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From Heredity to Genetics: Political, Medical, and Agro-Industrial Contexts

Staffan Müller-Wille and Christina Brandt

The essays collected in this volume follow up on an earlier volume, *Heredity Produced: At the Crossroads of Biology, Politics, and Culture, 1500–1870*, that dealt with the cultural history of heredity from the early modern period to the middle of the nineteenth century.[1] They provide a fresh approach to the history of the life sciences from the late nineteenth century to the first decades of the twentieth century—a period which has sometimes been characterized as a period of thorough transformation in the life sciences more generally.[2] This present volume, *Heredity Explored: Between Public Domain and Experimental Science, 1850–1930*, is devoted to the historical analysis of a broad variety of scientific and social arenas in which the phenomena of inheritance acquired far-reaching economic, cultural, and political relevance and was investigated both experimentally and theoretically. While the authors of this volume therefore present some very different perspectives, their studies have one thing in common: they show that a history of heredity includes much more than the history of genetics, and that knowledge of heredity was always more than the knowledge formulated as Mendelism.

The first volume, *Heredity Produced*, foregrounded the formation of what the two editors in their introduction described as an "epistemic space" of heredity in the late eighteenth and early nineteenth century. The origin of a general biological concept of heredity was a relatively late historical phenomenon, culminating in Francis Galton's and Charles Darwin's theories of heredity in the 1860s and 1870s. Previously, hereditary transmission had not usually been treated as a phenomenon that could be separated from the contingencies of conception, pregnancy, or embryonic development, or more generally, from generation and development.[3] If heredity was studied as a sui generis phenomenon, this typically happened in disciplines that addressed not the normal or the natural but the pathological and the artificial. It was physicians and breeders—with their interest in how a disease could become permanent, or a novel trait "fixed"—who were the first to describe the transmission of traits using legal metaphors of inheritance.[4]

At one and the same time, almost in the manner of an oxymoron, the concept of heredity thus drew attention to phenomena involving variation *and* constancy, deviance *and* permanence, divergence *and* common origin—hence the increasing political significance of the concept in the context of emerging European nation states and their imperial ambitions; heredity was (and continues to be) a concept that could be mobilized for a whole range of ideological purposes: to celebrate progress, reinforce identity, or denounce deviance.[5] The authors of *Heredity Produced* analyzed how the "epistemic space" of heredity was articulated by a step-by-step aggregation and integration of conceptual, representational, and practical tools that circulated within, and among, several domains. The works produced within these domains—asylum records and breeders' registers, species catalogs and racial classifications, pedigrees and analyses of trait distributions across populations and generations—all established heredity as a distributed phenomenon that was adequately addressed by classification, statistical analysis, and morphological reasoning.[6]

As with the first volume, this one also focuses on a period that can be considered a threshold in the history of heredity. The first volume was concerned with the historical dynamics that produced the diverse array of phenomena that "heredity," as a general biological concept, came to address in the second half of the nineteenth century. In *Heredity Explored*, we focus on the subsequent period in which the epistemic space of heredity was increasingly consolidated to eventually form the "epistemic object" of a dedicated discipline, genetics. In the course of this development, heredity changed from an object that was distributed in time and space to a more or less tangible entity that could be produced and directly assessed within the confines of specialized spaces, such as laboratories, experimental stations, and data collections. The advent of genetics at that time, seen from a *longue durée* perspective, thus confronts us with a fundamental inversion, one that could be represented visually as an hourglass figure.[7] In the second half of the nineteenth century a variety of discourses flourished in which different concepts of heredity took shape. From 1900 onward, knowledge of heredity, in all its diverse aspects, appears to have been shaped by a highly specialized discourse: the new discourse of genetics, which soon began to colonize a variety of scientific and cultural domains with its concepts, standards, and technologies.

Historians of biology, especially those with a professional background in biology, have therefore long been fascinated with the history of genetics. Quite naturally, this historical focus often led to a preoccupation with the "milestones" in the development of the discipline, such as Mendel's experiments in the early 1860s, the "rediscovery" of his laws in 1900, the debates between biometricians and Mendelians, or the origins and achievements of the Morgan school of *Drosophila* genetics.[8] The gene has appeared as the very manifestation of the concept of heredity ever since. In hindsight, the gene therefore seems like an inevitable outcome of the protracted attempts of late-nineteenth-century biologists to identify the agents of heredity and to discern the laws they obeyed. And so too does the gene appear as the foundation stone on which the thoroughly molecularized biology of today has been built.[9]

This collection of essays is also concerned with the period around 1900 as an important turning point, but in contrast to previous scholarship we intend to go beyond the focus on Mendel's rediscovery. Our authors describe a complex period in the history of European countries and their "offshoots" in the New World, a period which witnessed the second industrial revolution, the demographic transition, and the so-called "laboratory revolution" in medicine. Their contributions demonstrate that a focus on the discipline of genetics, or even a history of heredity that takes the advent of genetics as its end point or starting point, is much too narrow to get an appropriate historical understanding of developments in the life sciences at that time. This does not mean that we intend to play down the significance of genetics (nor the significance of an earlier generation of historians). But the centrality of the gene for twentieth-century life sciences or, even more specifically, for the continuing history of heredity, is far from self-evident and needs to be accounted for by a different set of factors than the mere dynamics of scientific inquiry.[10]

We have therefore arranged the chapters of this volume in five sections that start with the broader cultural and political contexts that shaped knowledge of heredity and then gradually "zoom in" on increasingly specialized fields of inquiry, ending with a section that readdresses the origins of genetics from what we hope is a newly gained vantage point. The first section deals with heredity as an ever-present theme in the debates about identity, kinship, and reproduction that accompanied the formation of modern nation states. The second section looks at biology in general as a source of new biopolitical conceptions of heredity, degeneration, and gender. The third section turns to detailed analyses of the agro-industrial contexts of the newly emerging genetic rationality around 1900. In the fourth section, the authors explore different approaches to heredity in a variety of medical research fields from the late nineteenth to the mid-twentieth century. And finally, the last section deals with the genealogical constructs and experimental systems of genetics that turned heredity into a representable and manipulable object. Before we turn to the question of what this strategy of "zooming in" reveals about genetics and its lasting legacy, we would like to take the reader on a tour through the various contributions to this volume.

