dominant role for the chromosomes.

The notion of chromosomes being the only and decisive material substrate for Mendelian "Anlagen" was stabilized by those experimental systems, which traced the transmission of invariant properties of male and female organisms through the generations. In the work of the Boveris the subtext of this focus becomes visible. In his 1902 paper on fertilization which obviously belongs to gender politics, Theodor Boveri discussed the evolution of sex difference and made it very clear that the cellular representative of the male was endangered by miniaturization.[38] The primordial unit of procreation was the omnipotent, dividing cell—"mother cell" dividing into "daughter cells," placing reproduction clearly in a matrilineal framework. Procreation evolved further by the invention of cell fusion, followed by a differentiation into sex difference of cells: a large cell containing plasma and chromosomes and a tiny cell containing chromosomes only, plus eventually one centrosome which occasionally was necessary to start cell division after fertilization. It was the evolutionary fate of the male cell to become smaller and smaller to the point when only the remaining chromosomes guaranteed its necessity by providing a mechanism to create inheritable differences in the organisms of the next generation. These differences and their continuous recombination were seen—and are seen today—as an advantage in evolution, a view based on Weismann's ideas of amphimixis.[39]

Identifying the chromosomes as the material locus of Mendelian "Anlagen" created gender equality in procreation. The father's contribution to the next generation was equal to that of the mother, despite the morphological and physiological difference between the germ cells, which were gendered according to the human model, where the female and male contributions to the offspring are unequal. With the focus on chromosomes the cytoplasm became the purely nurturing—and hence

female—element. Morgan and his colleagues used this model for their genetics and theory of the gene developed during the First World War. In the German genetics community the question whether the cell nucleus had the "monopoly" in heredity, or whether some plasmatic factors also acted as hereditary substance, was still prevalent in the 1920s.[40] Still, the relationship between cell plasma and chromosomes was modeled along maternal nutrition and paternal control over the cell and organism. A fundamental reconceptualization of this gendered order, however, never took place. As we have seen, Felix Mainx could not go beyond the gender order of cell components in 1933, even while de-gendering the germ cells themselves. Claims that the cytoplasm could and had to reorganize the chromosomes, at least in ontogenesis, and that the cytoplasm had a crucial role in early embryonic development, were left to the developmental biologists and remained excluded from genetics for decades to come.[41]

One might argue that it was simply the selection of the most productive experimental systems in the first decade of the twentieth century—the breeding experiments with *Drosophila melanogaster* and with maize—that pushed genetics toward the search for genes as entities on the chromosomes, leaving the interplay of chromosomes and cytoplasm aside.[42] Looking for new breeding strategies and knowledge in the project of eugenics provided another motive for the concentration on organisms with a binary sex system. However, I would argue, the search for the paternal contribution to procreation must have been a hidden agenda as well, structuring thought and driving motivation, thus helping to overlook the "female" cytoplasm as a relevant factor in heredity.

8.3 Chromosomal Sex Determination—A Telling Delay

Theodor and Marcella Boveri, who always sought to unravel the interplay of chromosomes and cytoplasm, allow us to see this hidden agenda. Theodor Boveri must have been fascinated by the idea that the chromosomes would guarantee gender equality in the sense of an equal male relevance in heredity. His rhetoric on the miniaturization of the male cell is revealing in this respect. Furthermore, until 1909 he stuck to his notion of the full equality of the cell nuclei and chromosomes of male and female germ cells. By doing so he recognized only rather late that the new interpretation of sex difference as based in a chromosome difference supported his 1903 theory of the specific relevance of individual chromosomes as the locus for Mendelian "Anlagen."[43] Nettie Maria Stevens had proposed this radical new understanding of sex difference in 1905 after her stay as a visiting scholar in Boveri's Würzburg laboratory in 1902/1903 and after she had published a paper with Boveri in 1904.[44] Stevens claimed that male or female germ cells came in two versions, differing at the level of chromosomes, and thus creating two types of fertilized eggs, which developed into male or female organisms. In most cases the female cell had one chromosome more, or at least one larger chromosome, than the male. With this new interpretation, sex difference became an inheritable trait,

