MAX-PLANCK-INSTITUT FÜR WISSENSCHAFTSGESCHICHTE
Max Planck Institute for the History of Science

2008

PREPRINT 343

Conference

A Cultural History of Heredity IV: Heredity in the Century of the Gene

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Introduction

This volume contains contributions to a workshop that was the fourth in a series of workshops dedicated to the objects, the cultural practices and the institutions in which the knowledge of heredity became materially entrenched and in which it unfolded its effects in various epochs and social arenas.[1] It was organized collaboratively by the Max Planck Institute for the History of Science, Berlin, and the ESRC Research Centre for Genomics in Society, Exeter. Funds from the Academic Research Collaboration programme of the British Council and the German Academic Exchange Service allowed to prepare the workshop in two one-day-meetings of scholars from Berlin and Exeter. The workshop itself was funded by the British Academy and by the Government of the Principality of Liechtenstein.

The last workshop in the series had dealt with the period up until the very end of the nineteenth century when heredity had become a central problem for biologists and a wide variety of approaches to attack that problem had begun to flourish.[2] The fourth workshop was specifically designed to address a historiographic problem that had arisen within the wider context of our project 'A Cultural History of Heredity'. Up to the late nineteenth century, the knowledge of heredity took shape by a step-by-step aggregation and integration of discourses from various knowledge domains; while from 1900 onwards it began to condense into and to be shaped by a highly-specialized discipline, the discipline of genetics. This has resulted in a preoccupation of the historical literature with genetics. One of the basic assumptions of our project, however, has been that heredity was always and remained to be more than genetics as a discipline, and that wider notions of inheritance persisted in areas like practical breeding, medical counselling and therapy, eugenics, and anthropology (including cultural anthropology).

To widen the scope of inquiry, we therefore decided to focus the workshop on the *tools* of dealing with inheritance, that is genealogical records and model organisms, and to follow their provenances, metamorphoses, and trajectories.[3] The major results, as documented in this volume, can be summarized as follows.

1. During the era of classical genetics (1900-1940) a number of important concepts with respect to heredity were defined, or re-defined, in strictly genealogical terms. These concepts included: clones, pure lines, bloodlines (in animal breeding), family lines (in anthropology), generation, and mutations as instances of change in these lines. The operational definition of these terms allowed researchers like William Bateson, Wilhelm Johannsen, Erwin Baur, Victor Jollos, Herbert Spencer Jennings, and Albert F. Blakeslee to create what some of them referred to as 'synthetic species': breeding systems fine-tuned by systematic in- and out-breeding to instantiate particular cases of evolution, as Bateson once put it. The significance of these constructs for the cultural history of heredity is twofold. First, they all had a life prior to and outside biological laboratories or experimental gardens. Pure lines, for example, had been developed by plant breeders, especially

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1 For more information on the project see http://www.mpiwg-berlin.mpg.de/en/research/projects/DeptIII_Cultural_History_Heredity/index_html.

2 See *Conference: A Cultural History of Heredity III: 19th and Early 20th Centuries*, Berlin: Max Planck Institute for the History of Science (Preprint, vol. 294).

3 See original call for papers at http://www.mpiwg-berlin.mpg.de/workshops/en/HEREDITY/announcement4.html, 2008/01/07

the French seed company Vilmorin, in the late nineteenth century already. And genealogical concepts used in the analysis of human populations had an even longer prehistory in clinical records. Second, the construction of 'synthetic species' was largely independent of any specific theoretical assumptions about mechanisms of transmission. Clones of single-celled organisms like *Paramecium*, for example, could be regarded as 'naked germ-lines', thus opening the possibility to study germinal transmission in its own right, without any prior commitment to particular theoretical assumptions about the relationship of soma and germ-plasm. And mutation researchers like Blakeslee or Baur could rely on their systems producing novelties without having to make prior decisions about the nature of mutations. It was in this sense that Jennings insisted against Johannsen that genotypes had to be considered as 'things', rather than hypothetical entities.

2. Much research into heredity in the late nineteenth and early twentieth century took place in applied contexts like seed production, breeding yeast and cereals for large-scale beer production, mass-production of vaccines, efforts to further public health, or administration of psychiatric hospitals. Increasing levels of division of labour 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, however, Mendelism featured as only one among many methodologies to realize values that were endorsed by this culture, like analyticity, exactitude, calculability and predictability. Breeders and eugenicists in particular, whether they declared themselves Mendelists or not, 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.

3. 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 the corresponding inputs. It enabled practitioners to 'fix' characters and create identifiable and specifiable products. It created a set of discrete and stable life forms, rather than an uncontrolled continuum of variations. And it held a promise to divorce practices from the vagaries of history. Once entities could be held 'pure', they could be recombined without being subject to the unpredictable manifold of interactions that 'impure' entities like the so-called 'land races' in traditional agriculture elicited. Heritability rather than inheritance, prospect rather than retrospect thus became one of the chief criteria for assessing the quality of life forms. In order to advertise, trade-mark, or patent agricultural or microbiological innovations, production methods had to be made transparent and reliable reproduction guaranteed. Heredity was commodified to become heritability, a marketable quality.

4. Mendelism entailed conditions and costs that precluded many areas from adopting it. To do Mendelian experiments, organisms had to be first inbred, then cross-bred, and finally raised in large numbers, to be able to ascertain Mendelian ratios. Asexual organisms and humans, but also many agriculturally significant animals, like cows, could not be subjected to such a practice. This is one of the main reasons why animal breeding and clinical medicine became 'geneticized' only well after WWII, and why statistical approaches, developed by the so-called biometrical school

long before the advent of Mendelism already, persisted in these areas to finally merge with population and quantitative genetics. It was with respect to human populations, in psychiatry, medicine and anthropology, in particular that sophisticated genealogical and statistical techniques –trait pedigrees of various cut, statistical and combinatory tables – were developed and applied to populations by researchers like Wilhelm Weinberg, Ernst Rüdin, or Wilhelm Nussbaum. Originating in administrative record-keeping practices of mental asylums in the late nineteenth century, these techniques retained their bureaucratic character, with the result that key categories and concepts, like 'race' or 'heritability', were emptied of their biological content and became formal, purely classificatory or statistical notions, although constant slippage from statistical results to presumed 'genetic' and thus biological (as opposed to 'environmental' or 'epigenetic') causes occurred regularly. Such slippages could be productive in terms of posing new research problems, but they were also mobilized to justify oppressive and outright murderous bio-policies.

