Women in Early Human Cytogenetics: An Essay on a Gendered History of Chromosome Imaging

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Alongside the renowned male pioneers of medical cytogenetics, many women participated in investigations at the laboratory bench and the bedside, both in Europe and the Americas. These women were committed to this new biological and clinical practice—cytogenetics, the origins of contemporary genetic diagnosis—and contributed to the creation of new biological concepts and settings centered on the study of chromosome imaging. This paper will review the contributions made by a group of woman scientists from a wide geographical distribution, situating their names and research agendas within the history of a field dating back to early plant and insect cytogenetics. Rather than an exhaustive compendium of women geneticists, this essay presents a kind of historical reconstruction that can be achieved by placing women at center stage in their geographies and networks of circulating cytogenetic knowledge and practices thereby relating a history of genetic images though the work carried out by women, retrieving their agency and constructing an inclusive history of an influential contemporary biomedical practice as it gained increasing influence in the laboratory and the clinic.

Keywords: women geneticists, visual cultures, medical genetics, twentieth century, circulation of knowledge and practices

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1. Introduction

The biographical approach in history generally relies on a one-person focus. Any reconstruction of a scientific life, however, to be satisfactorily comprehended in all its complexity, includes a collective—of individuals, objects, and institutions—in order to account for the emergence of new research spaces, agendas, and authority of a given person, discipline, or technique.¹ A collective biography—or, in the case of this essay, a historical reconstruction of the early days of a scientific collective—is based on a narrative that includes a wide assemblage of agents from diverse geographical spaces and aspires to provide a sense of the genealogy, links and connections, contacts and inspirations at the roots of creating a network; a transnational community of expertise.

In the historiographical time in which we live and conduct research, genetics, cytogenetics, and medical genetics in general have their own clinical and research space, the historical reconstruction of which still conforms to the established grand narratives of the history of science. Historians and geneticists have provided their own reconstructions, the publication of such texts being mediated by the scientific authority their authors have accumulated.²

Places, institutional settings of Anglo-Saxon cultures and practices have attracted the attention of scholars on science studies, either history, philosophy or sociology. It is the consideration of networks of practitioners and places, of the travels and circulations of knowledge and practices what allows to identify both women and the skills they deployed in cytogenetics, beyond geography and male predominance. By following women and their practices in cytogenetic imaging, additional agents appear whose identification allows to “representing the subtleties of cooperation” (Leigh Star and Strauss 1999, p. 9). That is, not only women and their geographies but also circulation and travels exhibit agency, by allowing the geographical distribution of authority and expertise and its dynamics to emerge.

The gendered organization of scientific work and the materialities of its memories generally combine with academic hierarchies within the laboratory, clinic, and field. Helga Satzinger (2004, 2009, 2012) has insightfully

1. Particularly insightful for this essay has been the work of Govoni and Franceschi (2015) and von Oertzen (2012), as well as the pioneering reconstructions of women scientists in the US by Margaret Rossiter (1998, 2012) and Cabré (1996). See also Santesmases, Cabré, and Ortiz Gómez (2017).

2. Kevles (1985) is one of the few persuasive *grand narratives* of the history of human genetics; an inclusive conceptual framework is provided in Müller-Wille and Rheinberger (2012). Diverse approaches can be found in Lindee (2005), the contributions in Fortun and Mendelsohn (1998), Gaudillière and Rheinberger (2004), Rheinberger and Gaudillière (2004), and Müller-Wille and Brandt (2016). For an example constructed by a geneticist see Harper (2008). Some provide beautiful details about experiments and techniques, of which probably the best known is Hsu (1979).

analyzed the cultures and practices of geneticists in the laboratories and their private lives. An entire social culture participated in maintaining a border between genders and a gendered order of objects and tasks, including recollections and their legitimacy: who carries the power to reliably remember whom and what. Our own stories, those that many of us as historians have helped construct, rely in part on sources provided by men deemed to have such authority. Archives, highly cited papers, discoveries and highlights, award speeches, memoirs, workshops and conferences, homages and *festschriften*, and, particularly in the case of medical genetics, agreements on nomenclature and classifications, all pertain to a set of sources elaborated from the privileged position of male authority.

By focusing on women, an inclusive historical narrative can be provided to historicize and chronicle achievements in genetics and their integral position in contemporary clinical practice (see Richmond 1997, 2007, 2015; Satzinger 2009, 2012; Stamhuis and Monsen 2007). It has been in the temples of wisdom—universities and hospitals—that genetics has secured its enduring role in contemporary biomedicine (Keating and Cambrosio 2003; Santesmases and Suárez 2015). As a space of knowledge and practices that have contributed to the creation of biomedical laboratories as platforms relating to healthcare and scientific practices, genetics provides a scenario that deserves profound exploration in order to situate the women, men, and the material culture they helped create, within the geographical, transnational history of the field.

What gender means in this history goes beyond the straightforward participation of women; it includes a mindful handling of techniques, a conscientious craft with handling biological material and precision instruments, and in the majority of cases, women in a secondary position (Jordanova 1989; Rossiter 1993). It was because those positions were created for and occupied by women that those workplaces were regarded as assistantship and backstage. This paper will focus on reviewing the contributions made by women, including their names and research agendas within the history of the field dating back to early plant and insect cytogenetics in Europe and North America. This is of course not an exhaustive compendium of women geneticists but rather a test run—a suggestion for the kind of historical reconstruction that can be achieved by placing women at center stage. This proposal aims to bring a group of woman cytogeneticists from a set of geographical settings to the heart of a historical narrative on an influential contemporary biomedical field in biological research and medical practice.³

3. The *Journal of the History of Biology* 40, 3 (2007), included a “Special Section on Women in Genetics,” with four papers on women in genetics in what I believe to be a pioneering collection. See also those included in Ogilvie and Harvey (2000).

Cytogenetics has a long history as a visual epistemology: it has been through the manufacturing of images—drawings and photomicrography—that knowledge and practices have been produced (Santesmases 2017b). To develop this genealogy of woman cytogeneticists, I have therefore included a number of their drawings, a display of their expertise, one exercised in the field of genetics since its earliest days in which artful and scientific experimental skills appeared as superimposed.

2. Gender in Research

In the history of science and professions, the norms and hierarchies of working spaces have been governed by a gendered culture articulated around dichotomies: women and men, of course, but also female and male issues, tasks and objects (Satzinger 2012; Richmond 2006). This meant women and men rarely interchanged jobs, and a logic was constructed around the need to have educated women in science: only when provided with comparable education and training would women and men carry out similar roles. They did so in the twentieth-century research laboratory and in university teaching, once women had been accepted as students by right rather than as the exception, even if before this happened without permission, as a *fait accompli* policy. Between the late-nineteenth and early-twentieth century, women were given the right to access higher education across many European countries, most of which did not create colleges specifically for women: women started to enter a space previously reserved for men. As education became a legal right for women (Núñez 1992; Flecha 1996), education and training began to have the same effect on sex segregation as on social segregation; they initiated the mitigation of inequality. The number of women students at Spanish universities increased faster than the number of men between 1940 and the late 1960s, so the extraordinary influence of 1968 on contemporary culture was in part due to the increasing presence of women in universities: women graduate students were a cause, rather than a consequence, of the changes experienced in Spanish society and its universities during the late 1960s. These women were instrumental in changing universities precisely by being university students (Santesmases 2000).

3. A Genealogy of Chromosome Images from Plants and Insects

Through cytological observation, plant biologists have systematically investigated the shape and number of chromosomes possessed by known species. By the mid-twentieth century, species with high numbers of chromosomes were familiar to cytologists, botanists, and plant biologists who observed cell division through the microscope (Fig. 1).

In 1907 at the Cold Spring Harbor Station for Experimental Evolution (New York), Ann May Lutz produced a hybrid evening primrose (*Oenothera*)

that had double and quadruple numbers of chromosomes, leading Lutz and her contemporaries to talk of triploid and tetraploid mutants. Plant cytology was becoming a competitive field of study, and polyploidy one of its most keenly explored phenomena (Richmond 2010), including the observation of induced polyploidy in plants through the action of alkaloid colchicine in 1937. Colchicine proved to produce polyploidy by multiplying chromosomes during cell division. To the naked eye, the effect of colchicine was usually an increased size in plant parts: leaves, plant stature, branches, flower parts, fruits, and seeds (Curry 2016, Campos 2015).

Genetics research on *Drosophila* (initially classified as *amphelophila* and later as *melanogaster*) was based on chromosomes before phenotyping and genotyping focused on the lineal genes observed, drawn and printed from chromosomes. The fly's chromosomes were first described and drawn by Nettie Stevens (1908, 1912), who in 1905 identified the “heterochromosomes”

Figure 1. Ann M. Lutz 1912: 387. The 21 chromosomes observed by Ann May Lutz of a hybrid of *Oenothera lata* and *Oenothera Lamarckiana*.