following Mendelian rules and challenging older assumptions of nutrition or other factors as responsible for the development of sex difference.[45] Also in 1905, Boveri's old friend Edmund B. Wilson (1856–1939) had realized the correlation of sex difference and chromosomal difference. At that time, he, and Boveri, interpreted the additional chromosomal material in the female differently from Stevens. They saw it as an indicator of the female's higher assimilative powers, thus positioning the female in the classically gendered realm of nutrition.

Stevens's interpretation, however, made sex difference a binary, discontinuous one, caused by the random distribution of chromosomes in the creation of germ cells. Her work and her later identification of the chromosomes of *Drosophila melanogaster* were crucial preconditions for the project undertaken by Morgan's group to map genes onto chromosomes. This became the foundation stone of Sturtevant and Beadle's chromosomal sex-difference paradigm of genetics described at the beginning of this chapter.[46]

Theodor Boveri was chosen in 1913 to act as director of the newly founded Kaiser Wilhelm Institute for Biology in Berlin-Dahlem. He appointed the institute's scientific staff, among them Max Hartmann and Richard Goldschmidt, and made the problem of sex determination, its inheritance, and development a central topic of the well-funded research institute. He ultimately resigned from the directorship before the institute's inauguration, but, still, he can be credited for the support of a research program which in the 1920s investigated sex difference as the paradigmatic problem for genetics and embryology and finally helped to challenge the unquestioned assumption of a binary, discontinuous sex difference as its basis.[47]

8.4 A New Binary Sex Difference—Paradoxes for Genetics and Gender Politics

Genetics and research into the processes of inheritance in the first decade of the twentieth century were intertwined with the concept of a binary sex difference, where equality or hierarchy were the negotiated alternative orders. This gender concept had implications which moved in various and sometimes conflicting directions. In the sense of "doing gender," the chromosomes became male and the crucial cellular structure to embody Mendelian genes. In this reconfiguration the paternal contribution to heredity equaled the maternal contribution, and the cytoplasm in turn acquired an auxiliary role and became female. A cellular asymmetry or generative difference in procreation was thus transformed into gender equality to compensate for a perceived male inferiority. In the order of the cell components, on the other hand, chromosomes and cytoplasm became gendered in a hierarchical way. By attributing to the cytoplasm an auxiliary role only, a blind spot was created in the conceptualization of genetics.

For gender politics, however, this development helped to support the attempts made for female emancipation in the first decade of the twentieth century. Referring to the

new findings of genetics, the female medical doctor Hope Adams-Lehmann (1855–1916) and the doctor and geneticist Agnes Bluhm (1862–1943) stressed the point that women inherit 50% of their qualities from their fathers. Therefore they should be regarded as equals to their brothers. The Berlin zoologist Oscar Hertwig (1849–1922) argued for women's access to university education using the findings of genetics.[48] It is probably difficult to imagine today how powerful the genetics-based equality claim was in the realm of the gender politics of that time. Genetics challenged male superiority and the usual male-centered genealogies.

However, the chromosome-dependent positive political support for gender equality had a price for biology: Mendelian inheritance was based on a hierarchical concept of sex difference, applied to the biological entities participating in procreation. In an ironic twist, it was exactly this hierarchical concept which helped to challenge women's inequality in the realm of politics and social order. The new concept of chromosomal sex determination had multiple and incongruent effects. To provide another example, it also helped to undermine the customary censure of women when they did not give birth to the desired boys and heirs. Now the responsibility lay with the father, and it was the chromosomal constitution of his sperm that determined whether the child became male or female.