1.1 Heredity between the Sciences and the Public Sphere

The peculiar role of thinking in terms of heredity, in political and cultural discourses around 1900, was, as mentioned above, grounded in the historical developments of a period that saw a massive wave of industrialization and associated demographic changes. As a consequence, liberal values of a rising middle class began to clash with political and social movements centered on ideas of shaping populations and engineering social life, reinforcing developments that had been going on since the 1860s when evolutionary theories began to nourish ideas of social and cultural progress in general, and eugenic hopes for "improvement," and corresponding fears of "degeneration," in particular. Heredity provided a very convenient tool for the proponents of such visions since it foregrounded the formation of identity and difference on a whole range of levels, beginning with the bourgeois family and ranging from ethnic or racial minorities to entire classes and nations. The transfer of meanings that the concept of heredity brought about went in both directions: heredity served as a frame for the technological and cultural appropriation of nature, just as much as it was used to interpret the political and cultural manifestations of human history and diversity.[11] The notion of "biohistorical narratives" that Veronika Lipphardt develops in her chapter captures this Janus-faced character of heredity very well and highlights that "heredity" around 1900 was inseparably both an object of the natural sciences and their applications in agriculture, industry, and medicine, as well as a powerful metaphor deployed in the service of identity formation and political struggle. Societies came to be seen as "transmission machineries"—as Ulrike Vedder puts it in her contribution—from which nobody was able to escape.

Vedder provides a fresh perspective on the history of heredity by tracing the literary figure of the "bachelor." At first glance an unlikely figure to enter the scene of our inquiry, the bachelor nevertheless has a lot to reveal about family, property transmission, genealogy, and heredity in the nineteenth and early twentieth centuries. The bachelor was (and remains) a controversial figure, being both a product of the emerging bourgeois society, as well as a challenge to it. The nineteenth-century tendency to naturalize the family, and the emerging discourse on degeneration, became crystallized in the figure of the bachelor, a paradox personified, being both sterile and productive at the same time. In the mid-nineteenth century, the bachelor was still depicted as an integral part of family networks. However, toward the end of the century, he became more and more viewed as a "natural failure" that terminated genealogies. At the same time, the bachelor was increasingly regarded as a paragon of cultural productivity, free from the constraints of tradition.[12]

By comparing public and legal debates about marriage between cousins from the 1830s until the early twentieth century, Diane B. Paul and Hamish G. Spencer throw light on interesting—and also unexpected—aspects of the links between popular beliefs, state regulation, and scientific research. The question of whether or not marriage between cousins was a harmful cultural practice was highly controversial in both the United States and Great Britain, and some U.S. states legislated against it. Eugenicists were often approached to provide expertise about the benefits and risks of cousin marriage, among them George Darwin, whose own family background was perceived by many as problematic (the Darwin and Wedgwood clans cultivated cousin marriage to such a degree that historian Jim Moore has referred to them as the “Darwoods”). Whereas eugenicists often came to no clear statement in favor of, or against, cousin marriage, folk beliefs at the time increasingly associated the practice with increased risks of degeneration. Paul and Spencer conclude that the enactment of state laws against marriage between cousins in the United States, but not in Europe, is principally explained by the fact that in the former the practice was associated with rural-dwelling, poverty-stricken lower classes and in the latter with elites, and by the porous and decentralized character of the American political system. The debate about cousin marriage thus provides a historical case, showing that eugenics experts had a very limited influence on state policies, and that the eugenics movement was driven “from behind” by strong sociocultural undercurrents.[13]

Theodore M. Porter presents us with a glimpse into the world of late-nineteenth- and early-twentieth-century institutions for the mentally ill, which, alongside prisons, military conscription, compulsory schooling, and census taking, provided the institutional frameworks that channeled the sociocultural undercurrents just mentioned. From his analysis it becomes clear that statistical approaches to human heredity predated and encompassed human genetics. These approaches were closely associated with modern notions of the state—in particular, the notion of its “population” which became as important as the territory it encompassed for definitions of the nation state. Starting with German asylum policies in the late nineteenth century, Porter goes on to analyze the practices of the Eugenics Record Office in Cold Spring Harbor, New York, which was initiated by Charles Davenport in 1911 in order to create a comprehensive database on human genetics. Statistics, and in particular new methods of gathering and managing huge amounts of data, such as filing systems, played a fundamental role in the formation of the new science of human genetics. As a science, human genetics has from its inception been closely entangled with the bureaucratic control and management of institutionalized populations, and this, in turn, shaped popular understandings of human heredity around 1900.[14]