XY of the common mealworm *Tenebrio molitor* and, alongside Edmund B. Wilson and Thomas H. Morgan, established the chromosomal theory of sex determination. Stevens's work and presentation of evidence preceded Wilson's and Morgan's efforts and was also more comprehensible (Ogilvie and Choquette 1981). In a paper in which Stevens identified the chromosomes of a wide set of flies and midges from the genus *Diptera*, among the four plates of chromosome drawings were twenty-seven figures showing *Drosophila* chromosomes at different stages of cell division (Stevens 1908; four are reproduced in Fig. 2). Stevens introduced a detailed technique to make *Drosophila* chromosomes visible and fixed for a number of weeks (Delgado Echeverría 2007, pp. 254–60), from which she created images of chromosomes using the *camera lucida* technique of projecting what was revealed to the eye by microscopic magnification onto paper. Since that time, the majority of chromosome images of *Drosophila* and other species would be drawn using this method.

Nettie Stevens graduated from Bryn Mawr College, a women's college committed to providing students with opportunities for research. Working with Theodor and Marcella Boveri during a stay at the University of Würzburg, Germany, Stevens practiced the experiments involved in Boveri's chromosome theory of heredity in her research on sex determination (Satzinger 2008). Her

Figure 2. Nettie Stevens 1908: from Plate IV. Chromosomes of *Drosophila* ampelophila at different stages in anaphase (78 and 79) and metaphase (81 and 82).

chromosome-centered view of heredity and images of fruit fly chromosomes became the basis upon which *Drosophila* cytogenetics was constructed when a group led by Thomas H. Morgan at Columbia University in New York began cross breeding *Drosophila* in the 1910s in an effort to locate genes as particular sites within chromosomes.

Married to Bryn Mawr zoology graduate Lilian Vaughan Morgan, Thomas Morgan became influential and provided evidence for the chromosomal theory of heredity. Later, in 1916, Calvin Bridges, a member of Morgan's group, provided a schematic version of the *Drosophila* chromosomes that Stevens had drawn (Morgan et al. 1915, p. 7; Allen 1978). From that time forward *Drosophila* chromosomes tended to be drawn showing the particularities of a fly or a given line: these chromosome images, along with other material from *Drosophila* cultures and practices, continually referenced Morgan, Sturtevant, Muller and Bridges. In the laboratory that became known as "the fly room," however, Morgan worked in collaboration with many women, the names of whom were included in some of Morgan's publication acknowledgements: M. B. Abbott, Anna Dorothy Bergner, Elizabeth Cattell, Clara Lynch, Ann Elizabeth Rawls, Helen Redfield, Mary Stark, Sabra Tice, and Edith Wallace (Kohler 1994; Delgado Echeverría 2007; Dietrich and Tambasco 2007).

Lilian Morgan, once their four children were in school, began to work as a geneticist and independent researcher in Morgan's laboratory. When she drew the chromosomes of *Drosophila* she was studying (Morgan 1922), referencing Bridges (1916) enabled her to correlate his images with her own analysis of the genetic "behavior" of triploid females in *Drosophila* that "occasionally" appeared to exhibit two "inseparable" X chromosomes (Keenan 1983). Lilian Morgan depicted the inseparable X chromosomes of the triploid females as broader than usual, as shown in Figure 4, in which her females *b* and *c* are presented next to *a*, the wild type drawn "after Bridges" (Morgan 1922, p. 273); Bridges himself styled his drawings "after Miss Stevens" (Fig. 3).

Chromosome was the biological term associated with these images provided by Nettie Stevens, and later Calvin Bridges and Lilian Morgan.

Figure 3. Lilian V. Morgan 1922. *Drosophila* wild-type (a) chromosomes drawn "after Bridges" and two triploid-X females.

Flies themselves were drawn by the zoologist Edith Maynard Wallace, whose images articulated the whole set of genetic practices and knowledge provided by experiencing with both wild-type and breded flies. Graduating in 1903a Mt. Holyoke College, Edith Wallace took a master's degree at Clark University and in 1908 was hired by Thomas H. Morgan (<http://archives.caltech.edu/news/wallace.html>; Kohler 1994). Her drawings became a recognized visual culture of the *Drosophila* genetics manufactured by the "Fly Room" and shared epistemic authority with the accompanying texts (see below).

Nettie Stevens's studies of "sex-limited" inheritance in *Drosophila* participated in the origins of the chromosomal theory of heredity and she herself helped persuade T. H. Morgan of the theory's validity (Ogilvie and Choquette 1981). Thus, the genealogy of genetics dates back to zoology and botany and includes—among others less studied—Nettie Stevens, Edith Wallace, and Lilian Vaughan Morgan.

Women continued work in the new area of cytogenetics, and by the 1920s were receiving PhDs (Richmond, this issue). Among these was Barbara McClintock, gaining a PhD from Cornell in 1927, presented the first diagram of maize chromosomes in 1929 using the iron-acetocarmine staining method described by British cytologist John Belling working at Cold Spring Harbor (Keller 1984; Comfort 2001, p. 51; Kass and Bonneuil 2004, p. 105). This was a "representation of the haploid set" composed of the ten chromosomes of *Zea mays*, as she observed them in the "first division in the microspore where only the haploid complement is present." (Fig. 4) McClintock depicted an interchange of pieces between two chromosomes by drawing the event both with the aid of a *camera lucida* and as a diagram (Fig. 4). This combination, based on images—that is to say, on visual evidence, was a result of her research. The image of the interchange shown in figure 4 exhibits clear portions of each chromosome sharing some pieces in a particular shape. On the following page she presented a diagram making her vision of the phenomenon even clearer: normal components appear ready to interchange segments of the chromosomes with a pair that was already an interchange. Note the straight lines and right angles of figure 4b compared with the circular shape of the *camera lucida* drawing in figure 4a: straightforward idealization appears to make the knowledge contained in such images far more evident. McClintock's trained eye (Comfort 2009; Anderson and Dietrich eds. 2012) led her to "present evidence indicating the serial order" of a number of genes (McClintock 1929). Her diagrammatic and visual culture was part of her way of working, producing images that repeatedly alluded to each other. From the late 1920s onwards McClintock's genetic research on maize provided a set of practices and knowledge relating to heredity that was textual and artful, her drawings usefully demonstrating how cell division takes place. Her work on the so-called

Figure 4. Barbara McClintock 1929: p. 792, 793. The interchange as Barbara McClintock observed it through the microscope in an “outline drawing made with the aid of a camera lucida,” and the schematized version on the following page depicting the interchange between non-homologous chromosomes.

jumping genes, transposons, contributed to a dynamic and complex view of both genetics and the meaning of “the gene” (on the gene see Keller 2000; Barahona 1997; Comfort 2012; Rheinberger and Müller-Wille 2017).

McClintock appears to have relied on the powers of microscopy and her trained eye to see maize chromosomes and draw them, thereby providing correlations between the crop’s colors, shapes, fertility features, and the size and shape of chromosomes. She complemented the forms and colors she observed in the field and greenhouse with those observed through the microscope. Her celebrated skills as a cytologist were related to her powerful sensibility for new forms and shapes and her ability to correlate images that crossed and rearranged themselves in unknown ways (Keller 1984).

The growing community of cytogenetics would enthusiastically engage with the first *Drosophila* handbook, published in 1944, circulating knowledge produced through the medium of this fruit fly. It was authored by Calvin Bridges and Katherine Brehme. A geneticist educated at Wellesley College, Brehme was a fellow of the Carnegie Institution in Washington, DC, when she edited the handbook, 1939–1941, and until 1958 when she edited the *Cold Spring Harbor Symposia of Quantitative Biology*, a set of publications of papers from annual meetings on genetics and early molecular biology organized by the geneticist Milislav Demerec.

Under the title, *The Mutants of Drosophila Melanogaster*, the handbook was based on mutants initially elaborated by Bridges, but following his unexpected death in 1938, the project was completed, updated, and edited by Brehme.

The 253-page book described a collection of *Drosophila* “mutants and aberrations” listed by symbols in alphabetical order and included hundreds of figures drawn by Edith Wallace, many previously unpublished. Wallace’s accuracy and artistic touch, according to Brehme’s preface, had become “a standard all over the world” (Bridges and Brehme 1944). Brehme’s work participated in the growing authority of *Drosophila* genetics, providing a handbook that became a reference not only for *Drosophilists* but for genetics more widely.