For genetics, chromosomal sex determination created a useful experimental tool. It had a key function in the development of Morgan's theory of the gene by allowing the localization of genes, like the gene for white eyes, for example, on a sex chromosome, thus starting the creation of chromosomal gene maps for *Drosophila melanogaster*. However, chromosomal sex determination also created a problem. It conceptualized sex difference as a binary, discontinuous, inheritable difference between either male or female, based on the presence or absence of chromosomal material. By doing so, genetics became incompatible with embryology's older notion of sex determination according to which the development of male or female organisms derived from an organism with bisexual potency.

8.5 Challenging Binary Differences and Racial Purity

In the 1920s Richard Goldschmidt succeeded in harmonizing the genetic and embryonic understanding of sex determination.[49] Based on his experiments with the gypsy moth *Lymantria dispar*, he proposed the theory that inheritable factors determining maleness or femaleness cooperated in one and the same organism. It was the actual balance of the two factors within one organism, and the correct timing of their activity, which led to the development of a male or female animal. This model allowed an explanation for the existence of so-called "intersexual" organisms, which showed features of both sexes. Goldschmidt used it to depathologize sexual ambiguity and homosexuality in humans. A detailed account of Goldschmidt's work is beyond the scope of this chapter.[50] Only two aspects can be mentioned here in a rough abbreviation.[51] The

1927 genetic concept based on the *Lymantria* experiments entailed the notion that genes were not stable in their effects. They could vary in their "strength" to create a particular feature in an organism. For this reason Goldschmidt's politically right-wing colleagues in Germany did not accept his genetic model. It did not conform to their efforts to establish a new genetics-based racial anthropology—racial features had to be caused by stable, invariant genes; otherwise races were fluid and changeable units.

However, another aspect of Goldschmidt's work proved to be very useful in the context of right-wing politics. The crossbreeding of some different geographical populations of insects had resulted in "intersexual" animals. Against Goldschmidt's intentions this result was used as the scientific proof for an old anti-Semitic, anti-feminist, and anti-democratic trope used in Imperial Germany: that miscegenation would blur a clear-cut gender dichotomy in humans, thus causing the degeneration of the supposedly most developed Nordic race. Again, the scientific and political uses of the same gender concept had conflicting consequences. On the one hand we find the integration of genetics and embryology, and support for a policy of emancipation for homosexuals; on the other hand we see the propaganda for racial purity, pure masculinity and femininity, dismissing every new invention on the human gender front as a sign of degeneration in Weimar Germany.

When the Nazis came to power, Goldschmidt was forced to emigrate. He survived in the United States, but he never achieved as elevated a position there as that which he had held in Germany. His pre–World War II work was positively received in the United Kingdom.[52] However, his genetic concepts, which he further developed after 1936, did not become mainstream. The new concepts of molecular genetics developed in the 1950s and thereafter did not integrate Goldschmidt's work and its questions. They were only reconsidered in the late 1980s.[53]

8.6 Epilogue: The Gender of DNA and Aristotle Rediscovered in the 1970s

In the 1960s and 1970s the problem of sex difference was seemingly irrelevant for genetics, but a closer look reveals that it was central. In 1970 François Jacob began his highly influential book, *The Logic of Life: A History of Heredity*, with a statement similar to that of Beadle and Sturtevant in 1939 in its claim of something "immediately evident," but different from it in its focus on identical reproduction: "Few phenomena in the living world are so immediately evident as the begetting of like by like. A child soon comes to realize that dog is born of dog and corn comes from corn."[54] Jacob continued,

> Heredity is described today in terms of information, messages and code. […] What are transmitted from generation to generation are the "instructions" specifying the molecular structures: the architectural plans of the future organism. They are also the means of executing these plans and of coordinating the activities of the system. In the chromosomes received from its parents, each egg therefore contains its entire future. […] The organism thus becomes the realisation of

a programme prescribed by its heredity. […] The aim is to prepare a completely identical programme for the next generation. The aim is to reproduce.[55]

Jacob conceptualized genetics as the science that investigates the reproduction of the same. Genetics was no longer based on the tracing of differences; sex differences appear to be completely absent, fertilization processes irrelevant.