5. The era of classical genetics was marked by a close, yet conflict-ridden relationship of heredity and history. Prominent biologists 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 could be made, or constructed, eliminating the power that history and tradition used to have over life. It was in this sense that Alfred L. Kroeber spoke of culture as the 'superorganic': Weismann's separation of soma and germ-line also, in a way, divorced culture from the organic, leaving culture behind as subject to its own 'systems of inheritance', systems that varied from culture to culture, and could be studied in their own right by anthropologists. But histories of nations and peoples were also recast as 'bio-historical narratives' whose dramatic turning points consisted in race mixtures, migrations, phases of strong selection or isolation, resumed intermarriage, in short: events entirely human, and not enforced by some higher law of history. Knowledge of heredity had evolved into an instrument, not only to analyze the past, but also to shape the future.

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Leaving Inheritance behind: Wilhelm Johannsen and the Politics of Mendelism

Staffan Müller-Wille

Abstract

In 1912 Wilhelm Johannsen codified the distinction of genotype *and* phenotype *to distinguish a space of heredity with an independent logic and metrics from another, physiological and developmental space represented by the cytoplasm and standing for the organism. In addition, for the elements of the genotype, he proposed the notion of the* gene. *This terminology was gradually taken up by the genetics community. Johannsen's codification, which was based on breeders' practices of separating "pure lines," has profoundly marked all of twentieth century genetics. What has largely escaped the attention of historians of science, however, is the polemical context in which Johannsen made these distinctions. In introducing his neologisms, Johannsen explicitly turned against "historical" notions of inheritance prevalent in eugenics and breeding. Yes, he even denounced the terms "heredity" and "inheritance," taken in their everyday sense, as inadequate to capture the "modern view of heredity." "Ancestry by itself is irrelevant; dispositions are decisive," as he put it in his 1905 textbook* Arvelighedslærens elementer. *In making such statements, Johannsen was far from denouncing eugenics and breeding as "unscientific" as such. He rather wanted to put these applied sciences on a thoroughly instrumental and constructive basis, with chemistry as a paradigm. In my contribution I will discuss Johannsen's roots in industrial research and how his view of Mendelism resonated with certain political ideas. Science, for Johannsen, was a modernizing force in as much as it was able to cut ties with tradition.*

> There is some kind of link, some kinship, among burdocks and beggars, singing in the fields, electricity, a locomotive and its whistle, and earthquakes—there is the same birthmark on all of them and some other things too … Growing grass and working steam engines take the same kind of mechanics.
>
> (Andrei Platonov, 1922)[1]

Looking at the cultural history of heredity in the "century of the gene" poses a number of historiographical problems as explained in the introduction to this volume. I would like to add an additional layer of complication: Current biological research is steering away from gene-centrism.[2] Heredity, as a consequence, is again supposed to involve much more than the transmission of genes. Such contemporary developments are not neutral with respect to how historians of science conceive of their object, that is, the history of a concept, theory, or discipline. While historians of science, for their own explanatory purposes, must be symmetrical, the historical object they deal with rarely, if ever, is. More often than not, science is radically asymmetrical, by claiming to "progress" and overcome what then turns out to have been "error"

1 From a letter to a publisher, quoted in Tolstaya (2000), p. xvi.
2 Keller (2005).

or "prejudice." If it were not, it would simply not have a history.[3] So if gene-centrism now turns out to have been mistaken, how are we to asses its history in twentieth century biology?

There are several ways to answer this question. One is straightforwardly whiggish: Gene centrism was always mistaken, and the century of the gene was simply a century of error. A less whiggish, but still anachronistic answer, is that gene-centrism was a fiction necessary for heuristic reasons, a "stage" that biology had to go through to reach its present state of art. There are finally two reflexive answers, which turn on the presuppositions that have informed the histories written so far. One may want to question that genetics was central to twentieth century biology at all, and argue that a lot more than genetics was going on all along, but has been unduly overlooked by historians. Or one may want to question the meaning of genetics, and argue that genetics was about something entirely different than historians have so far told us.

I will follow the latter line of argument in this paper. My aim in this is to open up classical genetics in order to see how it might fit into a cultural history of heredity. A lot of what I am going to say is derived from looking at the life and work of Wilhelm Johannsen, a key figure of early genetics. Yet the structure of my paper will be neither narrative, nor discursive, but rather aphoristic. I want to present a series of observations, all of which, in one way or other, turn around heredity, and all of which, in one way or other, turn around the notion of progress—a fundamentally political notion, as I see it. My overarching claim will be that classical genetics was the expression of an industrial culture that valued the future over the past, progress over tradition, autonomy over authority, and parts over wholes.

1.

The first observation I want to make is trivial, but essential, I believe. Classical genetics emerged during a time when Europe was undergoing demographic, economic, and social changes on a massive scale, a development that has become known as "the demographic transition." Some of the main parameters of the demographic transition are: fall of death-rate and fall of birth-rate, the latter occurring with a characteristic time lag, resulting in rapid population growth; rise in agricultural and industrial productivity; migration from rural communities to urban centres; and an overall rise in living standards, including nutrition and health care. To provide an illustration of the scale of these developments from a small European nation: In Denmark, between 1801 and 1901, 360,000 individuals migrated from agricultural areas to cities—or rather one city, Copenhagen. 143,000 of these went between 1881 and 1890 alone. From 1901 to 1950, the net-loss for agriculture was over 850,000 people. The population as a whole grew from 929,000 to 4,281,000 during the same time.[4]

The term "demographic transition" was coined in 1929 by the American population scientist Warren S. Thompson, director of the Scripps Foundation for Research in Population Problems.[5] The changes that the demographic transition encompassed, that is, had been under close scientific scrutiny—as is well-known, at least since Malthus. Moreover, the demographic transition associated a number of knowledge domains that arguably had some import for the knowledge of

[3] Canguilhem ([1994] 2002), p. 16–20.
[4] Andersen (1979), p. 102.
[5] Thompson (1929).

heredity: eugenics and reproductive medicine, of course; agricultural science, in particular breeding research; and—probably less obviously—microbiology in its medical, agricultural, and industrial applications.[6]

2.