Edith Wallace participated in many of the copious publications originating from Morgan’s group. The California Institute of Technology (Caltech) Archive website has a photograph of Wallace wearing a white-coat, signifying her worth as an assistant and draftsman of the original drawings of numerous *Drosophila* specimens. Another photograph, taken in 1912 by embryologist Alfred Huettnner and shown on the historical webpage of the Marine Biological Laboratory in Woods Hole, depicts Wallace in a more powerful stance, seated and hands crossed.

The CalTech archive preserves many drawings by Edith Wallace, which “survived in the papers of Morgan and his students”; her pictures remain a source for the historical reconstruction of *Drosophila* genetics. Additional original drawings by Wallace include those published in successive editions of the Red Book (as later editions of the *Mutants of Drosophila* were called) held at the CalTech Archives. Her artistic skills, held in wide esteem, were honed while studying biology at Mt. Holyoke College.

Katherine Brehme’s archival material is preserved under the heading “Kitty Brehme Warren” at Cold Spring Harbor Laboratory Archives—a diminutive that co-constructed Brehme dependent identity on other scientist. Her

Figure 5. Two drawings by Edith Wallace of two mutants of *Drosophila melanogaster*. From Bridges, Calvin B., and Katherine Brehme. 1944. *The Mutants of Drosophila Melanogaster*. Washington DC: The Carnegie Institution, p. 20. Reproduced by permission from the Carnegie Institution.

annotated scrapbooks contain valuable visual material, including photographs of those who participated in the symposia at Cold Spring Harbor, with many of the women and men identified by Brehme herself.⁴ Photographs are testimonies that participate in identification of the many scientists involved in those meetings, including a wide group of women who deserve historical attention. Such testimonies provide a sense of genealogy and belonging to those whose participation in the history of genetics has frequently been overlooked.

4. Transitions to Human Genetics

In the first edition of her popular book *Genetics in the Atomic Age*, Charlotte Auerbach (1956) from the Institute of Animal Genetics at Edinburgh University explained how chromosomal accidents that produce mutations affect the cell and the developing embryo (Richmond 2017; Carlson 1981, pp. 244–57). Auerbach together with John M. Robson was the first to prove that chemicals were able to induce mutations (Auerbach and Robson 1944). A German-born Jewish researcher, Auerbach fled Nazi Germany to get a PhD in genetics, and after the Second World War and the advent of nuclear testing, she dedicated herself to popularizing radiation genetics in work that was translated and circulated widely. Her presentations of genetic knowledge on the effects of radiation—which Hermann Muller himself had warned against for the case of X-rays since the 1920s—show an additional trajectory of expertise from *Drosophila* to human genetics through research on mutations and radiation effects in chromosomes (Auerbach 1956, pp. 78–9). An expert in *Drosophila* genetics, according to Richmond (2017) Auerbach's work also helped promote women's authority as scientific experts.

As Auerbach summarized in 1978, radiation produces both chromosome breaks and mutations: following the emergence of nucleic acids and enzymes as explicators of mutagenesis and cell biology, the unresolved issue of chromosome structure was leading back to biology (Auerbach 1978, pp. 322, 333). Charlotte Auerbach was talking about living beings, both *Drosophila* and human beings. It was the study of the effects of industrial chemicals and radiation on chromosomes, and genes as lineal pieces of chromosomes, that created a shared focus for *Drosophila* and human genetics. Auerbach's experiments during WWII on the mutagenic effects of radiation in *Drosophila* provided the basis for radiobiology and her own genetic thinking about radiation. The atomic age participated in the growing ontology of chromosomes in genetic epistemology.⁵

4. <http://library.cshl.edu/personal-collections/kitty-brehme>.

5. Fiona Miller (2006), Soraya de Chadarevian (2006) and also Rheinberger (2010) inspired this reflection. On the debates about the effects of radiation in human beings during the 1950s, see Hamblin (2007).

Fig. 16. Kinky tails of mutant mice.

Fig. 17. Brachydactylous (top) and normal hand.

Figure 6. From Charlotte Auerbach 1956, p. 20. These illustrations by Inge G. Auerbach—a distant cousin (see Richmond 2017)—show the transition Charlotte Auerbach made from animals to human beings and her use of images to popularize her research.

As Anne May Lutz had in the early-twentieth century, during the 1930s Albert Levan used root-tips, onions in his case, to produce clear images of chromosomes through a microscope, a process he termed the *Allium* test (Levan 1932; Santesmases 2015). In this space of cytological practices, between plants and mice, tumor cells appeared as polyploids of normal cells. Tumors as accumulations of cells and chromosomes became biological entities in transit themselves. By participating in the growing funding provided for cancer research in the US and Europe, studies of cell growth, its normalities and pathologies, became increasingly focused on human biology while coexisting with the experimental systems that took part as inspirers and living tests: mice (Rader 2004) and *Drosophila* (Kohler 1994) among them.

A network composed of Albert Levan, Theodore Hauschka, Joe Hin Tjio, Eva Klein, George Klein, and Helene W. Toolan produced research that linked polyploid cells with cancer (Santesmases 2015). This set of practices included the creation of experimental mice as living laboratories for cancer research (Rader 2004). At the Karolinska Institute in Stockholm, Eva Klein and George Klein developed the project they had envisaged together upon their arrival from Hungary in the late 1940s. According to the Kleins' recollections, Eva suggested that cells could be cultured in the peritoneal cavity of the mouse (Fig. 7). After infecting mice with ascites (liquid) tumors introduced intraperitoneally, cancer chromosomes were produced *in vivo* and obtained by extraction following the animals' deaths. The samples were then treated and chromosomes observed through the microscope in a preparative slide.

At the Sloan-Kettering Institute for Cancer Research (New York) in the 1950s, Helene W. Toolan invented a method, apparently inspired by

Figure 7. Klein Preparation showing 86,3 per cent of tumor cells produced from cultures of ascite fluid (tumor) in mice. From Klein, Eva. "Gradual Transformation of Solid into Ascites Tumors. Permanent Difference between the Original and the Transformed Sublines." *Cancer Research* 14.7 (1954): 482–485, plate 2, figure 7. Reprinted by permission from the American Association for Cancer Research.

Klein's logic, for introducing human solid tumors into mice. Her technique of treating mice with cortisone prior to the introduction enabled samples of the same tumor to be obtained over and over again. Along with providing a method for transplantation, Toolan also made a comprehensive study of many types of tumors (Fig. 8). Her transplantation method enabled prospective cancer therapeutic agents to be tested, thereby boosting Sloan-Kettering's public renown in cancer research and therapy.

By creating living conditions for a tumor, the bodies of mice themselves became laboratories. With the methods they developed, both Eva Klein and Helen Toolan participated in the testing of chemotherapeutic agents against cancer and in providing techniques to study chromosomes. These implants enabled to obtain tumor chromosomes, and it was as part of this project that in 1956 Levan and Indonesian cytogeneticist Joe Hin Tjio determined the number of human chromosomes to be 46 (Santesmases 2015). The genealogy of experiments leading to the one involving explants of human embryo chromosomes—the biological material in which Tjio and Levan investigated human chromosomes—reveals some of the women scientists who contributed to the set of practices through which the new human chromosome number was established.

5. Early Techniques and Achievements for Visualizing Human Chromosomes

It was research on tumors and cancer cells that led to the method for obtaining clear slides of apparently healthy chromosomes, thereby providing evidence of the new number of 46 human chromosomes, as presented by

Figure 8. A human carcinoma after 12 days implantation in the subcutaneous tissue of a rat x-radiated and treated with cortisone. From Toolan, Helene Wallace. 1953. "Growth of Human Tumors in Cortisone-treated Laboratory Animals: The Possibility of Obtaining Permanently Transplantable Human Tumors." *Cancer Research* 13: 389–394, plate after 394. Reprinted by permission from the American Association for Cancer Research.

Tjio and Levan in 1956 (de Chadarevian 2015; Santesmases 2015). The Swedish geneticist Maj Hultén was at Lund University's Institute of Genetics at the time of Tjio and Levan's investigations. She provided her own recollections of the circumstances of the new number, in both an anecdotal journal article (Hultén 2004) and when interviewed as a witness scientist (Arnason 2006; see Harper 2008). She was asked to clarify whether Tjio determined the new chromosome number alone or in collaboration with Levan (Kottler 1974; Martin 2004).

Maj Hultén was, however, a member of the community in her own right, a community whose women would retain their agency.⁶ As a genetics student at the University of Stockholm, she spent three months at the Lund Institute of Genetics in the autumn of 1955, working under Levan's supervision on a research training project on genetics in human chromosomes. Following Levan's suggestion Hultén looked at mice and ascites tumors, studying the effect of X-irradiation, and "found some very interesting things

6. To retrieve the contributions these women made, material on their male colleagues is instrumental and often the sole resource available for an initial approach to the woman who worked with them. This is indeed one of the main sources for any study on women in science: exploring reconstructions of male scientists with the eye fully focused on women's names. See Velasco Martín (2020, this issue).

of the chromosome behaviour after X-irradiation but I never published that” (Hultén 2002).