With the concept of “biohistorical narratives,” Veronika Lipphardt adds another dimension to the exchanges between public and expert discourse by pointing to narrative modes of identity construction in nation building and the consolidation of ethnic minorities. According to her account, biohistorical narratives emerge when historical processes and events are interpreted in biological terms. Endogamic practices of Jewish populations in Europe, for example, were frequently read as genetic isolationism. Lipphardt analyzes the genetic research of the German–Jewish anthropologist Wilhelm Nussbaum along these lines. Nussbaum was a student of the eugenicist Eugen Fischer and worked with Franz Boas in the United States after his forced emigration from Germany. Lipphardt’s chapter throws new light on well-known controversies between so-called neo-Darwinism and neo-Lamarckism around 1900. Not only were the deterministic views of heredity that underpinned Mendelism and neo-Darwinism used in eugenics and German “race hygiene” to support growing anti-Semitic views of the “inalterability of Jews,” but neo-Darwinian standpoints, as well as racial biology, were also used by some Jewish scientists as a means to defend their emancipation. The sad and tragic story of Nussbaum’s research serves as a strong reminder that there is no straightforward correlation between concepts of heredity and political convictions.[15]

Most studies that attend to the contexts of, for example, racial anthropology or eugenics in the nineteenth century take inheritance as a necessary component of nineteenth-century biologistic ideologies but do not further question that component themselves. With the great variety of hereditary theories we encounter in the late nineteenth century it seems, however, that the very notion of inheritance was not a stable one but deeply troubled in ways that are only inadequately understood by the standard oppositions of “soft” and “hard,” “blending” and “nonblending” inheritance. Questions of “heredity” touched long-standing problems in the life sciences such as the relationship between parts and wholes, between internal and external conditions, or between the origin and preservation of variation in evolution. Moreover, because heredity has become a central research problem in different fields such as psychiatry, medicine, breeding research, cell biology, and evolutionary theory since the mid-nineteenth century, the term “heredity” itself has been used with a multitude of slightly different meanings. Many, for example, reserved it for the transmission of species-specific characteristics, relying on other designations for the transmission of variable traits. Most importantly, however, a variety of hypothetical–speculative theories of heredity emerged toward the end of the nineteenth century that by no means gave a homogenous picture on a conceptual level, let alone generally accepted answers of how to understand heredity.

In his classic article “From Heredity Theory to *Vererbung*,” Fredrick Churchill has shown how *Vererbung* (the German term for “heredity”) had become a widespread theoretical problem in the 1880s, being part of a watershed in biology that was created with the rise of cytology. During this period, biologists raised the problem of heredity as a question that was separate from, and followed a different logic than, cell differentiation during ontogeny. New ideas of a “continuity that preserved the organized material of transmission” laid the basis for a “modern” conception of heredity, turning away from older assumptions in which reproduction, growth, and heredity were explained by the same principles.[16] However, if heredity could not yet be taken as a given by nineteenth-century biologists, the question remains why biologists were so deeply concerned about it? As is made clear in the chapters by Jean Gayon, Hans-Jörg Rheinberger and Staffan Müller-Wille, and Helga Satzinger in the second section of this book, the answer to this question, apart from cytological advances, is also to be sought out at the level of ideology. In his philosophical analysis of Darwinism, Jean Gayon has argued that evolution and heredity were two faces of the same coin.[17] With

Darwin's theory, however, the world was seen not only as full of evolutionary variation, but also as a world in which continuity and stability were not guaranteed and needed to be safeguarded against the endless vicissitudes of life, to paraphrase Charles Lyell.[18] It is therefore not surprising to find that heredity theories resonated strongly with contemporary debates about the relationship between citizen and state, between progress, decline, and tradition, as well as the contributions of the two sexes to social (re-)production.

In their discussion of "Heredity before Genetics" in this volume, Rheinberger and Müller-Wille provide an overview and comparison of the highly hypothetical theories of heredity that were proposed by Charles Darwin, Francis Galton, Rudolf Virchow, Carl Nägeli, Claude Bernard, Ernst Haeckel, August Weismann, Hugo de Vries, and Edmund Beecher Wilson. For some of them, heredity was still a kind of "force" (as for Haeckel, e.g.), but toward the end of the century, more and more approaches discussed the problem of heredity as a "morphological" question about the structure of the hereditary material, how it originated in the course of phylogeny, and how it related to the structure of the fully developed organism. Surprisingly, dichotomies between "soft" or "hard" inheritance did not, as Rheinberger and Müller-Wille argue, play any important role, not even after Weismann's theory of germ plasm. Instead, reasoning about heredity touched on organic relationships that were expressed in a great variety of metaphors, ranging from pianos to parliaments. In this respect, one can observe major shifts toward the end of the century: heredity as a direct relationship between ancestor and progeny became less and less important while the "horizontal" relationship of individuals to a shared hereditary substrate gained in prominence. In addition, another relational aspect was at the center of the discussion—in particular, once a clearer picture of the main mechanisms of cell division had emerged—namely, the relationship between the parts and the whole. Was the structure of the fully developed organism somehow prefigured in the overall architecture of the germ plasm or nucleus, as

Weismann believed, or were hereditary determinants relatively independent units, free to reappear and recombine under given circumstances, as Darwin and de Vries claimed in their theories of pangenesis? Frequent comparisons with the relationships among citizens, and the relationship between the citizen and the state, brought to the fore the concrete political issues with which these seemingly abstract debates resonated.