Much of nineteenth-century research into heredity was clearly motivated by a concern, or even fear of degeneration, and this remained true even for much of classical genetics. The five last chapters (out of twelve) of Ronald A. Fisher's *The Genetical Theory of Natural Selection* dealt with the "decay of civilizations."[7] As a phenomenon, however, degeneration was unwieldy. In a crude manner, it simply reflected the negative consequences of the demographic transition. Any number of causes—from racial dispositions to alcoholism, from economic depravation to contagious diseases—could be held responsible for degeneration. And any number of measures—from positive eugenics to temperance, from birth control to public hygiene—could reasonably be suggested to counter or even reverse its negative effects. In the eugenic movement, therefore, all of these concerns lay very close. Alcoholism, for example, was thought to be both an effect and a cause of "bad" inheritance, simply by "poisoning" the germ line.[8]

The metaphor of hereditary transmission covered the whole spectrum of causes and measures just mentioned, relying on the assumption that the "indefinitely numerous small causes" that generated variation in one generation would have some "average effect upon the offspring" of that generation.[9] "Nature" and "nurture," "heredity" and "environment," under this perspective, did not separate two organic systems, one responsible for transmission, the other for development, but two sets of causes, one acting from the past, through pedigrees, onto the present, the other acting more or less instantaneously, at a given point in time.[10] This perspective becomes particularly clear when Karl Pearson, in his 1910 presidential address to the annual meeting of the Social and Political Education League, titled "Nature and Nurture: The Problem of the Future," reaches the conclusion that "[t]here is no real comparison between nature and nurture"—a surprising conclusion, if one takes into account that the bulk of the address was actually devoted to a meticulous comparison of the statistical effects of "nature" *vs.* "nurture." As Pearson went on to explain his paradoxical conclusion,

> it is essentially the man who makes his environment, and not the environment which makes the man. That race will progress fastest where consciously or unconsciously success in life, power to reproduce its kind, lies with native worth. Hard environment may be the salvation of a race, easy environment its destruction.[11]

Hereditary superiority, that is, lies with the innate ability to shape one's environment, even under adverse conditions, in order to reproduce one's kind. Nurture, in this case, is not reduced to a mere accident, able to modulate nature only within strictly set limits. Nurture would rather be the

6 On microbiology see Bos and Theunissen (1995); Mendelsohn (2005); Müller-Wille (2007).
7 Fisher (1930), p. xii.
8 Snelders, Meijman, and Pieters (2005).
9 Pearson (1896), p. 255.
10 Pearson (1913), p. 11–12.
11 *Ibid.*, p. 27.

very expression of nature, if the latter were only left alone to exert its positive influence. In trying to avert degeneration, the eugenic movement endorsed a view of inheritance as a natural force which had the potential to preserve and promote positive characters, but whose positive effects would only supervene, if society invested a lot to create conditions that would actually foster, and not inhibit, that potential. Nature was glorified as a powerful source of progress and at the same time deeply mistrusted in its ability to bring about progress simply on its own.

3.

There was another, more specific, more precisely delineated phenomenon than degeneration, which excited research into heredity. This was reversion, regression, or atavism, the fact that ancestral characters sometimes reappear in more distant, descendant generations, while being absent from intermediate generations.

Several points are interesting about this phenomenon. First, it depended on a temporal structuring of populations by generations, on an analysis of descent, that is.[12] Second, it encompassed a wider scope than procreation, the immediate production of offspring by parents, by looking at three generations at least. And third, it connected with an important issue raised in the context of contemporary cell theory, the issue of the relative autonomy of the living, elementary units of which organized beings were supposed to be composed. In the last chapter of *The Variation of Plants and Animals under Domestication*, presenting his notorious theory of pangenesis, Charles Darwin highlighted two conclusions that attention to reversion suggested with respect to the issue of autonomy. First, he reasoned that the "principle of Reversion [sic]," that "most wonderful of all attributes of Inheritance [sic] ... proves to us that the transmission of a character and its development, which ordinarily go together and thus escape discrimination, are distinct powers."[13] Transmission, that is, and development of a character are independent phenomena. The second conclusion that Darwin drew from the "principle of Reversion" was that "[o]vules and the male element, before they become united, have, like buds, an independent existence. Both have the power of transmitting every single character possessed by the parent form. We see this clearly when hybrids are paired *inter se*, for the characters of either grandparent often reappear, either perfectly or by segments, in the progeny."[14] Individual characters, that is, may be transmitted independently of each other.

4.

The second conclusion quoted in the previous section is as close as Darwin ever should get at formulating what Mendel, just a few years earlier, had called the "law of development of the progeny of hybrids," and which we today would call the law of segregation.[15] It also allows us to understand why it was that Darwin thought that the "principle of Reversion" was the "most wonderful of all attributes of Inheritance." Drawing on the work of Claude Bernard and Rudolf Virchow, Darwin subscribed to the view that "[e]ach organ has its proper life, its autonomy," and

12 Parnes (2007).
13 Darwin (1868), vol. ii, p. 372.
14 *Ibid.*, p. 360.
15 On Mendel's formulation of this "law" see Müller-Wille and Orel (2007).

that each element of the living body "even though it derives its stimulus to activity from other parts, yet alone effects the actual performance of its duties."[16] Now, reversion, according to Darwin, was just the phenomenon that provided decisive evidence for this view, because it could only be explained under the assumption that "every character which occasionally reappears is present in a latent form in each generation ..., ready to be evolved under proper conditions."[17] To put it differently: the potential to develop a character "under proper conditions" was apparently retained by each transmitted unit—or gemmule, as Darwin called it—independently of the particular bodies it passed through, and independently, in particular, from its combination with other such units in the fertilized egg. This was a relative autonomy only, to be sure. The development of characters clearly depended on "proper conditions," more specifically, on the "union" of gemmules "with other partially developed cells or gemmules."[18] But once these conditions were realized, development would always ensue in the same way according to Darwin. The developmental potential of gemmules was supposed to remain unaffected—or untainted, so to speak—by the various organic systems that they became part of while being transmitted. If that were not the case, if gemmules were somehow "tainted" along their way, parents would always leave a trace in their children—which is clearly contradicted by cases of reversion, where grandparental traits reappear without having reappeared in the parents.