Hultén would later graduate in Medicine at the Karolinska Institute, and having completed her PhD in 1974, she moved to the UK the following year to pursue her interest in medical genetics. Appointed head of the Regional Genetic Service at the East Birmingham Hospital, she developed her research trajectory in medical genetics, combining teaching with research and clinical practice (Jones and Tansey 2015).

By the time Tjio and Levan were investigating human chromosomes, Eva Hansen-Melander and her husband Yngve Melander, working on ascites tumor chromosomes at the same institute, discovered that no matter how many times they counted, the number of healthy human chromosomes in explants of human fetal liver cells was 46. Although the Melanders did not publish their results—the established number of 48 had been confirmed in the US by Theophilus Painter and later Tao-Chiuh Hsu—plant geneticist Arne Muntzing, the director of the Lund Institute of Genetics, remembered the Melanders repeated discoveries of 46 (Hultén 2002). Swedish genetic laboratories were highly active pioneers in genetics, as were the women who worked there, and Eva Hansen-Melander was at the time conducting research on cancer chromosomes (Tunnlid 2018). The research activities carried out at Lund’s Institute of Genetics can be seen in publications, particularly their official journal, *Hereditas*. The human chromosome number detected by Eva Hansen-Melander and Ingve Melander suggests that experimental methods being established at the time, and circulating in the transnational community of expertise in chromosome preparation, were providing epistemic opportunities for counting the new number on a slide.

In Paris during 1959, Marthe Gautier identified the additional chromosome—initially labeled chromosome number 21—possessed by the “*neuf enfant mongolien*” displaying the condition now known as Down syndrome (Lejeune et al. 1959a, 1959b). As a young pediatrician trained in congenital heart diseases in infants and newborns in Paris, Gautier had also become skilled in cell culture techniques at Harvard. On her return to Paris she was offered a post as *chef de clinique* at l’Hôpital Trousseau with Raymond Turpin. It was after publication of the new human chromosome number by Tjio and Levan and their presentation at the International Congress of Human Genetics in Copenhagen in 1956 that Turpin went back to Paris planning to search for the chromosomes of “Mongolism,” a task for which Gautier volunteered. In a laboratory equipped with a refrigerator, centrifuge, low-definition microscope, and glass material purchased at her own expense, Gautier began her attempts to obtain chromosome slides from embryo extracts provided by the Pasteur Institute. Marthe Gautier preserved the cell membrane intact—contrary to the method described by Tjio and Levan (1956)—to guarantee she was dealing with a

reliable chromosome number and not obtaining a mix of chromosomes from more than one cell: she secured “an exact figure and beautiful elongated chromosomes, easy to pair and unbroken.” “The additional chromosome was small,” according to Gautier (2009, p. 4). She had no photomicroscope, so she passed the slides on to Lejeune, who, according to Gautier records, never showed her the resulting photomicrographs (one of them may be the one reproduced and available at <http://publications.fondationlejeune.org/article.asp?filename=fj1046.xml>, published by the three authors the same year of their first paper on the Down syndrome karyotype). In 1959, Jerome Lejeune, Marthe Gautier, and Raimond Turpin published their paper on the 47 chromosomes found in Down syndrome patients in the journal of the French Academy of Science (Gautier 2009). Following these experiments, Gautier returned to her earlier clinical project of pediatric cardiology.

By that time, British cytogeneticist Patricia Anne Jacobs had identified an additional chromosome in a sample extracted from a person diagnosed with Klinefelter syndrome. It was in 1958 when she started “to look at human chromosomes” with Michael Court Brown in a new group at Edinburgh funded by the Medical Research Council conducting research on the effects of radiation. Patricia Jacobs had studied botany and zoology at the University of St Andrews. Hired by the group for her experience with insect chromosomes, she proceeded to learn techniques relating to mammalian chromosomes from Charles Ford at Harwell and a method for growing bone marrow from the hematologist Laszlo Lajtha at Oxford (Jacobs 1982).

Following training, Jacobs remembers Court-Brown requesting that she look at the chromosomes of both radiation-induced and non-radiation-induced leukemia patients, at a time when radiation-induced leukemia was

Figure 9. Mittwoch 1952. 48 chromosomes counted from a “testicular biopsy of a Mongolian imbecile.” According to Mittwoch, X and Y appear to be united. © 1953 Blackwell Publishing Ltd/University College London.

extremely rare. At that time, human chromosomes were produced using bone marrow samples, painful to extract and difficult to handle. Jacobs, by then 23 years old and assisted by 20-year-old Muriel Brunton (later Brunton Lee), would later describe the experiments and emotions of that time, including the bone marrow extraction procedure, relationships with patients, and her admiration for the expertise shown by Lionel Penrose when classifying those with intellectual difficulties. These two young women, Patricia Jacobs and Muriel Brunton, were searching for chromosomes in people with Down syndrome by the same year Gautier was, 1958, precisely because these people were regarded to be at high risk of developing leukemia (Jacobs 2004; Lee 2004).

Leukemia induced by radiation was the target of MRC research programs at Harwell in the early atomic age, but Brunton and Jacobs focused on non-radiation-induced leukemia, which, as Jacobs herself reported, was far more common. They were part of the emergence of a new scientific culture focusing on the epistemology and experimental skills of the new biomedical domain of human cytogenetics. They were agents in a story centered on studying the effects of radiation on chromosomes, a field produced by wartime developments in atomic weapons and radiation (de Chadarevian 2006). Harwell was the base of the British Atomic Energy Research Establishment created immediately after the Second World War, which included research into nuclear power and the genetic effects of radiation among its duties (Gowing and Arnold 1974).

While working with Court-Brown, Patricia Jacobs confirmed the additional chromosome found in Down syndrome children immediately after the publication of the paper by Marthe Gautier, Jerome Lejeune and Raymond Turpin (Jacobs et al. 1959). But it was during Jacobs' and Brunton's research on a Scottish endocrinologist's Klinefelter patient that they detected their first case of a karyotype composed of three sexual chromosomes: XXY. Since then, this second type of aneuploidy—additional chromosomes—has been associated with the clinical diagnosis of Klinefelter, a condition found in those regarded as men and characterized by infertility, small testes, and learning disabilities. This cytogenetic result was the first in Patricia Jacobs' long career in human cytogenetics. The importance of her work in Edinburgh was instantly recognized and she was invited to the 1960 Denver conference intended to achieve a consensus on chromosome nomenclature and classification: Jacobs was the sole woman geneticist among the 14 participants (Penrose 1960; Böök et al. 1960).

Meanwhile, Ursula Mittwoch was one of the first scientists to carry out chromosome analysis at the Galton Laboratory in London, contributing to its transition—and that of its director, geneticist Lionel S. Penrose—from population genetics to cytogenetics based on chromosome images. “He

wanted some work done on chromosomes in Down's syndrome," Mittwoch later recalled (Harper, Reynolds, and Tansey 2010) (see Fig. 10). Ursula Mittwoch had joined Penrose's Galton Laboratory as a young graduate, after a long and difficult period following her family's flight from Nazi Germany, including an internment on the Isle of Man at the age of 16. Back at the family home, at the time in London, she tried to enroll at St Anne's College in Oxford but was unsuccessful due to war regulations. She was therefore "fortunate" to secure a place at the John Innes Horticultural Institution, and between 1943 and 1947, Mittwoch attended evening classes in order to attain a degree while serving as a technical assistant to botanist Kenneth Mather. She left in 1947 after graduating to pursue a doctorate. In 1950, after obtaining her PhD at University College London, Ursula Mittwoch was offered postdoctoral research work studying the genetics of cystinuria and also leucocytes and chromosomes in "mongolism." (Figure 10 shows a drawing of the chromosomes of a case she reported in 1952.) She later carried out research on the genetics of sex determination (Mittwoch 1995, also 2004).

The term "mongolism" would be replaced by Down syndrome after 1961, the year nineteen geneticists from around the world sent a letter to *The Lancet* decrying the original term's racial connotations (Allen et al. 1961). Because of the condition's association with genetic determinism, their concern suggests a debate among practitioners on the explanatory, or even legitimating, power of chromosomes and cytogenetic knowledge and practices. The term carried a long cultural history between disabilities and heredity, which have contributed not only to the emergence of bioethics but to a reflection of the social knowledge that such *in vitro* discrimination embodied in its conceptualization, tightly linked to racial and discriminatory practices (Stern 2012; Santesmases 2016). The biologization of differences and of diversity have not avoided discrimination; however, increasing geneticization continues to receive scrutiny from critical analysts and bioethicists. Through the practices of human cytogenetics, the geneticization of social identities as pertaining to preexisting groups in nature remained closely linked to the classification of human differences in society, as Jenny Reardon (2005, pp. 15–16) insightfully analyzed. Women and men geneticists participated in these debates, in the

Figure 10. Caspersson et al. 1971. Human chromosomes number 6–12 plus XX, showing the "characteristic banding patterns," bright and dark cross striations.

history of genetic practices, and in the geneticization of health and well-being (on Scandinavian countries, see Koch 2004).