Jacob's asexual concept of genetics and inheritance is surprising in view of the fact that in their practical work Jacob and his colleagues attributed a classic binary sex difference to their unicellular model organisms. They identified DNA donating cells as male, receiving cells as female.[56] They called their central experimental interventions "coitus interruptus."[57] This was the interruption of the DNA transfer between bacteria at a definite time to estimate the length of the transferred DNA.

This experimental technique became a central practice for bacterial genetics, in the mapping of bacterial chromosomes, and is usually called "mapping by mating."[58] It was exactly this modeling of inheritance in bacteria, viruses, and unicellular yeast according to the sexual processes in higher organisms which allowed the development of the new DNA-based gene concept in molecular genetics.[59] DNA replaced the chromosomes as the central player in heredity, and the old Mendelian, sex-difference-based gene concept could thus be applied to evolutionarily earlier processes of inheritance. For my point here it is not the main problem that Jacob and others attributed to bacteria the same processes of inheritance that had been deduced from that of higher organisms using sexual reproduction. Nor is it the transference in the other direction, when molecular genetics transferred genetic models from procaryotes to higher organisms. The problem rather lies in the unconscious nature of this transference from organisms with sexual reproduction to single cells dividing, which prevents a reflection on the implicit trajectories and limitations of the concepts used.

Jacob praised the genetic program, and it is known that Michel Foucault was fascinated by the idea that it provided instructions which were realized by the organism.[60] I want to stress only one point here: the concept of the genetic program re-producing the same way in every generation entails a classic figure of Aristotelian thought and the theory of procreation and inheritance that went with it. This concept was consciously brought into the debate by a colleague of Jacob. In his 1971 contribution to a Festschrift for Jacob's former superior André Lwoff (1902–1994), Max Delbrück (1906–1981), German émigré physicist and founder of the phage group, proposed, partly tongue-in-cheek, and partly seriously, that Aristotle should be given the Nobel prize for his discovery of the principle embodied in DNA.[61] According to Delbrück, the idea of the genetic program was equivalent to Aristotle's formal cause in male sperm, which shaped female matter. Delbrück even saw Aristotle's concept of the prime mover, the godlike first cause, as applicable to DNA.

The classic Aristotelian binary—the male formal cause and the female material cause—is a hierarchical one which disadvantages the female. It was developed and used

by Aristotle to legitimize the exclusion of women from political equality. He saw woman as a deviant man, almost a malformation. Man was the incorporation of the eternal ideal form, which was reproduced with the help of woman, in the chain of generations. Delbrück used German language studies on Aristotle to make his claim, but he completely missed the medical historian Erna Lesky's 1950 study of ancient theories of procreation, where she clearly demonstrated that Aristotle's theory was simultaneously a political gender theory to legitimize male superiority.[62]

By hailing the re-production of the same, Jacob and others hid gender difference, especially the generative difference and its hierarchization to the disadvantage of the female. They provide a textbook example for a binary order, which takes one side of the binary as the general and the other side as its derivation, dependent, or "other."[63] Genetics, for decades to come, treated DNA as the representative of the organism. Craig Venter's recent cyborgs made out of synthetic DNA and bacterial cell bodies function in this sense, and will never, according to his understanding, create spontaneously something different from that which he designed.

The history of the different gender concepts in genetics that I have reviewed in this chapter shows not only their relevance, but also how varied they have been in both their scientific and political implications. There were equality claims in a binary order, negotiations and acknowledgments of a mutual dependence of the two; the creation of inequalities up to the point that one element of the binary became the representative of the whole and the other one auxiliary or even irrelevant; and there was the concept of a binary gender order, which nevertheless allowed for intermediate forms, and more important than that, postulated that both elements of the binary entailed both qualities. These gendered orders were attributed to biological entities and processes at different times, and embedded in different experimental approaches to heredity.