Darwin thus broke down the organism into two levels of organisation in his theory of pangenesis: a level consisting of the "completely passive or 'formed material'" of the body, composed by fully developed cells; and a level consisting of the gemmules, thrown off by cells throughout their development, "circulat[ing] freely" through the body, and "multiplying by self-division" when supplied with "proper nutriment."[19] Gemmules, that is, represented the body in all its parts, but they did so in a manner that allowed them to circulate, recombine, and develop freely without changing their essential nature. It is in this sense that Darwin, towards the end of his Pangenesis-chapter, insisted that "[t]he child, strictly speaking, does not grow into the man, but includes germs which slowly and successively become developed and form a man."[20]

5.

Cell theory, and the associated issue of the autonomy of the elements of organisms, also lay at the ground of Johannsen's distinction of genotype and phenotype. This becomes especially clear in his contributions to a textbook in general botany that he co-authored with his teacher Eugen Warming in 1900. Among the chapters he contributed was one on the topic of the "periodicity in the life of plants." Johannsen started this chapter with a thought experiment:

> If we think about a bacterium in a continuously renewed nutritive fluid of unchanged composition, at constant temperature, in permanent darkness etc., in short, under constant living conditions, we can assume that the bacterium will divide after a certain amount of time, the daughter cells will grow up and also divide etc. Cell division is obviously a consequence of

16 Darwin (1868), vol. ii, p. 368–369.
17 *Ibid.*, p. 373.
18 *Ibid.*, p. 374.
19 *Ibid.*
20 *Ibid.*, p. 404. Darwin is playing here on a famous quote from a poem by William Wordsworth: "The child is the father of the man" (*My heart leaps up when I behold*, 1802).

> growth and nutrition, as well as of changes in the inner states of the cell provoked by growth and nutrition. And these periodic phenomena appear without the slightest change in external conditions. The nature and order of phases in the life history of bacteria is thus not dependent on a periodicity of external factors.[21]

Johannsen took this to show that "the course of development [of an organism], its 'Grundplan', is independent of external factors or at least not immediately dependent on them." The reasoning behind this is obvious: If the course of the life of organisms depended entirely on external conditions, conditions held constant should keep them from developing. But organisms do develop, even in a constant environment, in the simplest case undergoing cell division after a certain amount of time. Johannsen believed that the source of this "independent and autonomous periodicity was still entirely mysterious." So much could be said however: "In many cases there must be properties within the organism, which determine, that a certain activity, e.g. a growth process, causes a state after some time, which contravenes the continuation of that process, may be in an analogous manner as chemical processes 'cease by themselves' with the accumulation of their product."[22]

Johannsen's thought experiment, as well as the chemical analogy he used to explain the mysterious ability of organisms to develop, were not simply plucked out of thin air. In interesting ways, both show connections with another of Johannsen's contributions to Warming's textbook, a chapter that dealt with "fermentation and putrefaction" and the "occurrence and role of micro-organisms in nature." Here, Johannsen gave credit to Emil Christian Hansen, head of the bacteriology department at the Carlsberg Laboratory in Copenhagen, for the discovery "that there are whole series of yeast species or races that are of very different practical value" for the brewing industry.[23] In order to develop methods that could prevent beer from turning sour occasionally, Hansen had adopted the pure culture approach from Louis Pasteur and Robert Koch in 1883. Isolating single yeast cells by repeated dilution and under the microscope, and cultivating them under sterile and constant conditions, allowed him to produce yeast consisting of beneficial strains of brewer's yeast only. The strains were marketed successfully as *Carslberg Bottom-Yeast No. 1* in the same year, and soon spread over breweries world-wide.[24]

6.

Johannsen had himself started his research career at the Carlsberg Laboratory, a private research laboratory in Copenhagen associated with, but largely independent of, the famous beer brewery. In 1881, he entered its chemistry section as a research assistant with the task of applying analytic methods to determine the involvement of organic nitrogen in metabolic processes connected with the ripening and germination of plants, especially barley. In 1887 Johannsen left the Carlsberg Laboratory to take up a lectureship at the Royal Veterinary and Agricultural College in Copenhagen, but continued his collaboration with the Laboratory, now turning to experiments in breeding high quality strains of barley.[25] Both projects were intimately connected, because the

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21 Warming and Johannsen ([1900] 1909), p. 580–581.
22 *Ibid.*, p. 619.
23 *Ibid.*, p. 355.
24 Teich (1983).

nitrogen-content of barley was an important variable in the brewing process, and the quality of barley, in consequence, could be assessed, among other things, by measuring its protein content. Variation in plant form was thus reduced to variation in a single, measurable chemical variable.[26]

It is in this context that Johannsen must have picked up the "pedigree" method from plant breeders like the French Louis de Vilmorin. Just like pure cultures, pedigrees—or "pure lines" as Johannsen should later call them—were genealogical constructs. A pedigree, or pure line, consisted of all descendants derived from a single individual through self-fertilization. There was therefore, as Johannsen used to put it, "no doubt about the father" in pure lines.[27] The vagaries of ancestry were reduced to a minimum, just as in pure cultures of asexually reproducing organisms, and pure lines could thus be expected to always react in the same way to given environments. In 1903, Johannsen should use pure lines of beans to draw the distinction of genotype and phenotype by demonstrating that selection was ineffective in genetically homogenous populations.[28]

7.

Johannsen was clearly aware that the use of pure cultures and pure lines did not relieve practitioners from attending to environmental conditions. The quality of beer, as he put it in the Warming textbook—and as he well knew as a Danish *bonvivant*—would always depend on "the locality in which fermentation went on."[29] Pure cultures and pure lines were therefore not of immediate practical use in local contexts—as Johannsen stated in his 1905 textbook *Arvelighedens elementer* (Elements of Heredity)—but of use in the *circulation* of plant material among such contexts only. "Use and propagation (i.e. breeding) both pose their own demands which should never be confused. Use counts on the individual and exploits the most advantageous conditions that can be created for its development to meet the purpose. Continued propagation must count on life-types, and different conditions of life show us here, what potential lies in a respective race."[30] Pure lines did not exist locally, and they could not be intuited based on localized experience. "There are so many who have made experiences," as Johannsen polemisized against breeders, "starting from their experiences, [they] have formed notions of inheritance in which they believe like charburners."[31] Johannsen had similar views on eugenics, expounded in an article he wrote in 1927 for the Danish journal *Naturens verden* (The World of Nature) while serving as a member of the Danish state commission that was to draw up one of the first sterilization laws world-wide.[32] Johannsen was sceptical about the prospects of eugenic policies, arguing that individual phenotypes were the expression of equations with two, or rather two sets of, unknowns: elements of disposition and environmental factors. "This causes the varied and not always happily concluding lottery in the life and fate of generations," as the article concluded.[33]

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25 Roll-Hansen (2005).
26 Johannsen (1899) summarizes the results of these projects, discussing mutations and the correlation of morphological and chemical variables. See Bonneuil, this volume, for more details.
27 Quoted according to Roll-Hansen (2005), p. 47.
28 Johannsen (1903).
29 Warming and Johannsen ([1900] 1909), p. 356.
30 Johannsen (1905), p. 177.
31 Johannsen (1913), p. 4.
32 On Johannsen's engagement with eugenic policies of his time, see Koch (1996), p. 57–67.
33 Johannsen (1927), p. 235.