In 1959, Joy Delhanty also joined the Galton Laboratory. She underwent training on how to grow skin biopsies with David Harnden at the MRC Radiobiology unit at Harwell, while others, like Patricia Jacobs, used bone marrow in order to work on Down syndrome cytogenetics. Joy Delhanty started her working life in London as a “laboratory technician at the Institute for Cancer Research, on *Drosophila* chromosomes” for a year, before going to University College London. After Gautier, Lejeune, and Turpin’s paper on the additional chromosome associated with Down syndrome appeared, Delhanty went to see Penrose, who, appreciating her experience with *Drosophila* chromosomes, awarded her a studentship at Galton Laboratory. She started from scratch: “no equipment at all” (see Mittwoch 1995; Harper, Reynolds, and Tansey 2010). By that time, pediatrician Paul Polani, at Guys’ Hospital, London, had detected a chromosome translocation in a Down syndrome child and Delhanty tested its familial inheritance (Penrose and Delhanty 1962). A method for obtaining chromosomes from blood samples had recently been published by US geneticists from the Institute of Cancer Research in Philadelphia Peter Nowell and David Hungerford, leading to an expansion of cytogenetics studies, with the indispensable reactant phytohaemagglutinin obtained from the common bean *Phaseolus vulgaris*.

In 1962, the young physician Emilia Barreiro joined cardiologist Andrés Sánchez Cascos in establishing a laboratory for cytogenetic diagnosis at the Clínica de la Concepción in Madrid, Spain. She had been trained by Sánchez Cascos after his return from Guy’s Hospital in London, where Paul Polani had begun to collaborate with Charles E. Ford, leading to successive publications on the human chromosomes associated with congenital and inherited disorders, mental abilities, and fertility. Clinicians provided samples and then cytogeneticists obtained and examined the chromosome preparations. In the summer of 1962, Emilia Barreiro and Sanchez-Cascos began from scratch in a small laboratory with a large window on the ground floor of the Clínica, outfitted with a centrifuge, a microscope and a heater—a few simple instruments and a mindful hand, like all cytogenetic units set up at the time (Santesmases 2014).

Emilia Barreiro was an early Spanish pioneer in medical genetics and remained in the field until retirement, while Sánchez Cascos continued as a clinical cardiologist. From the mid-1960s onwards, as new hospitals were opened across Madrid, Barreiro secured a number of positions in new genetics units. In 1966 she was put in charge of the genetics department at La Paz Children’s Hospital, Madrid, a position she held for over a decade before moving to a new unit at the Hospital 12 de Octubre, also in Madrid, which she led until retirement. María Jesús Lautre, who trained with Barreiro and

Sánchez Cascos, returned to Madrid in 1967 following a stay at Guy's Hospital in London. She settled on the other side of the street, at the Hospital Clínico, also a university hospital, to head up their work in cytogenetics. As the Spanish health care system expanded in large new hospitals, so did their cytogenetic units, establishing medical genetics within the medical care agenda of Spanish health policies.

6. Banding Techniques

During the late 1960s, at the laboratory headed by Torbjörn Caspersson in the Karolinska Institut, Stockholm, Lore Zech established the staining method of using fluorescence to reveal banding patterns, enabling every chromosome to be clearly distinguished (Zech 2013). By that time photomicrography was being used in cytogenetics to make amplified photographs of a tiny point on a slide: the spot containing the chromosomes of a solitary cell. Less clear and sharp than drawn images, karyotypes obtained through photomicrographs were then cut and placed in size order (de Chadarevian 2015; Santesmases 2015). Staining chromosomes with the chemical substance quinacrine mustard produces fluorescence that can be seen in the dark and recorded by a fluorescence microscope (Caspersson et al. 1970; Hogan 2014, 2016; Schlegelberger 2013). Following the method established by Lore Zech, this fluorescence reveals bands within the chromosomes, each exhibiting a particular banding pattern, enabling an observer to distinguish one from another, not only by size and the centromere position but, in chromosomes of similar size, by the inner shape of their bands (Fig. 10).

Lore Zech had followed her husband during the Second World War from Germany to Sweden, where he was working at the Karolinska Institute as a virologist. As Caspersson had little interest in chromosomes, preferring to focus on the study and measurement of nucleic acids, Zech recalls working on chromosomes by herself. Funding was not available for microscopes: "I had some jewelry and sold it and bought a microscope because if we wanted to make a thesis at the Institute, we needed a microscope" (Zech 2013). She started her banding work in plant chromosomes before moving to mice and then humans. Quinacrine mustard became the standard tool for clarifying chromosome banding, and Zech delivered a presentation on her method in 1971 at the Paris conference on human chromosomes.

By increasing the ability to distinguish between chromosomes, the banding technique led to detection of the Philadelphia chromosome. This chromosome was initially identified by Peter Nowell and David Hungerford from Philadelphia, as a smaller than usual chromosome 22 found in the leukemia cells of patients suffering from chronic myeloid leukemia. It was initially attributed to a deletion—the chromosome lacks a part—until Janet Rowley, provided with the banding technique established by Lore Zech,

demonstrated in 1973 that it resulted from a reciprocal translocation—that is, an interchange of parts during cell division—with the part lost from chromosome 22 found in chromosome 9 (Schlegelberger 2013; Gahrton et al. 1973; Rowley 1973).

Janet Rowley had followed her husband, pathologist Donald Rowley, to Oxford twice. During the first stay in 1958 she worked with the hematologist Latzlo Latja—who had trained Patricia Jacobs—and during the second, 1970–71, she learned the banding technique during a visit to Lore Zech, who had already detected the translocation (Schlegelberger 2013). On her return to the University of Chicago, where her husband was now a professor, applying methods being developed in British and Swedish laboratories to enable human chromosomes to be clearly distinguished, Rowley used the fluorescence microscope to study the karyotypes of leukemia patients to develop her research on the translocation. In media reports of this breakthrough, cutting skills honed at the dining room table were invoked as gendered gestures attributed to her: the kitchen as women's space and domestic craft considered a minor *métier*. The technique of cutting karyotypes could certainly have been considered a gendered activity.⁷ Typing “Janet Rowley” into an internet search engine will not only reveal Rowley's pioneering contributions to cancer genetics and leukemia research, but also the recognition and numerous accolades she received.

7. As a Conclusion

The succession of images presented here demonstrate the extent to which plant and *Drosophila* genetics inspired early human genetics. Mitosis promotion with colchicine and other techniques from plant cytology made the transition to human chromosomes, as did image-making practices (Campos 2015; Curry 2016; Santesmases 2017b). Image trajectories suggest cultures—visual cultures, or even cultures of making visuals—of creating images to make genetics reliable to an audience-in-progress.

This brief history of cytogenetics, from contexts in zoology and botany to the Philadelphia chromosome, leads me to propose a number of ideas relating to the creation of history, of cytogenetics, and of disciplinary networks. A particularly useful technique has been focusing on women's names in order to trace the trajectory of images and techniques, agreements and training, personal interchanges, and professional recognition. The scientists revisited here belong to a genealogy that allows us to recreate the history of their common identity. It was my intention here to reconstruct stories of preparative slides, drawings, and photographs in a way that would bring some of the many women that participated in the early practices of cytogenetics to the core of a historical narrative.

7. I cover this briefly in Santesmases 2017b.

So many intertwined biographies reveal the agency of women and of gender in the history of human genetics since its early days. Some of the women geneticists I reflect on started their professional lives as assistants, then went on to graduate programs, while others graduated and then followed their husbands. Lore Zech and Janet Rowley were both prepared to adjust their interests and acquire experimental skills, and were therefore able to construct their professional identity as researchers in the course of their marital transits.

These women participated fully in the early and influential manufacture of this new medical field of genetic diagnosis, from which genetic determinism—or as Rosenberg (2002) has termed it, the “tyranny of diagnosis”—would originate. They participated in debates, reconstructed their genetic thinking, and revised their thoughts about causality and correlations (as Emilia Barreiro once told me Patricia Jacobs had done).