Jean Gayon's contribution picks up on an aspect of late-nineteenth-century speculations about heredity and evolution that has largely been neglected by historians, namely, their entanglement with different concepts of "regression." Regression, or reversion to a presumed original "type," had long been an important topic of discussion among breeders since it constituted a constant threat to their efforts to "improve" their breeds. In the light of evolutionary thinking, this turned into a problem of more general scope because regression seemed to suggest a kind of reversibility of modifications of species. Alfred Russel Wallace, for example, firmly believed that regression was nature's response to the degenerative effects of domestication, whereas for Darwin, who accepted domestication as a model for natural selection, all variations, including apparently regressive ones, had to be understood as a consequence of adaptive processes. Such debates about regressive evolution, as Gayon suggests, have to be understood in the broader cultural context of "a period in which, in almost all areas of culture, progressivist thinking was harshly criticized and challenged by declinist thinking." Moreover, this background explains the very different role that concepts of heredity came to play in different evolutionary theories. Galton endorsed a typological perspective, where heredity in effect limited the power of natural selection. Weismann, on the other hand, turned heredity into a subordinate principle of evolution since natural selection was for him the sole and primary force responsible for both transformation and conservation of species.

In order to understand the peculiar role that concepts of heredity have come to play since the second half of the nineteenth century, we have to consider not only evolutionary contexts but also wider shifts in theories of biological reproduction. Helga Satzinger throws light on the gender categories that unavoidably enter these theories. Her analysis of the emergence of chromosomal theories of inheritance reveals a surprising ambivalence in the understanding of male and female contributions to reproduction. On the one hand, the focus on chromosomes as the main material locus of heredity not only suggested an equal male and female contribution to the processes of procreation, but also supported ideas of gender equality in political debates. On the other hand, the chromosome theory of heredity reinstated a higher-level gendered dichotomy, ascribing a superior, "male" role to the chromosomes as compared to the auxiliary role of other cellular components, especially the cytoplasm, which often carried female connotations. Interpreted as a reaction against an impending "miniaturization" of the paternal contribution to procreation, this attributed cellular asymmetry created "a blind spot […] in the conceptualisation of genetics" that had lasting consequences for twentieth-century developments in biology. However, as Satzinger's analysis of the work of Richard Goldschmidt from the 1920s demonstrates, there were also alternative approaches that suggested more flexible concepts of sex difference.

1.2 Heredity in Applied Contexts

The weight of ideology with which theories of reproduction and inheritance became charged around 1900 was no doubt fueled by the rapid social and demographic changes that went hand in hand with the second industrial revolution. For the special case of early Mendelian genetics, the agro-industrial contexts of scientific change have long since caught the attention of historians of biology. The conceptual and institutional consolidation of this discipline was broadly promoted by a new class of scientifically educated experts, agricultural engineers, who engaged in new forms of applied research. Their work received substantial support from state bureaucracies and large philanthropic organizations like the Carnegie Institution and the Rockefeller Foundation.[19] The contributing authors to the third section of this volume cast their net wider by analyzing how elements of the new genetic rationale were shaped by the biotechnologies of the second industrial revolution. A first wave of massive commercialization of nature's products challenged definitions of creatorship and invention, and through an industrialization of such fields as breeding and microbiological applications, serial mass production of standardized organisms became a valuable economic factor.[20]

Christophe Bonneuil provides an analysis of the rationalization of life around 1900 that casts a new light on the familiar struggle between Darwinism and the new genetics. Whereas the dominant Darwinian views of the late nineteenth century emphasized fluidity, continuity, and individuality in the living world, the new genetics brought out opposite concepts: new ideas of immutable types that could be recombined, as well as notions of sudden ruptures or mutations. What Bonneuil calls the "pure-line paradigm" was the product of a new epistemic space of acceleration and the economic values of efficiency, reliability, and fairness. Evolutionary approaches, with their strong emphasis on slow processes and individuality, were regarded as insufficient to fulfill the economic needs of breeding research and were replaced by ideas of reliable mass reproduction, by a logic of seriality, and views that focused on the "horizontal," instead of "historical," relationships between living individuals. Bonneuil traces the manifestation of this new epistemic and economic space in programmatic statements of leading geneticists at the time, as well as in the ways in which research and administrative practices were organized in influential sites of industrial research, such as the French seed company Vilmorin or the Carlsberg Laboratory in Copenhagen.

J. Andrew Mendelsohn explores the impact that late-nineteenth-century bacteriological practices had on notions of hereditary stability. He presents us with an unexpected, but nevertheless convincing, comparison in order to understand the impact that the young field of bacteriology had on industrialization. Comparable to the “early physical standards laboratories of the same period,” Mendelsohn argues that “vaccine laboratories helped make a world in which local science could become global.” By focusing on Pasteur’s laboratory and his commercial agents, Mendelsohn shows how the mass production and worldwide distribution of vaccines supported global processes of standardization. Independent of, and at the same time supportive of, other approaches to inheritance like the search for underlying cytological mechanisms or Mendelism, bacteriological theorizing on hereditary variation within species considerably contributed to a shift from heredity as a gradual force toward a combinatorial understanding of the absence and presence of distinct and stable hereditary factors. The point here is that the fixity of virulent and nonvirulent bacterial strains was not just a matter of ontological presuppositions but imposed itself onto the industry in the form of a practical demand that had to be fulfilled if the safety of vaccines was to be warranted. Produced with immense care and effort, the attenuated strains of bacteria that made up vaccines thus literally came to embody heredity as fixity, that is, the ability to retain an unchanged character despite contextual changes.