It will be interesting to see in what way genetics will be reconceptualized in the future.[64] This process will not only have to consider new gender concepts but will also have to face deeply embedded biological concepts, experimental approaches, powerful machinery, and vested interests which place hope for future medical therapies and agricultural and biotechnological developments on the dominant concept of DNA as providing the crucial tools and information.

Notes

1. Sturtevant and Beadle (1939) 1988, 11.
2. Sturtevant and Beadle (1939) 1988, 11.
3. Sturtevant and Beadle (1939) 1988, 17.
4. Kohler 1994; Sturtevant and Beadle (1939) 1988, 10.
5. Sturtevant and Beadle (1939) 1988, 11.

6. See Lesky 1951.

7. Fischer-Homberger 2001 introduces the notion of a male insecurity with regards to paternity, which she sees as lying behind biological theories of procreation.

8. See Kohler 1994.

9. Conklin cited in Sapp 1987, 17. On the relevance of cytoplasmatic inheritance in German genetics in the 1920s, see also Harwood 1993.

10. Before World War I Theodor and Marcella Boveri regarded this question as an essential part of the investigation into hereditary processes and used experimental systems not tailored to the needs of Mendelian genetics; see below. Consequently, Mendelian genetics in the 1930s needed an array of additional hypothesis to accommodate the difference between genotype and phenotype. See also Rheinberger and Müller-Wille 2009.

11. For the early critique of gendered concepts cf. Spanier 1995; Biology and Gender Study Group 1989; Keller 1995. More recently: Satzinger 2005, 2008; Richardson 2013.

12. See Satzinger 2009a, 2009b, 2012.

13. See the "romance" attributed to the meeting and fusion of germ cells in Martin 1996.

14. See, e.g., Correns and Goldschmidt 1913; Hertwig 1913 (paper presented at the 2nd main meeting of the Kaiser Wilhelm Society, 1913, in Berlin); Plate 1933; Mainx 1933.

15. Mainx 1933.

16. Satzinger 2009a, 154–159; Chen 2003.

17. Martin 1996.

18. Fischer-Homberger 2001.

19. Schatten and Schatten 1983.

20. Mainx 1933, 81. All translations, if not otherwise stated, are by the author.

21. Mainx 1933, 81.

22. Harwood 1993.

23. Pringsheim 1933.

24. Mainx 1933, 30–41.

25. Schiemann 1931. Review by Oehlkers 1933. On Schiemann, see Scheich 2002; idem 1997.

26. The concept of "doing" or "undoing gender" is based on the understanding of "gendering" as a social or symbolic activity to attribute power, responsibility, relevance/irrelevance to people or things by calling them male or female. The actual meaning of male and female, however, is highly flexible and always a matter of negotiation. To "undo gender" means to avoid or dismantle this allocation process for the sake of a gender-free social or symbolic order. On the problem

of gender difference in the realm of procreation or generativity—the generative difference—see Landweer 1994; for an instantiation of this difference, see Vedder, this volume, on the trope of the bachelor.

27. See Satzinger 2009a, 85–123 and 45–51; also Satzinger 2008, and forthcoming. Walter Sutton is usually credited with being the cofounder of the chromosomal theory of heredity. His contribution is one short paper where he compares the behavior of chromosomes during germ cell development (later called meiosis) with the behavior of Mendelian "Anlagen." Boveri's work has much more depth and complexity, identifying the material, intracellular processes of inheritance as observable under the microscope, combined with sophisticated experiments to show the individual relevance of each chromosome for the development of an organism.

28. Satzinger 2009a, 85–91.

29. For the complicated international, English, and American history of the chromosomal theory of heredity, see Brush 2002; Rushton 2014.