To retrieve the contributions made by these women, source material on and originating from their male colleagues may at times be the only resource available for an initial approach (Velasco 2020, this issue). The presence of the women discussed here has been identified in reconstructions preserved and written by their male colleagues: at some point these women eventually attained recognition. In the early days of human cytogenetics, every experiment mattered; every new experience with chromosomes and chromosome preparations provided new data, new images, and new knowledge. Such a small group, who were invited *en masse* to Denver in 1960 by Theodore Puck, included more women than the sole female participant at the 1960 conference (Patricia Jacobs), where names and classifications of chromosomes would be organized and standardized for the foreseeable future.

By focusing not only on women’s names but also women’s skills I have shown that genetic methods not only circulated transnationally but also crossed species spaces and ontologies. Zoology and botany were the institutionalized disciplines that provided the path to cytology and cytogenetics. This style of work circulated quickly and efficiently, from Lund and Harwell to London, Madrid, Stockholm, and Chicago. Not only did women, places, and methods play their part, but communication was an essential agent, erasing the obstacles produced by geography and geopolitics. As in many historical reconstructions, time and space took effect. This means that even if geography matters as a representation of the geopolitics not only of experimental research but of the historiography as well, travels of journals, and researchers—to meet each other, to acquire experimental abilities, to attend meetings—participate in the dynamics of networks of authority and recognition. For the case of woman scientists, a diversity of skills is required for a historian who aspires to offer inclusive

histories. In addition to retrieve women's names, it is women's skills that needed to be retrieved as instrumental in knowledge production: drawings, techniques, laboratory work, women's remembrances of their male advisors, colleagues and chief are the set of sources and categories to be regarded as indissoluble part of scientific authority. Between Europe and the Americas, circulating between New York, Pasadena, Washington, Lund and Stockholm, Edinburgh, Harwell, Madrid and Chicago, many woman scientists have stood out, and more would subsequently obtain recognition in periods and experimental domains not covered by this essay.

It is generally acknowledged that a focus on the achievements of an individual generates an incomplete picture: research has always been, as it still is, a collective endeavor in which women have been engaged for centuries. Therefore, it is through observing collectives that the practice of history will be able to demonstrate the diverse set of agents involved in reconstructing human genetics and its genealogies.

The promotion of genetic research played its part when the funding priorities for radiobiology—the biology of radiation—began to include genetics, genetic damage, and chromosomal reactions to radiation, while biological heredity was at the root of contemporary life sciences, cytogenetics included (de Chadarevian 2006; Creager 2013; Müller-Wille and Brandt 2016). Nettie Stevens and Barbara McClintock in the US, Marcella Boveri in Germany, and later Ursula Mittwoch, Joy Delhanty, Patricia Jacobs in the UK, Marthe Gautier in France, Emilia Barreiro and María Jesús Lautre in Spain, Lore Zech in Sweden, and Janet Rowley in Chicago, are but a few of the women who participated in the early days of human cytogenetics, at the beginning of contemporary medical genetics. They belonged to a lineage of cytogeneticists, of woman researchers and the practices of microscopy, the same lineage traced by their inspirational predecessors, those woman botanists and zoologists who attempted to deduce a theory of heredity through the study of plant and insect chromosomes: among them Nettie Stevens, Anne May Lutz, Barbara McClintock, Lilian Vaughan Morgan, Jannaki Amal who worked at John Innes Horticultural Institution (UK), distinguished British geneticist Mary Frances Lyon for her work on the X chromosome and many others not included in this brief account of woman geneticists in Europe and the Americas. The careers of these women not only illustrate their participation as scientists from the very beginning of the field of genetic research, but also the set of agents involved. In addition to their renowned male colleagues, the fields of botany, entomology, and zoology, the arts and crafts of producing images, the microscopes, the delicate preparative skills, and various biological epistemologies all played a part. By visualizing the women in cytogenetics, the history of these practices emerges as one composed by a collective of objects,

subjects, and researchers, as part of the material and gendered cultures of knowledge production within contemporary biomedical heredity.

Professional skill's geographies, a cartography of practices, have been included here by focusing on women, the scientific authority of whose experiments and practices would be later recognized after women were classified as illustrators of those drawings that embodied a centuries old set of both knowledge and practices of the sciences and the arts.

References

- Allen, Garland E. 1978. *Thomas Hunt Morgan: the Man and his Science*. Princeton: Princeton University Press.
- Allen, Gordon, C. E. Benda, J. A. Böök, C. O. Carter, C. E. Ford, E. H. Y. Chu, E. Hanhart, George Jervis, W. Langdon-Down, J. Lejeune, Hideo Nishimura, J. Oster, L. S. Penrose, P. E. Polani, Edith L. Potter, Curt Stern, R. Turpin, J. Warkany, and Herman Yannet. 1961. "Mongolism." *The Lancet* 1: 775.
- Anderson, Nancy, and Michael R. Dietrich. 2012. *The Educated Eye: Visual Culture and Pedagogy in the Life Sciences*. Hanover, NH: Dartmouth College Press.
- Arnason, Ulfur. 2006. "50 Years After—Examination of Some Circumstances Around the Establishment of the Correct Chromosome Number of Man." *Hereditas* 143: 202–11.
- Auerbach, Charlotte. 1978. "A Pilgrim's Progress through Mutation Research." *Perspectives in Biology and Medicine* 21: 319–34.
- Auerbach, Charlotte. 1956. *Genetics in the Atomic Age*. Edinburgh: Oliver & Boyd.
- Barahona, Ana. 1997. "Barbara McClintock and the Transposition Concept." *Archives internationales d'histoire des sciences* 46: 309–329.
- Böök, J. A., et al. 1960. "Nomenclature in Human Mitotic Chromosomes." *Annals of Human Genetics* 24: 320–325.
- Bridges, Calvin B. 1916. "Non-disjunction as Proof of the Chromosome Theory of Heredity." *Genetics* 1(1): 1–52.
- Bridges, Calvin B., and Katherine Brehme. 1944. *The Mutants of Drosophila Melanogaster*. Washington DC: The Carnegie Institution.
- Cabré, Montserrat. 1996. "Mujeres científicas e historias 'científicas'. Una aproximación al pasado desde la experiencia femenina." Pp. 13–32 in *Mujeres de ciencias. Mujeres, feminismo y ciencias naturales, experimentales y tecnológicas*. Edited by Teresa Ortiz Gómez and Gloria Becerra. Granada: Universidad de Granada-Instituto de Estudios de la Mujer.
- Campos, Luis A. 2015. *Radium and the Secret of Life*. Chicago: University of Chicago Press.

- Carlson, Elof A. 1981. *Genes, Radiation, and Society: The Life and Work of H. J. Muller*. Ithaca, NY: Cornell University Press.
- Caspersson, Torbjörn, Gösta Lomakka, and Lore Zech. 1971. "The 24 Fluorescence Patterns of the Human Metaphase Chromosomes—Distinguishing Characters and Variability." *Hereditas* 67(1): 89–102.
- Caspersson, Tjioborn, Lore Zech, C. Johansson, and E. J. Modest. 1970. "Identification of Human Chromosomes by DNA-binding Fluorescent Agents." *Chromosoma* 30(2): 215–217.
- Comfort, Nathaniel. 2001. "From Controlling Elements to Transposons: Barbara McClintock and the Nobel Prize." *Trends in Genetics* 17(8): 475–478.
- Comfort, Nathaniel. 2009. *The Tangled Field: Barbara McClintock's Search for the Patterns of Genetic Control*. New Haven: Harvard University Press.
- Comfort, Nathaniel. 2012. *The Science of Human Perfection: How Genes Became the Heart of American Medicine*. New Haven: Yale University Press.
- Creager, Angela NH. 2013. *Life Atomic: A History of Radioisotopes in Science and Medicine*. University of Chicago Press.
- Curry, Helen Anne. 2016. *Evolution Made to Order: Plant Breeding and Technological Innovation in Twentieth-Century America*. Chicago: University of Chicago Press.
- de Chadarevian, Soraya. 2006. "Mice and the Reactor: The 'Genetics Experiment' in 1950s Britain." *Journal of the History of Biology* 39: 707–735.
- de Chadarevian, Soraya. 2015. "Chromosome Photography and the Human Karyotype." *Historical Studies in the Natural Sciences* 45(1): 115–46.
- Delgado Echeverría, Isabel. 2007. *El descubrimiento de los cromosomas sexuales: un hito en la historia de la biología*. Madrid: Editorial CSIC.
- Dietrich, Michael R., and Brandi H. Tambasco. 2007. "Beyond the Boss and the Boys: Women and the Division of Labor in *Drosophila* Genetics in the United States, 1934–1970." *Journal of the History of Biology* 40(3): 509–28.
- Flecha, Consuelo. 1996. *Las primeras universitarias en España, 1872–1910*, vol. 3. Madrid: Narcea ediciones.
- Fortun, Michael, and Everett Mendelsohn, eds. 1998. *The Practices of Human Genetics*. New York: Springer.
- Gahrton G., J. Lindsten, and Lore Zech. 1973. "Origin of the Philadelphia Chromosome. Tracing of Chromosome 22 to Parents of Patients with Chronic Myelocytic Leukemia." *Experimental Cell Research* 79: 246–247.
- Gaudillière, Jean-Paul, and Hans-Jörg Rheinberger, eds. 2004. *From Molecular Genetics to Genomics: The Mapping Cultures of Twentieth-Century Genetics*. London: Routledge.
- Gautier, Marthe. 2009. "Cinquantenaire de la trisomie 21-Retour sur une découverte." *médecine/sciences* 25: 311–316.