A key element of genetic rationality, which Bonneuil interprets with the help of Jean Baudrillard’s notion of “industrial simulacra,” is addressed in more detail in the chapter by Alain Pottage—namely, the view that manufactured organisms can be replicated reliably. Pottage chooses the U.S. Plant Patent Act of 1930, the first statute that treated organisms as inventions, for his starting point. Framing his analysis within a brief history of the parallel conceptual developments of ideas of “invention” and notions of inheritance since the early modern period, Pottage points out major shifts in how patents were legitimized when the logic of patenting law became relevant in plant breeding. At the center of these debates was the concept of “clonal plants” that fundamentally challenged the logic of novelty and the view of the creative act that makes something patentable. Pottage argues that the first U.S. Plant Patent Act was a consequential historical moment since it turned the idea of invention "from a discursive to a biological medium"—whereas in chemistry, for example, the act of innovation that legitimized a patent was seen in the creation of a novel chemical "recipe," but not in its materialization, in plant patents it was the material thing itself, the "clone," that became patented. Debates about plant patents were hence shaped by ambiguities of the clone concept itself and the impossibility of ensuring whether or not a plant was indeed of clonal descent.

The developments in the broad field of medical and physiological research around 1900 provide another important field of concepts and practices which shaped hereditarian thinking. The chapters in this section show that the historical relationship between medicine and human heredity is far less straightforward than one would suspect on the basis of what we know about eugenics and its historical impact alone. However, with a little reflection, it becomes clear that medicine and Mendelian ideas of heredity are not readily compatible. Furthermore, it is not clear how statistical knowledge of hereditary "tendencies" applies to clinical contexts where individual patients are the target of diagnosis and treatment, nor can human populations simply be broken down into genealogical constructs like "pure lines"—an important precondition for any Mendelian experiment. While heredity may be abstracted from development for the purposes of biological inquiry, the same abstraction is highly problematic in medical contexts. As Ilana Löwy and Jean-Paul Gaudillière have remarked in their introduction to the influential volume *Heredity and Infection: The History of Disease Transmission*, as far as the epidemiology of disease is concerned, questions of infection, immunization, and heredity remained confounded in such a way that the vertical and the horizontal dimensions of the transmission of diseases could not be disentangled.[21]

The complex and multilayered relationship between medical and hereditarian thinking has thus far not gained much attention from historians of science and medicine, apart from the very special case of eugenics.[22] Medical contexts such as psychiatry had developed specific theories of heritable diseases—with the notion of “hereditary constitution” or “diathesis” at the center—long before biologists, and more specifically, geneticists started to redefine ideas of inheritance as the presence or absence of traits. Furthermore, since the medical perspective in everyday practice is primarily directed toward the individual body, medical thinking about inheritance developed in quite different directions than in agro-industrial contexts where tools were developed that aimed at standardization and mass reproduction. The “narrowing down” of heredity to transmission and genotypic stability, as it occurred in plant breeding and microbiology, played almost no role in dealing with human pathologies. Physicians, when thinking along the lines of “hereditary dispositions,” usually had in mind something much more fluid and variable that was readily influenced by a wide range of cultural and natural preconditions. The Lamarckian idea of an inheritance of acquired characteristics was hence quite widespread among eugenicists, especially in socialist and Catholic contexts.[23] Conversely, early geneticists like William Bateson, Thomas Hunt Morgan, and Wilhelm Johannsen invested quite some energy in the refutation of what they thought was a widespread misconception of heredity as a transmission of parental traits, the roots of which could be traced to eugenic thinking.[24]

Caroline Arni takes us into the field of gynecological and physiological–embryological knowledge of procreation and generation in the late nineteenth century where protogenetic ideas of heredity were alive and well around 1900. In her chapter, she focuses on the idea of a psychic influence that the mother (and, in turn, the environment to which she was exposed) exerts on her unborn child. As Arni shows, the assumption that “a mother’s present becomes her child’s future” was still prevalent in the 1880s, continuing the ancient idea of the power of “maternal imagination,” an idea currently experiencing a renaissance in epigenetic understandings of inheritance.[25] In her contribution, which presents a chapter from the history of artificial insemination in the late nineteenth century, Arni explores the origins of what later would become labeled as "prenatal psychology." She sheds light on the ways in which concepts of cultural inheritance, parental transmission, "generation," and "procreation" were still deeply intermingled in physiological and embryological research fields that were concerned with the "coming into being of new human beings." Even if the act of procreation was widely understood as a material process involving the union of two cells—a historical precondition in order to advance medical practices of artificial insemination—the separation of hereditary transmission from the act of procreation and its contingencies never quite happened in gynecology and embryology.

Jean-Paul Gaudillière and Ilana Löwy identify, in the first decade of the twentieth century, a similar mismatch between new genetic research and the persistence in practice of older ideas. Although, as they emphasize, "during the first half of the twentieth century, 'heredity' was omnipresent in medicine, […] invariant 'factors' transmitted according to Mendelian rules were very rare." From their detailed analysis of clinical research on diseases such as anaphylaxis, cancer, or "mongolism" in France, Great Britain, and the United States between 1900 and 1940, they draw the conclusion that most physicians were well aware of what was going on in experimental research in genetics but most of them found these investigations irrelevant to the medical understanding of diseases with a hereditary component. Besides the usual incommensurability of experimental and clinical practice, Gaudillière and Löwy refer to a further reason why Mendelism was widely received as a new order of knowledge but had almost no practical effects on medicine, a historical situation they describe as "Mendelism without Mendel's laws." For professional reasons, medical researchers were interested in hereditary diseases, where the disease itself had priority over its mode of transmission and left little room for the geneticist's freedom to focus on traits that reveal clear-cut Mendelian transmission patterns.[26] Particularly in France, genetic thinking was thus regularly accompanied by physiological approaches until World War II. As the case of the physiologist and Nobel Prize winner Charles Richet shows, the belief in the existence of constant hereditary traits did not preclude the promotion of a new version of humoral theories in which "acquired traits" became chemically inscribed in the body.