8.

We meet the same kind of contempt for popular conceptions of heredity in Johannsen's 1911 paper in the *American Naturalist*, that introduced the expressions genotype and phenotype to the English speaking world. The paper started out with a veritable diatribe against what Johannsen conceived as "the most naïve and oldest conception of heredity," namely the "view of natural inheritance as realized by an act of transmission, viz. the transmission of the parent's (or ancestor's) *personal qualities* to the progeny." "The *personal qualities* of any individual organism," as Johannsen went on after sketching out the history of the transmission conception of heredity,

> do not at all cause the qualities of its offspring; but the qualities of both ancestor and descendent are in quite the same manner determined by the nature of the sexual substances—i.e., the gametes—from which they have developed. Personal qualities are then *the reactions of the gametes* joining to form the zygote; but the nature of the gametes is not determined by the personal qualities of the parents or ancestors in question. This is the modern view of heredity.[34]

This short passage contains the distinction of genotype and phenotype in a nutshell. It must be seen against the background of what Jean Gayon has called the "Mendelian break," seperating biometricians from early geneticists, William Bateson in particular. In Darwinism, specifically in the version endorsed by the biometricians, inheritance was conceived of as a force or tendency that could be measured by the statistical "effects" that ancestors had on their descendents. Heredity became synonymous with the descent, lineage, or "pedigree" of an individual. A major characteristic of this approach was its descriptive character, in other words, its independence from any hypothesis about the mechanism of hereditary transmission. Mendelians, in contrast to that, regarded pedigrees not as objects, but as tools to uncover the genetic constitution, understood as an organic structure, of a given parental generation. To quote Jean Gayon: Heredity was not the sum total of ancestral influences; it was a question of structure in a given generation. What happened to the progeny did not depend on what happened to the ancestors of its parents, but only on the genetic makeup of its parents."[35]

For Johannsen ancestral inheritance was a "mystical expression for a fiction," and his contempt for biologists endorsing such views, especially Ernst Haeckel, was profound.[36] The genotype conception represented an "'ahistoric' view of the reactions of living beings" that was analogous to a "chemical view." "Chemical compounds have no compromising ante-act, H_2O is always H_2O, and reacts always in the same manner, whatsoever may be the history of its formation or the earlier states of its elements. I suggest that it is useful to emphasize this 'radical' ahistoric genotype conception in its strict antagonism to the transmission- or phenotype view."[37] "Ancestry by itself is irrelevant; dispositions are decisive," as Johannsen put it provocatively in his 1905 Textbook *Arvelighedens elementer*.[38]

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[34] Johannsen (1911), p. 130.
[35] Gayon (2000), p. 77.
[36] See Johannsen ([1914] 1917), p. 20, where Haeckel is referred to as the "high priest" of German Darwinism.
[37] Johannsen (1911), p. 139.
[38] Johannsen (1905), p. 216.

9.

What was modern about Johannsen's "modern view of heredity"? First of all, I would like to maintain, the uncompromising willingness to detach the production of knowledge from tradition, from experience accumulated in the past. Tradition, in Johannsen, appears as a reservoir of myths and prejudices only, which mathematics in conjunction with experiment allows to overcome. Johannsen's theory of heredity was an exact match of his epistemology. Johannsen was always proud of coming as a largely self-taught outsider to biology. "I am, and always will be, a free-lancer in science," as he once stated.[39] Johannsen's father, a corporal in the Danish army, had been unable to pay his son a university education, and Wilhelm therefore had to seek his way into academia through an apothecary apprenticeship.

Another aspect of Johannsen's modernity is much more difficult to pin down. Nils Roll-Hansen has remarked, that Johannsen "successfully bridged the gap" between early Mendelians and biometricians.[40] Providing this bridge was not, however, only a matter of conceptual innovation. Johannsen's emphasis on the importance of pure cultures and pure lines demonstrates a technological dimension, the creation of new entities, genes, that allowed to view and to deal with organisms as if they were constituted, quasi-mechanically, of independent elements, which could be transposed and combined at will, while retaining their propensity to produce definite effects under given circumstances. As James Griesemer has argued, genetics did not divorce transmission from development. Far from it, genetics, in its search for "developmental invariants," was in a sense all about development.[41]

10.

It needs to be emphasized that Mendelism comprised an impossible view of the organism, which is probably no better expressed than by William Bateson's stunningly self-confident formula: "We can pull out the yellowness and plug in greenness, pull out tallness and plug in dwarfness." Such statements contain an attractive promise of control over life, and many Mendelians were enthusiastic eugenicists. Not so Johannsen and Bateson. In the latter's case, as Mackenzie and Barnes have argued, this correlated with conservative political convictions and a deeply rooted aversion against any "ideas of interventionist reformers [like Karl Pearson] riding the tide of advanced industrialism."[42] With Johannsen, the matter seems to have been a bit more complicated.

In 1914, Johannsen published a booklet titled "False analogies with respect to similarity, kinship, inheritance, tradition, and development." It was a sweeping attack against all attempts to analogize the social and the biological world. In particular, Johannsen directed biting comments against the assumption that "an active historical moment" was involved in the formation of individual organic beings, that heredity consisted in a kind of "memory" of the past that played a causal role in individual development.[43] There was another assumption, however, that drove

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39 Quoted in Winge (1958), p. 87.
40 Roll-Hansen (1980), p. 512; cf. Gayon (1998), p. 512.
41 Griesemer (2000).
42 MacKenzie and Barnes (1979), p. 205.
43 Johannsen ([1914] 1917), p. 38.