- Govoni, Paola, and Zelda Alice Franceschi, eds. 2015. *Writing about Lives in Science: (Auto)Biography, Gender, and Genre*. Goettingen: V & R Unipress.
- Gowing, Margaret, and Lorna Arnold. 1974. *Independence and Deterrence: Britain and Atomic Energy, 1945–52*. London: Macmillan.
- Hamblin, Jacob D. 2007. “‘A Dispassionate and Objective Effort’: Negotiating the First Study on the Biological Effects of Atomic Radiation.” *Journal of the History of Biology* 40(1): 147–177.
- Harper, Peter S. 2008. *A Short History of Medical Genetics*. Oxford: Oxford University Press.
- Harper, Peter S., Lois A. Reynolds, and E. M. Tansey. 2010. *Clinical Genetics in Britain: Origins and Development*. London: The Wellcome Trust.
- Hogan, Andrew J. 2014. “The ‘Morbid Anatomy’ of the Human Genome: Tracing the Observational and Representational Approaches of Postwar Genetics and Biomedicine.” *Medical History* 58(3): 315–36.
- Hogan, Andrew J. 2016. *Life Histories of Genetic Disease: Patterns and Prevention in Postwar Medical Genetics*. Baltimore, MD: Johns Hopkins University Press.
- Hsu, Tao Chiuh. 1979. *Human and Mammalian Cytogenetics: An Historical Perspective*. New York: Springer-Verlag.
- Hultén, Maj A. 2002. “Numbers, Bands and Recombination of Human Chromosomes: Historical Anecdotes from a Swedish Student.” *Cytogenetic and Genome Research* 96: 14–19.
- Hultén, Maj A. 2004. Interview by Peter Harper. <https://genmedhist.eshg.org/fileadmin/content/website-layout/interviewees-attachments/maj-hulten-interview.pdf>
- Jacobs, Patricia A. 1982. “The William Allan Memorial Award Address: Human Population Cytogenetics: The First Twenty-Five Years.” *American Journal of Human Genetics* 34(5): 689–98.
- Jacobs, Patricia A. 2004. Interview by Peter Harper. <https://genmedhist.eshg.org/fileadmin/content/website-layout/interviewees-attachments/Jacobs,%20Pat.pdf>
- Jacobs, Patricia A., W. C. Brown, A. G. Baikie, and J. A. Strong. 1959. “The Somatic Chromosomes in Mongolism.” *The Lancet* 273(7075): 710.
- Jones, Emma M., and Elisabeth M. Tansey. 2015. *Human Gene Mapping Workshops c.1973–c.1991*. London: The Wellcome Trust. <http://www.histmodbiomed.org/witsem/vol54.html>
- Kass, Lee B., and Christophe Bonneuil. 2004. “Mapping and Seeing: Barbara McClintock and the Linking of Genetics and Cytology in Maize Genetics, 1928–1935.” Pp. 91–118 in *Classical Genetic Research and its Legacy*:

- The Mapping Cultures of Twentieth-Century Genetics*. Edited by Jean-Paul Gaudillière and Hans-Jörg Rheinberger. London: Routledge.
- Keating, P., and A. Cambrosio. 2003. *Biomedical Platforms: Realigning the Normal and the Pathological in Late-Twentieth-Century Medicine*. Cambridge, MA: MIT Press.
- Keenan, K. 1983. "Lilian Vaughan Morgan (1870–1952): Her Life and Work." *American Zoologist* 23(4): 867–76.
- Keller, Evelyn Fox. 1984. *A Feeling for the Organism: The Life and Work of Barbara McClintock*. Macmillan.
- Keller, Evelyn Fox. 2000. *The Century of the Gene*. Cambridge, MA: Harvard University Press.
- Kevles D. J. 1985. *In the Name of Eugenics: Genetics and the Uses of Human Heredity*. Cambridge, Mass.: Harvard University Press.
- Klein, Eva, N. B. Kurnick, and G. Klein. 1950. "The Effect of Storage on the Nucleic Acid Content and Virulence of Mouse Ascites Tumor." *Experimental Cell Research* 1(1): 127–134.
- Koch, Lene. 2004. "The Meaning of Eugenics: Reflections on the Government of Genetic Knowledge in the Past and the Present." *Science in Context* 17: 315–331.
- Kohler, Robert E. 1994. *Lords of the Fly: Drosophila Genetics and the Experimental Life*. Chicago: University of Chicago Press.
- Kottler, M. J. 1974. "From 48 to 46: Cytological Technique, Preconception, and the Counting of Human Chromosomes." *Bulletin of the History of Medicine* 48(4): 465–502.
- Lee, Muriel Brunton. 2004. Interview by Peter Harper. <https://genmedhist.eshg.org/fileadmin/content/website-layout/interviewees-attachments/Lee%2C%20Muriel.pdf>
- Lejeune, J., M. Gautier, and R. Turpin. 1959a. "Etude des chromosomes somatiques de neuf enfants mongoliens." *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences (Paris)* 248: 1721–1722.
- Lejeune, J., M. Turpin, and M. Gautier. 1959b. "Le mongolisme, premier exemple d'aberration autosomique humaine." *Annales de Genétique* 1(2): 41–49. <http://publications.fondationlejeune.org/article.asp?filename=fjl046.xml>
- Levan, Albert. 1932. "Cytological Studies in Allium II: Chromosome Morphological Contributions." *Hereditas* 16: 57–95.
- Lindee, Susan M. 2005. *Moments of Truth in Genetic Medicine*. Baltimore: Johns Hopkins University Press.
- Lindsley, Dan, and E. H. Grell. 1972. *Genetic Variations of Drosophila melanogaster*. Second printing. Washington: The Carnegie Institution. http://publicationsonline.carnegiescience.edu/publications_online/genetic_variations/

- Lutz, Anne May. 1912. "Triploid Mutants of *Oenothera*." *Biologisches Centralblatt* 32(7): 385–435.
- Martin, A. 2004. "Can't Any Body Count? Counting as an Epistemic Theme in the History of Human Chromosomes." *Social Studies of Science* 34(6): 923–948.
- McClintock, Barbara. 1929. "Chromosome Morphology in *Zea mays*." *Science* 69(1798): 629.
- Miller, Fiona Alice. 2006. "'Your True and Proper Gender': The Barr Body as a Good Enough Science of Sex." *Studies in History and Philosophy of Biological and Biomedical Sciences* 37(3): 459–483.
- Mittwoch, Ursula. 1952. "The Chromosome Complement in a Mongolian Imbecile." *Annals of Eugenics* 17, Part 1: 37.
- Mittwoch, Ursula. 1995. "Living History-Biography." *American Journal of Medical Genetics* 55(1): 3–11.
- Mittwoch, Ursula. 2004. Interview by Peter Harper. <https://genmedhist.eshg.org/fileadmin/content/website-layout/interviewees-attachments/Mittwoch,%20Ursula.pdf>
- Morgan, Lilian V. 1922. Non-Criss-Cross Inheritance in *Drosophila melanogaster*. *The Biological Bulletin* 42: 267–274.
- Morgan, Thomas H., A. H. Sturtevant, H. J. Muller, and C. B. Bridges. 1915. *The Mechanism of Mendelian Inheritance*. New York: Holt.
- Müller-Wille, Staffan, and Christina Brandt, eds. 2016. *Heredity Explored: Between Public Domain and Experimental Science, 1850–1930*. Cambridge, MA: MIT Press.
- Müller-Wille, Staffan, and Hans-Jörg Rheinberger. 2012. *A Cultural History of Heredity*. Chicago: University of Chicago Press.
- Núñez, Clara Eugenia. 1992. *La fuente de la riqueza: educación y desarrollo económico en la España contemporánea*. Madrid: Alianza Editorial.
- Ogilvie, Marilyn B., and C. J. Choquette. 1981. "Nettie Maria Stevens (1861–1912): Her Life and Contributions to Cytogenetics." *Proceedings of the American Philosophical Society* 125(4): 292–311.
- Ogilvie, Marilyn B., and Joy Harvey, eds. 2000. *Biographical Dictionary of Women in Science*. 2 Vols. New York: Routledge.
- Penrose, Lionel S. 1960. "A Proposed Standard System of Nomenclature of Human Mitotic Chromosomes (Denver, Colorado). Editorial comment." *Annals of Human Genetics* 24: 319.
- Penrose, Lionel S., and Joy D. A. Delhanty. 1962. "Familial Langdon Down Anomaly with Chromosomal Fusion." *Annals of Human Genetics* 25: 243–252.
- Rader, Karen. 2004. *Making Mice: Standardizing Animals for American Biomedical Research, 1900–1955*. Princeton: Princeton University Press.
- Reardon, Jenny. 2005. *Race to the Finish: Identity and Governance in an Age of Genomics*. Princeton: Princeton University Press.