This does not mean that Mendelism had no impact in medicine. However, as Bernd Gausemeier's chapter on developments within German psychiatry demonstrates, the very subject of human heredity had to be shaped in specific ways before it could become amenable to Mendelian analysis. Gausemeier distinguishes three major, successive forms in which human heredity presented itself to psychiatrists—asylum statistics, family pedigrees, and statistical cohorts expressly constructed for the purpose of Mendelian analysis. Since the establishment of psychiatric clinics in the early nineteenth century, psychiatrists regularly recorded and analyzed data on their patients in order to assess the relative importance of "hereditary dispositions" for different forms of mental diseases. Transmission, as Gausemeier argues, was not yet the main focus in the study of degenerative diseases while psychiatrists were still occupied with definitions for these diseases. This changed in the years around 1900 when pedigrees moved center stage in psychiatric discussions. However, despite the fact that pedigrees were often used to demonstrate the Mendelian transmission of mental diseases—the most notorious example being provided by Charles Davenport and his Eugenics Record Office at Cold Spring Harbor[27]—they ultimately turned out not to provide adequate proof of Mendelian ratios. The incompatibility of genealogy and Mendelian genetics was first fully realized by medical statistician Wilhelm Weinberg and the psychiatrist Ernst Rüdin. Their "sibling method" aimed at an exact calculation of the occurrence of a well-defined pathological trait in two successive, coherent generations of a large number of families. Weinberg and Rüdin treated their populations as if they had been the product of a large number of independently executed Mendelian breeding experiments.

1.3 Origins of Mendelism

The last set of chapters in this volume revisits the origin of Mendelian genetics. The "delayed" reception of Mendel's work has been a topic that has intrigued many in the history of the life sciences.[28] Equally impressive is the speed with which Mendel's rediscovery led to the consolidation of a new discipline within the life sciences that was often hailed as revolutionary. However, if we give due consideration to the results of the previous sections in this collection, it becomes clear that in fact Mendelism entailed conditions and drawbacks that precluded many practitioners from readily adopting it. In order to carry out Mendelian experiments and ascertain Mendelian ratios, organisms had to be first inbred, then crossbred, and finally raised in large numbers. Humans, but also many agriculturally significant organisms, could not easily be subjected to such practices. This is one of the main reasons why animal breeding and clinical medicine became thoroughly "geneticized" only well after World War II, and why statistical approaches, developed by the so-called biometrical school long before the advent of Mendelism, persisted in these areas to finally merge with population and quantitative genetics in the mid-twentieth century.[29]

One explanation for the success of Mendelism, proposed long ago by Garland E. Allen, relies on its appeal to biologists trained in the experimentalist traditions of nineteenth-century biology.[30] Several features of the rhetoric in which early Mendelians engaged to bolster the credentials of their new science indeed resonate with an experimental style of reasoning. First of all, there was the rejection of historical understandings of heredity. Physiological concepts of hereditary particles as "living units" that reproduced and evolved were replaced by genetic concepts of discrete factors that could be recombined but in essence remained unaffected by the combinations they entered. The new geneticists thus expelled life from hereditary units, a stance that also came to the fore in frequent references to the thriving field of synthetic chemistry. Analogies between heredity and chemistry, between reproduction and recombination, became widespread on both sides of the Atlantic and across zoological and botanical disciplines.[31] Mendelism was thus defined by a new set of experimental tools and research objects, a new style of how to do experiments, how to collect data, and how to apply statistical analyses. One of the three "rediscoverers" of Mendel, the botanist Carl Correns, expressed the peculiar epistemic status of what misleadingly became known as Mendel's "laws" when he—even years after Mendel's rediscovery—stated that Mendelism "despite its name is not a theory at all but a group of facts [*Tatsachen*] that comes before any interpretation."[32]

Staffan Müller-Wille and Marsha L. Richmond make a similar point by following the research trajectories of William Bateson and Wilhelm Johannsen, two figures that played crucial roles in the consolidation of genetics as a discipline, across the annus mirabilis of 1900. Bateson and Johannsen converged on Mendelism from extremely different starting points, both institutionally and theoretically, and they both stuck to their original research agendas with a certain tenacity, even after accepting the basic tenets of Mendelism. Comparing their careers before and after 1900 reveals, however, that Mendelian experiments, first and foremost, offered a wealth of opportunities to cross the boundaries between general biology and its application to problems of industry and agriculture. "What Mendel's paper paradigmatically incorporated," the authors argue, "was thus less a certain, dogmatic view of living nature, but a certain way of doing science and making one's reputation." The most striking element of this new way of doing biology was its constructivism, its reliance on a heterogeneous set of tools and methods—most importantly among them, the use of "pure lines" of organisms for the construction of populations—that formed an experimental system of great versatility. While Mendelism thus clearly shared a lot with the way in which the exact sciences approach nature through instruments and apparatuses that create phenomena of interest, it was not being reductionist in the usual sense of reducing biological phenomena to physicochemical processes—fertilization, after all, remained an irreducible element of Mendelian experiments.