Johannsen mad, and that he saw instantiated by Darwin's theory of pangenesis: the assumption, namely, that the organism is an ensemble of independently reproducing parts.[44] This is surprising, given Johannsen's own reliance on the tenets of cell theory. And did not his own conceptual creation, the gene, constitute an element of the organism that reproduced itself independently of circumstance?

Well, as Lenny Moss and Rafi Falk have shown, Johannsen always remained critical of "gene for" talk, of "genes" being and representing parts of the organism.[45] He consistently resisted the temptation to follow the Morgan school in locating genes on chromosomes.[46] It thus seems that Johannsen, in some sense, wanted to have it both ways. His analytical skills had made his career, initially in an industrial context, where advancing over traditional procedures was what counted to achieve success, and where "atomizing" life into constituent units that could be moved around and recombined at will was a good strategy to make such advances. It was here, indeed, where ancestry was irrelevant, and where dispositions were decisive. Faced with the prospects and projects of eugenicists eager to avert "degeneration," on the other hand, Johannsen tended to emphasize the haphazard nature of genetic recombination, and the inability to effectively control the future on the basis of genetics. Here, life essentially became a gamble.

Johannsen's writings thus exhibit a deep ambiguity. "Personally," he wrote in 1923, "I believe in a great central 'something' as yet not divisible into separate factors", and he identified this "something" with the "specific or generic nature of the organism. The pomace-flies in Morgan's splendid experiments continue to be pomace-flies even if they loose all 'good' genes necessary for a normal fly-life, or if they be possessed with all the 'bad' genes, detrimental to the welfare of this little friend of the geneticist."[47] Genetic analysis, on one level, was a safeguard of personal autonomy, as it allowed to escape the weight of history, and to literally make one's own life. On another level, however, it constituted a threat to personal autonomy, by dissolving the life of individuals into ponderable elements and putting this life at the mercy of powers beyond their control. Johannsen, it seems, was acutely aware of this political dilemma that the science of heredity posed.

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44 *Ibid.*, p. 40.
45 Falk (1986), 135–141; Moss (2003), p. 28–44.
46 Churchill (1974).
47 Johannsen (1923), quoted in Moss (2003), p. 38.

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Mendelian Factors and Human Disease: A Conversation

Jean Paul Gaudillière & Ilana Löwy

A fictitious conversation, in 1930s, between

—Miss **Mina Mauser**, an indefatigable laboratory worker and enthusiastic follower of the new theories on heredity, who has dedicated all her life to studying hereditary phenomena in inbred mice. Miss Mauser is a typical spinster: austere and slightly fanatical;

and

—Professor **Adolph Influence**, a brilliant clinician, who has dabbled in multiple domains of medical investigation, is a pro-natalist, believes in the superiority of "intransmissible" clinical knowledge. Professor Influence is a highly successful doctor and has the charm and polished manners of his profession.

MM: Doctors are always talking about "heredity," "hereditary predisposition," and "hereditary conditions." But if you listen to them carefully, you can see that the term "heredity," as they use it, is far from clear. They confuse true hereditary conditions with vague "parental influence," and they include under the same heading the "degeneration" induced by diseases such as syphilis or tuberculosis and behavioural traits such as alcoholism, and even the effects of the poor health of mothers during pregnancy on the newborn child. They've never really understood what the new science of heredity is all about.[1] Take for example Charles Richet. He is a great scientist, he has won the Nobel prize for his investigations in anaphylaxis, but he is also an enthusiastic supporter of eugenics.[2] Richet has suggested that interracial marriages should be prohibited, that men found unfit for military service should not be allowed to marry, that the marriages of sick and mentally handicapped people and of those with identified criminal inclinations should be regulated, and that the sterilization of recidivist criminals should be mandatory.[3] He has supported these rather

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1 See, e.g., papers by Andrew Mendelsohn and Patrick Zylberman. In Jean Paul Gaudillière and Ilana Löwy (eds.). *Heredity and Infection. The History of Disease Transmission.* London: Routledge 2001.

2 On Richet, see Charles Richet. *Souvenirs d'un physiologiste.* Paris; J. Peyronnet & Cie 1933; André Mayer. "Notice Nécrologique sur M. Charles Richet." Académie de Médecine. Session of 14 January 1936; *CR Académie de Médecine.* 1936. pp. 51-64; Gustave Roussy. "Éloge de Charles Richet." *Académie de Médicine.* Session of 18 December 1945. *CR Académie de Médecine.* 1945. pp. 725-731; Stuart Woolf. *Brain, Mind and Medicine. Charles Richet and the Origins of Physiological Psychology.* New Brunswick and London: Transaction Publishers 1992; Pierrette Estingoy. DEA thesis. "Charles Richet, 1850-1935. Esquisse biographique et bibliographie." PhD in History. University of Lyon III. Jean Moulin 1993; Pierrette Estingoy. "Charles Richet et la découverte de l'anaphylaxie. Histoire d'un prix Nobel de médecine." Thesis in Medicine. University of Lyon I. Claude Bernard 1996.

3 Charles Richet. "La sélection humaine." *Eugénisme, Organe de la société française d'eugénique* 1923, 3(1). This study was written in 1912, first published in 1919, and in 1921 a revised version of this essay was published by the French Eugenic society.

extreme measures because he believes in invariable hereditary traits. On the other hand, he also believes that heredity could be modulated by the environment. For him, not all transmissible traits are fixed. Some are, but others are plastic and can be changed by the appropriate manipulation of external conditions. Really, according to these people, anything goes! Richet has even declared that Darwinism should blend with Lamarckism.[4] What kind of scientific approach is that?

AI: That is precisely the point. We are not dealing with the artificial conditions of a laboratory but with real human beings. We are not breeding homogeneous mice, but trying to help parents have healthy children and provide healthy citizens. You seem to believe that eugenic measures are in contradiction with efforts to improve the health of expectant mothers—but where is the contradiction? We all know that some people—those suffering from advanced tuberculosis or syphilis, those with important physical handicaps, those with a family history of mental diseases—are unfit to be parents.[5] Charles Richet wants such people to be formally prohibited from marrying. Most physicians will not go that far but do think that people with hereditary handicaps should be persuaded to refrain from having children. Responsible family doctors are expected to advise their patients on these issues.