- Rheinberger, Hans-Jörg. 2010. *On Historicizing Epistemology: An Essay*. Stanford: Stanford University Press.
- Rheinberger, Hans-Jörg, and Jean-Paul Gaudillière, eds. 2004. *From Molecular Genetics to Genomics: The Mapping Cultures of Twentieth-Century Genetics*. London: Routledge.
- Rheinberger, Hans-Jörg, and Staffen Müller-Wille. 2017. *The Gene from Genetics to Postgenomics*. Chicago: The University of Chicago Press.
- Richmond, Marsha L. 1997. "'A Lab of One's Own': The Balfour Biological Laboratory for Women at Cambridge University, 1884–1914." *Isis* 88: 422–55.
- Richmond, Marsha L. 2006. "The 'Domestication' of Heredity: The Familial Organization of Geneticists at Cambridge University, 1895–1910." *Journal of the History of Biology* 39(3): 565–605.
- Richmond, Marsha L. 2007. "Opportunities for Women in Early Genetics." *Nature Reviews Genetics* 8(11): 897–902.
- Richmond, Marsha L. 2010. "Women in Mutation Studies: The Role of Gender in the Methods, Practices, and Results of Early Twentieth-Century Genetics." Pp. 11–47 in *Making Mutations: Objects, Practices, Contexts*. Edited by Luis Campos and Alexander von Schwerin. Berlin: Max-Planck Institut für Wissenschaftsgeschichte.
- Richmond, Marsha L. 2015. "Women as Mendelians and Geneticists." *Science & Education* 24(1–2): 125–150.
- Richmond, Marsha L. 2017. "Women as Public Scientists in the Atomic Age: Rachel Carson, Charlotte Auerbach, and Genetics." *Historical Studies in Natural Sciences* 47(3): 349–388.
- Rosenberg, Charles E. 2002. "The Tyranny of Diagnosis: Specific Entities and Individual Experience." *The Milbank Quarterly* 8(2): 237–260.
- Rossiter, Margaret W. 1993. "The Matthew Matilda Effect in Science." *Social Studies of Science* 23(2): 325–341.
- Rossiter, Margaret W. 1998. *Women Scientists in America: Before Affirmative Action, 1940–1972*. Baltimore: Johns Hopkins University Press.
- Rossiter, Margaret W. 2012. *Women Scientists in America: Forging a New World since 1972*. Baltimore, MD: Johns Hopkins University Press.
- Rowley, Janet D. 1973. "Letter: A New Consistent Chromosomal Abnormality in Chronic Myelogenous Leukemia Identified by Quinacrine Fluorescence and Giemsa Staining." *Nature* 243(5405): 290–293.
- Santesmases, María Jesús. 2000. *Mujeres científicas en España: profesionalización y modernización social*. Madrid: Instituto de la Mujer.
- Santesmases, María Jesús. 2014. "The Human Autonomous Karyotype and the Origins of Prenatal Testing: Children, Pregnant Women and Early Down's Syndrome Cytogenetics, Madrid 1962–1975." *Studies in History and Philosophy of Biological and Biomedical Sciences* 47: 142–153.

- Santesmases, María Jesús. 2015. "Human Chromosomes and Cancer: Tumors and the Geographies of Cytogenetic Practices, 1951–1956.." *Historical Studies in the Natural Sciences* 45(1): 85–114.
- Santesmases, María Jesús. 2016. Discriminación *in vitro*: cuerpos y cariotipos en los orígenes de la genética del síndrome de Down. Pp. 79–91 in *Justicia ¿para todos?* Edited by Catherine Heeney, Jordi Maeso y David Rodríguez-Arias. Madrid: Plaza y Valdés.
- Santesmases, María Jesús. 2017a. "Imaging the Super-Female: Women, Gender and Handbooks in the History of a Genetic Term." *Medicina nei Secoli* 29(1): 189–210.
- Santesmases, María Jesús. 2017b. "Circulating Biomedical Images: Bodies and Chromosomes in the Post-Eugenic Era." *History of Science* 55(4): 395–430.
- Santesmases, María Jesús, Montserrat Cabré, and Teresa Ortiz Gómez. 2017. "Feminismos biográficos aportaciones desde la historia de la ciencia." *Arenal* 24(2): 379–404.
- Santesmases, María Jesús, and Edna Suárez. 2015. "A Cell-Based Epistemology, Human Genetics in the Era of Biomedicine." *Historical Studies in the Natural Sciences*. Special Issue. 55(4).
- Satzinger, Helga. 2004. Women's Places in the New Laboratories of Genetic Research in the 20th Century: Gender, Work, and the Dynamics of Science. Pp. 265–94 in *Women Scholars and Institutions. Proceedings of the International Conference (Prague, 8–11 June, 2003)*. Edited by Soňa Štrbáňová and Ida H. Stamhuis. Prague: Výzkumné centrum pro dějiny vědy.
- Satzinger, Helga. 2008. "Theodor and Marcella Boveri: Chromosomes and Cytoplasm in Heredity and Development." *Nature Reviews Genetics* 9(3): 231.
- Satzinger, Helga. 2009. *Differenz und Vererbung: Geschlechterordnungen in der Genetik und Hormonforschung 1890–1950*. Köln: Böhlau Verlag.
- Satzinger, Helga. 2012. "The Politics of Gender Concepts in Genetics and Hormone Research in Germany, 1900–1940." *Gender & History* 24(3): 735–754.
- Schlegelberger, Brigitte. 2013. "In Memoriam: Prof. Dr. rer. nat. Dr. med. h.c. Lore Zech; 24.9.1923–13.3.2013. Honorary Member of the European Society of Human Genetics, Honorary Member of the German Society of Human Genetics, Doctor Laureate, the University of Kiel, Germany." *Molecular Cytogenetics* 6: 20–21.
- Stamhuis, Ida H., and Arve Monsen. 2007. "Kristine Bonnevie, Tine Tammes and Elisabeth Schiemann in Early Genetics: Emerging Chances for a University Career for Women." *Journal of the History of Biology* 40(3): 427–66.

- Star, Susan L., and Anselm Strauss. 1999. "Layers of Silence, Arenas of Voice: The Ecology Of Visible And Invisible Work.." *Computer Supported Cooperative Work (CSCW)* 8(1–2): 9–30.
- Stern, Alexandra Minna. 2012. *Telling Genes: The Story of Genetic Counseling in America*. Baltimore: Johns Hopkins University Press.
- Stevens, Nettie Maria. 1908. "A Study of the Germ Cells of Certain *Diptera*, with Reference to the Heterochromosomes and the Phenomena of Synapsis." *Journal of Experimental Zoology* 5(3): 359–74.
- Stevens, Nettie Maria. 1912. "The Chromosomes in *Drosophila ampelophila*." Pp. 380–381 in *Proceedings of the 7th International Zoological Congress, Boston, 19–24 August, 1907*. Cambridge: Cambridge University Press.
- Tjio, Joe Hin, and Albert Levan. 1956. "The Chromosome Number of Man." *Hereditas* 42: 1–6.
- Toolan, Helene Wallace. 1953. "Growth of Human Tumors in Cortisone-treated Laboratory Animals: The Possibility of Obtaining Permanently Transplantable Human Tumors." *Cancer Research* 13: 389–394.
- Tunnlid, Anna. 2018. "Eva Hansen-Melander and the Circulation of Knowledge within the Cancer Chromosome Network." Paper presented at the *ESHS Conference*, London, 14–17 September 2018.
- Velasco-Martín, Marta. 2020. "Women and Partnership Genealogies in *Drosophila* Population Genetics.." *Perspectives on Science*, this issue.
- von Oertzen, Christine. 2012. *Science, Gender, and Internationalism: Women's Academic Networks, 1917–1955*. New York: Palgrave.
- Zech, Lore. 2013. Interview with Peter Harper. <https://genmedhist.eshg.org/fileadmin/content/website-layout/interviewees-attachments/zech-interview.pdf>