The complex research dynamics that Mendelian genetics, even in its early years, was thus able to generate is explored in the chapter by Luis Campos and Alexander von Schwerin on the botanist Albert Francis Blakeslee, second director of the Cold Spring Harbor Laboratory and the German plant geneticist Erwin Baur. Campos and Schwerin stress a historical point that can hardly be overstated, namely, that classical genetics cannot be equated with the "gene-centrism" that the historiography has suggested for Thomas Hunt Morgan's *Drosophila* school. With an eye on the possibilities of "genetic engineering," Blakeslee was interested in exploring how new variations and new species occur in evolution, which led him to artificially induce (with the help of Radium) and investigate chromosomal mutations in *Datura* (jimsonweed). Baur, on the other hand, had started to work with *Antirrhinum majus* (the snapdragon) in the context of an integrative view of how heredity and environment act together in producing minute variations. His main idea was that not only were the main traits in plants Mendelian units, but even the smallest variations corresponded to Mendelian rules. Both scientists developed dynamic experimental systems that turned, in the course of two decades, into a techno-epistemological realm of what the authors call an "industry of mutations." Moreover, their conceptual work shows that within Mendelian approaches, the focus on the level of the gene was not at all the only option nor even the dominant one. Since Blakeslee was concerned with variations on the level of chromosomes, and Baur was searching for so-called *Kleinmutationen* (minute mutations), their experiments focused on scales above and below that of the classical gene.

Christina Brandt and Judy Johns Schloegel's chapter about *Paramecium* research in early genetics resumes the well-known studies by Jan Sapp and Jonathan Harwood, which pointed to differing styles of genetic thought.[33] Considering the different scientific research contexts in the United States and in Germany, and again comparing the work of two scientists—Herbert Spencer Jennings and Victor Jollos—the authors argue that *Paramecium* became an early model system in genetics that was treated as a material representation of the unknown entity of the genotype. The authors thus call into question another widely held view about classical genetics, namely, that it was based on a clear-cut separation of a stable genotype and the phenotype as the product of fluctuating environmental conditions. The first two decades of the twentieth century saw a surge of newly coined terms and concepts, entailing much more than a mere distinction of genotype and phenotype. Among these new concepts were not only "mutation," and "clone"—terms that are still central concepts in today's life science—but also a variety of concepts and theories that are forgotten today. The origin of such different concepts as "norm of reaction" (Richard Woltereck), "biotype" (Jennings), or "plasmotype" (Jollos) illustrates that for many scientists the relationship between the organism and the environment was still the main focus, and that a lot of scientists believed that a conceptual genotype–phenotype distinction alone was not sufficient to fully understand heredity and development. As Brandt and Schloegel demonstrate, this was not least due to the fact that the genealogical constructs with which these geneticists worked often came to represent for them material instantiations of inheritance. "Clones" and "pure lines," especially in the case of unicellular organisms, embodied processes of inheritance to such a degree that the analytic distinctions between genotype and phenotype often collapsed.

1.4 Genetics and Heredity

In hindsight, it is certainly no overstatement to claim that the gene became the "central organizing theme of twentieth-century biology."[34] The ground was certainly well prepared for its reception, as many contributions to this volume show, by the centrality afforded, in the wake of the theory of evolution, to the question of the laws governing variation and inheritance in populations, and the wider ramifications such laws held for understandings of societal progress. Although undoubtedly speculative, nineteenth-century theories of heredity bestowed onto twentieth-century genetics a spectrum of ideas about the constitution of the peculiar space in which germs and hereditary dispositions circulated. Above all, they showed that this space could not be reduced to the individual relationships between ancestral progenitors and their descendants. Instead, questions focused on the relationship between populations and a common hereditary substrate. The reason for this "devaluation of ancestry" in favor of a view that sees (cultural as well as biological) inheritance as a common stock of dispositions seems to lie in the association of heredity with the future rather than the past, with projection rather than with legitimization, associations that occurred in the context of the all-pervading late-nineteenth-century theme of progress. Prominent geneticists like Wilhelm Johannsen saw Mendelism as a way to free technology and society from the weight of tradition. Mendelism's reductionist view of the organism as composed of modular and largely independent, to some degree even autonomous, entities was prefigured by the debates about cell theory in the nineteenth century and resonated with an industrial culture that placed value on the specificity and reproducibility of innovations. If one were able to atomize life to the degree that its elements would not be affected substantially by the combinations they entered in the course of history, then there would be virtually no limit to the future production of innovations through combination. The future—and this, notably, included the future shape of humans—could be made, or constructed, thereby overcoming the power that history and tradition used to have over life.

And yet, the origin of genetics remains underdetermined by its nineteenth-century forebears, as evinced by the fact that a variety of non- or pregenetic conceptions of heredity persisted far beyond 1900. This is true even in practical research fields like breeding, eugenic counseling, and medical therapy. It should not be forgotten that the gene was initially a rather narrowly defined conceptual tool that served to investigate patterns of trait transmission. Only eventually did it come to be deployed successfully for the investigation of other phenomena as well, ranging from problems of plant pathology to the theory of natural selection.[35] To understand this process, another set of factors has to be taken into consideration, one that points to a transformation of the life sciences on the same scale as the much better understood "laboratory revolution" in medicine.[36] Whereas biology had established itself around 1800 in contradistinction to physics and chemistry, it now pursued its agenda by turning the methods of the physical and chemical sciences to the study of particular organisms. The idiosyncratic properties of these organisms held the promise of the experimental characterization of the most general properties of living beings.[37] What plainly characterized the new dynamics of research around 1900, and what evidently distinguished the new genetics from earlier approaches to heredity, was the emphasis on doing experimental studies on variation and inheritance; the concomitant occurrence of new methodological tools; and, most importantly, the resulting emergence of new research objects. These objects were part of a new scientific endeavor for which a distinction between applied and pure science, between the artificial and the natural, made no sense. The new research objects were characterized by being both highly artificial, since they were results of procedures of standardization, purification, and controlled variation, and natural, since they were regarded as representing hidden, natural entities.