On the other hand, even individuals without hereditary handicaps can produce sickly and unfit children. The French paediatrician Professor Pinard's studies have shown that a child's weight at birth and its subsequent health strongly depend on the health status of the mother during pregnancy. Pinard has also demonstrated that women who work under difficult conditions while pregnant have higher rates of spontaneous abortion, more frequent pregnancy complications and can give birth to sick children. Helping poor women to have healthy children is important for the nation. Paid maternity leave for women who are forced to work for economic reasons and free medical service for all pregnant women are also excellent investments, because a small expenditure during the mother's pregnancy will save much larger amounts of money spent on an ailing child and, if the child survives, on a sickly adult.[6]

Charles Richet is a great experimental physiologist, but above all, he is a clinician. He is familiar with the complexity of physiological and pathological conditions and, for this reason, does not treat animals—or humans—like test tubes with legs. His understanding of anaphylaxis—a violent reaction to a "sensitizing" protein—has led him to a more complex view of the interactions between hereditary and acquired conditions. Anaphylaxis, argues Richet, illustrates the impossibility of separating innate physiological reactions from acquired components. Some anaphylactic reactions, such as sensitization by injection of horse serum—the so-called "serum sickness"—are induced by a repeated contact with an external antigen. Other "anaphylactic type" reactions, such as allergies to foodstuffs or drugs, occur with no previous contact with the allergen and are therefore probably induced by innate mechanisms. Nonetheless, both kinds of

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4 On Richet's concept of occasional inheritance of acquired traits, see "Autobiographie de professeur Charles Richet recueillie par le Dr. Pierre Maurel." *Les Biographies Médicales – Revue Mensuelle Illustrée.* 1932, 6(8), Part II, pp. 173- 188.

5 See, e.g., William Schneider. *Quality and Quantity. The Quest for Biological Regeneration in Twentieth Century France.* Cambridge: Cambridge University Press 1990.

6 William Schneider. "Puericulture and Style of French Eugenics." *History and Philosophy of Life Sciences.* 1986, 8, pp. 265-277; Charles Richet. "La protection de la maternité." *Bulletin de l'Académie de Médecine.* 1917, 77 (3), pp. 605-634.

anaphylaxis are rigorously identical from a physiopathological point of view.[7] And the first concern of a doctor treating a patient with severe allergic manifestations is not to find out if the patient is suffering because he was born sensitized to an allergen, acquired such sensitization sometime in the past, or from a mix of both of these mechanisms. What a doctor really needs to do is find a way to alleviate the patient's suffering and prevent future incidents.

MM: But if we really want to understand disease, not just to try to provide symptomatic treatment of bothersome symptoms, we need to develop a rigorous scientific approach, tested under well-controlled experimental conditions. We need to study diseases that run in families and find the Mendelian distribution of diseases known to be hereditary, such as haemophilia.

AI: Haemophilia is precisely a very good example. Some scientists believe that this is a true "Mendelian disease," but the French paediatrician Eugène Apert, who published the genealogical tree of a family with haemophilia, explained that in this case we were dealing with a modification of Mendelian transmission through "maternal inheritance." Professor Apert provided a good explanation of the complexity of human heredity. Allow me to quote him:

> Identical transmission of a disease from one generation to the next, which may be called inheritance of the same, is rare. It is, however, the rule for a few illnesses, known as familial diseases. Although these are exceptional, the study of hereditary disorders must begin with them, because they represent the least complex form of morbid inheritance. It should be borne in mind that they are just a small corner of a vast field. If, for instance, the father is a drunkard, he will produce a son differing from the normal type within his lineage. Within this family, there will be a tendency to degenerate, since the father's sperm, or rather the cell from which it derives, has been the target of obnoxious effects originating in the bad condition of the paternal organism.[8]

Professor Apert understood that normal inheritance is Mendelian. But he also made it clear that pathological inheritance is more complex than normal inheritance. He also pointed to the fact that familial disorders are rare and that these pathologies are marginal when viewed from a medical and public-health perspective. Geneticists love to draw pedigrees. Pedigrees, to be sure, are very useful, but only if we take them, not as a demonstration of the exclusive role of Mendelian factors but as a means for revealing how these factors are modified by other influences, whether they are environmental, social or physiological.[9]

Another French doctor, Professor Raymond Turpin, has studied "mongolism." Other researchers had previously shown that although the condition was inborn, there was no familiar

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7 Charles Richet. "Humorisme ancien et humorisme moderne." *La Presse Médicale*. 1 October 1910. English version. Charles Richet. "Ancient Humorists and Modern Humorism." *British Medical Journal*. 1910. ii. pp. 921-926; Charles Richet. *L'Anaphylaxie*. Paris: Felix Alcan. 1911. English translation. Charles Richet. *Anaphylaxis*. (translated by J. Murray Blight). London: Concable & Company 1913; Charles Richet, "Anaphylaxis." Nobel Lecture, 11 December 1913. *Nobel Lectures. Physiology or Medicine*. Amsterdam and London: Elsevier Publishing Company 1967. Vol. 1, pp. 473-492.

8 Eugène Apert. "Traité des maladies familiales et des maladies congénitales." Paris: Baillière 1907. In Jean Paul Gaudilliere. "Mendelism and Medicine. Controlling Human Inheritance in Local Contexts. 1920-1960." *CRAS* 2000, 323: pp. 1117-1126.

9 Raymond Turpin. "L'avenir des caractères acquis." *Le Progrès Médical*. 16 April 1932.

clustering, and they had decided that the condition was not inherited. Turpin has a different view. "Mongol" children have a furrowed tongue. Turpin claims that this trait is often displayed by their parents as well, which might be an indication of simple Mendelian transmission. On the other hand, Turpin and his co-workers have shown that the birth of a "mongol" child is often associated with late pregnancy; the older the mother, the higher the frequency of mongolism. Their conclusion is that there is no simple Mendelian transmission, but a twofold "familial imprint," genetic and physiological, that favours mongolism.[10] We can perhaps demonstrate the inheritance of a simple trait, but complex traits are, well … complex.