30. On Weismann's and Nägeli's theories of heredity, see Rheinberger and Müller-Wille, this volume.

31. Satzinger 2009a, 113–123; Boveri 1889.

32. Scientists today appreciate Theodor Boveri for his identification of two independent cycles of doubling and division in the process of cell division: the doubling and division of the chromosomes and the doubling of the centrosomes, which become the endpoint of the spindle apparatus during mitosis. Moritz and Sauer 1996; Davidson 1983.

33. Sea urchin egg cells fertilized by two spermatozoa had more than one spindle apparatus, causing irregular distributions of chromosomes in the resulting cells and, consequently, disturbances in embryonic development which could be analyzed by means of statistics to show the individual relevance of each chromosome. Satzinger 2009a, 85–91; Boveri 1904.

34. This observation was also the basis for the cytological identification of the germ line in Ascaris development by Theodor Boveri (1899).

35. Boveri 1910.

36. Satzinger 2009a, 91–93 and 135–137; Boveri 1918.

37. Satzinger 2009a, 111–122; Laubichler and Davidson 2008.

38. Boveri 1902.

39. Satzinger 2009a, 95–111. On Weismann's evolutionary theory, see Gayon, this volume, also.

40. See Harwood 1993; Sapp 1987.

41. The gendered order of the cell—with a "female" cytoplasm being subject to the "male" control of the chromosome—has been criticized by feminist scholarship for a long time. See Biology and Gender Study Group 1989; Keller 1995. At that time the work of the Boveris on chromosome diminution was unknown; therefore it remained unnoticed that—while the gendered order of

cell components was formed—biological observations and hypotheses were available which acknowledged a considerably active contribution of the cytoplasm and its power to reorganize the chromosome, at least in development.

42. Kohler 1994; Keller 2000; Rheinberger and Gaudillière 2004; Gaudillière and Rheinberger 2004; Sapp 1987; Keller 2000.

43. The following is based on Satzinger 2009a, 124–141; Boveri 1909. Boveri's favorite scientific opponent, Oscar Hertwig, had seen the cell nucleus as a site of sex difference; he denied the individuality of chromosomes, so crucial for Boveri's work. So it is possible to argue that this, in addition to his effort to uphold male equality in heredity, contributed to Boveri's blind spot concerning the interpretation of "accessory chromosomes" in germ cells as those that determined sex difference.

44. Boveri and Stevens 1904.

45. See Arni, this volume, on the importance of discourses of the mother's influence on the unborn in the nineteenth century.

46. Ogilvie and Choquette 1981; Brush 1978.

47. Satzinger 2009a, 82–84.

48. Satzinger 2009a, 40–44; Bleker 2005.

49. Satzinger 2009a, 247–281; Satzinger 2009b; Richmond 1986.

50. For more on Goldschmidt, see also Richmond 1986, 2007; Dietrich 1995, 2000, 2003. These references are necessarily incomplete.

51. Satzinger 2009b.

52. Richmond 2007.

53. Schmidt 2000.

54. Jacob (1970) 1989, 1. (French first edition: *La Logique du vivant*. Paris: Gallimard, 1970.)

55. Jacob (1970) 1989, 1–2.

56. Whether there was any reference to the earlier work at the Kaiser Wilhelm Institute for Biology on single cells' sexuality is as yet unknown. Possible channels of transmission might have run via Esther and Joshua Lederberg, Goldschmidt, and Franz Moewus.

57. Jacob 1988, 275–284 and 281. See Morange 2002 and Spanier 1995, 56–59.

58. Rheinberger 2002, 350.

59. Creager 2004; Bivins 2000.

60. Foucault, cited in Stingelin 2003, 14–15.

61. Delbrück 1971. Jacob must have known this text, as he himself contributed to the anthology.

62. Lesky 1951, 120–163. See also Heinz 2002; Tuana 1988.

63. See Klinger 2005.

64. See, e.g., Keller 2000; Rheinberger and Müller-Wille 2009.

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