This is reflected in the fact that much fundamental genetic research in the late nineteenth and early twentieth centuries did take place in applied contexts like seed production, breeding of yeast and cereals for large-scale beer production, mass production of vaccines, efforts to further public health, administration of psychiatric hospitals, or eugenic programs. Increasing levels of division of labor and bureaucratic control in these areas—the seed company Vilmorin in France had 400 employees around 1900—led to the establishment of a culture of expertise and scientificity. In these contexts, Mendelism featured as one of many methodologies to realize values that were endorsed by this culture, like analyticity, exactitude, calculability, and predictability. Breeders and eugenicists in particular shared a combinatorial approach that held a promise for the transparent and reliable production of intergenerational effects. Synthetic chemistry, not physics, provided the model science in this context. An important property of this culture of expertise was its obsession with purity. Purity connects a number of issues that were at stake. It was an instrument of control, as results could be "checked" against their inputs. It enabled practitioners to "fix" characteristics and create identifiable and specifiable products. It created a set of discrete and stable life forms, rather than an uncontrolled continuum of variations.

This obsession with purity confers upon genetics a curious status within the life sciences. Mendel's laws do not at all describe what happens "naturally"—or "happens all or most of the time," as Aristotle would have formulated it. As R. A. Fisher long ago argued, Mendel's achievement rather consisted in having demonstrated "the truth of his factorial system."[38] Like the "pure" substances and compounds that populate the shelves of chemical laboratories, "genes" are entities that serve both as the target and the instrument of successful experimental manipulation. With the advent of genetics in the twentieth century, heredity did not therefore become further entrenched as an inescapable bequest—or burden, depending on one's perspective—from the past. It was rather turned into the malleable, technical object of desires and fears that haunt us to this day.

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Notes

1. Müller-Wille and Rheinberger (eds.) 2007.

2. See, e.g., Benson, Maienschein, and Rainger (eds.) 1988; Gooday 1991; Kohler 2002.

3. Jacob 1970; Bowler 1989; Müller-Wille and Rheinberger 2012.

4. López Beltrán 1995; Wood and Orel 2001; Waller 2002; López Beltrán 2004a; Müller-Wille 2014.

5. López Beltrán 2004b; Waller 2012.

6. On statistical approaches, see Porter 1986 and Gayon 1998. On late-nineteenth-century morphological approaches to heredity, see Bowler 1989, chap. 3 and 4.

7. Cf. Barahona, Suárez-Díaz, and Rheinberger (eds.) 2010.

8. Allen 1978; Olby 1985; Bowler 1989; Harwood 1993 to quote just some of the classic accounts. For a review of more recent literature, see Müller-Wille and Richmond, this volume.

9. Schwartz 2008.

10. For a similar approach to the discourse of reproduction, see Clarke 1998.

11. See Paul 1998 for some incisive case studies of eugenics along these lines.

12. Willer 2007 and Müller-Sievers 2007 explore notions of genius and productivity for the late eighteenth and nineteenth centuries.

13. See Sabean 2007 on heredity and changes in marriage patterns and kinship in the early modern period from which cousin marriage emerged as a preferred strategy for the transmission of family property in the early nineteenth century.

14. Cartron 2007 documents the prehistory of this relationship in early-nineteenth-century French hospitals. For accounts of the continuing history of human genetics in the twentieth century, see Gausemeier, Ramsden, and Müller-Wille (eds.) 2013.

15. Due to the renewed significance of race as a "marker" in recent years, there has been an upsurge of interest in the history of racial anthropology and genetics. See Wailoo, Nelson, and Lee (eds.) 2012 as well as two recent special issues of *BioSocieties* (vol. 5, issue 3, 2010) and *Current Anthropology* (vol. 53, suppl. 5, 2012).

16. Churchill 1987, 355, 362.

17. Gayon 1998.

18. Lyell 1830–1833, vol. 2, 66.

19. Paul and Kimmelman 1988; Olby 1991; Palladino (1993); Roll-Hansen 2000; Wieland 2004; Harwood 2005; Bonneuil 2006.

20. Teich 1983; Kloppenburg 1988; Bud 1993; Kevles 2007; Thurtle 2007.

21. Gaudillière and Löwy 2001.

22. For classic accounts of the well-documented history of eugenics in different national contexts, see Kevles 1985; Weingart, Kroll, and Bayertz, 1988; Adams (ed.) 1990; Stepan 1991; Carol 1995; Paul 1995; Broberg and Roll-Hansen (eds.) 1996. For a critical review and reflection on some of the underlying assumptions of this literature, see Müller-Wille and Rheinberger 2012, chap. 5.

23. See Paul 1984 and Schneider 1986, respectively.

24. See Moss 2003, chap. 1, and Radick 2012.

25. Jablonka and Lamb 1995; Spector 2012.

26. Even diseases like hemophilia, which do show some rather striking Mendelian transmission patterns, were first of all defined physiologically, in this case as a blood disease; see Pemberton 2011, chap. 1.

27. See Allen 1986.

28. For a historiographical review, see Sapp 1990.

29. For human heredity, see Gausemeier, Ramsden, and Müller-Wille (eds.) 2013; for animal breeding, see Theunissen 2008.

30. Allen 1979, 194.

31. Allen 2003.

32. Correns 1937, 132. Our translation.

33. Sapp 1987; Harwood 1993.

34. Moss 2003, xiii; cf. Keller 2000, 9.

35. Beurton, Falk, and Rheinberger (eds.) 2000; Müller-Wille and Rheinberger 2009.

36. Cunningham and Williams (eds.) 2002.

37. Müller-Wille and Rheinberger 2012, 127–129.

38. Fisher 1936, 133.

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