MM: I disagree! Suppose we look at cancer. Cancer is without doubt a very complicated disease. Nevertheless, there are important differences in the distribution of malignant tumours in populations. So-called "savages" rarely suffer from cancer: the disease is much more frequent in "civilized" countries. The distribution of types of cancer in specific populations is also very different: people in Northern Europe suffer more from different malignant tumours than people in central Asia, and Negroes in the United States have a much higher incidence of cancer than their African ancestors.[11] In addition, we all know about "cancer families." In some families, every single member seems to die of cancer, often at a relatively young age. This is even known by insurance firms, as they are reluctant to sell life insurance to people who have several relatives who have died young from a malignancy.[12] This is something your fellow physicians refuse to admit: they want to persuade the general public that cancer is not hereditary so the disease is seen as curable and people are encouraged to consult a doctor as soon as they detect a symptom that could indicate the presence of malignancy.[13] They have therefore opted to avoid the question of the heritability of cancer and hide behind vague terms such as "hereditary influence." For example, an editorial in the Journal of the American Medical Association stated in 1932:

> Cancer is a disease of such protracted development and course, so variable in its manifestations and duration, often so difficult of diagnosis and differentiation, that satisfactory study of many fundamental problems on the basis of clinical observations is almost or quite impossible. At the present time it seems safe to maintain that the existence of an hereditary influence on the susceptibility and resistance to cancer has been established for both man and animals. The exact mechanism of the hereditary influence has yet to be determined. The evidence offered by human material is conflicting and inadequate both in amount and character to permit satisfactory analysis.[14]

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10 Raymond Turpin. "Le mongolisme, étude clinique et fonctionnelle." *Semaine des Hôpitaux de Paris*. 31 December 1931; R. Turpin, A. Caratzali. "Conclusion d'une étude génétique de la langue plicaturée." *CRAS* 1933, 196: 2040-2045; R. Turpin, A. Caratzali."Remarques sur les ascendants et les collatéraux des sujets atteints de mongolisme." *La Presse Médicale*. 25 July 1934, pp. 1186-1190.

11 Federick L. Hoffman. "Cancer in the North American Negro." *American Journal of Surgery and Gynecology*. 1931, pp. 229-263, quotation p. 241.

12 J. Paterson MacLaren. *Medical Insurance Examination. Modern Methods and Rating of Lives*. New York: William Wood and Company 1943. pp. 530-531.

13 E.E. Bashford. *The Influence of Heredity on Disease*. London: Longmans, Green & Co. 1909. pp. 63-66; James Ewing. "Heredity and Cancer." *Bulletin of American Society for the Control of Cancer*. August 1942, 24(8); pp. 4-7.

14 Editorial. "The Influence of Heredity on Cancer." *JAMA*. 7 May 1932, reproduced in *Bulletin of ASCC,* 1932, 4 (8): pp. 3-4.

Fortunately, some researchers have not been discouraged by this muddled argumentation and have set up specific experimental systems to study inheritance in cancer. In the 1910s, the 1920s and now in the 1930s, researchers such as Clara Lynch, Maud Slye, Nathalia Dobrovolskaia Zavadzkaia and Clarence Cook Little have developed "cancer prone" lines of mice and attempted to display the genetic mechanism that made these mice specially susceptible to malignancies. This has not, to be sure, been an easy task, and these researchers have not always agreed among themselves. For example, Maud Slye investigated spontaneous tumours surfacing in mice "families" that were kept under constant investigation and systematically autopsied to identify and document the cause of each death. This strategy has mainly produced pedigrees showing cancer families and non-cancer families of mice, which can be compared with human pedigrees but display clearer patterns of transmission, and has permitted the computation of Mendelian ratios. On the basis of several thousand necropsies and hundreds of charts, Slye claimed in the 1920s that cancer was not only a transmissible factor, but that a common recessive gene was involved in the appearance of tumours in utterly different locations.

The geneticist Clarence Little strongly opposed this form of experimental practice, because it did not involve true "pure lines" of mice. Only models based on such lines, Little argued, would allow the development of reliable knowledge on the input of genetic factors to the genesis of cancer. Little opposed the "messiness" and semi-qualitative nature of Slye's work, while the latter considered Little's inbred mice as by-products of an artificial selection process that made comparison with humans impossible. This controversy notwithstanding, the breast-cancer mice Little and his co-workers have developed lately have become widely-circulated research tools. Thanks to this and similar animal models such as the "cancer lines" of mice developed at the Curie Institute in France, we will soon be able to understand the true input of heredity to cancer.[15]

AI: Of heredity to cancer *in mice!* Look what has happened to studies that have attempted to investigate more precisely the links between heredity and cancer in human beings. About 10 years ago, the Sub-Committee on Statistics of the Cancer Committee of the League of Nations funded an extensive investigation on the racial determinants of cancer.[16] The study on the "relationships between cancer and race" conducted by Professors Alfredo Nicoforo and Eugène Pittard relied above all on anthropological measures to define "race." The study was limited to European populations. These populations were divided into three main racial types: *Homo europeus, Homo alpinus* and *Homo mediterraneus*, according to the distribution of physical traits such as eye and hair colour, height and build, the shape of the nose and the form of the skull. Nicoforo and Pittard painstakingly mapped racial traits on one side and the distribution of tumours on the other, and tried to correlate the two maps. And what did they find? Not much, really. At best, some vague

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15 Ilana Löwy and Jean Paul Gaudillière. "Disciplining Cancer: Mice and the Practice of Genetic Purity." In J.P. Gaudillière and I. Löwy (eds.). *The Invisible Industrialist. Manufactures and the Production of Scientific Knowledge*. London: Macmillan 1998. pp. 209-249; Jean Paul Gaudillière. "Circulating Mice and Viruses: The Jackson Memorial Laboratory, the National Cancer Institute and the Genetics of Breast Cancer." In Michael Frotrun and Everett Mendelsohn (eds.). *The Practices of Human Genetics*. Dordrecht: Kluwer 1999. pp. 89-124.

16 The commission was headed by Major Greenwood, and its members were Professor H.T. Delman, Dr. Janet Lane-Claypon, Dr. Henri Methorst, Professor Alfred Niceforo, Professor Eugene Pittard, Major P.G. Edge and Professor Goustave Roussy.

indication that the *Homo mediterraneus* seemed to be more cancer-prone than the *Homo alpinus*. They blamed their relatively unconvincing work on the inadequacy of data on cancer mortality and on the distribution of racial traits in Europe, and they recommended that collection of this type of data should be reinforced, but one just wonders if better data could provide more interesting results.[17]

And when the British statistician Janet Lane-Claypon investigated correlations between family antecedents and the prevalence of breast cancer, she also failed to show statistically meaningful data.[18] The questionnaire for cases of breast cancer and control cases developed by Lane-Claypon included the question, "Is there any information as to other forms of tumour in the family?" For practical reasons—given that people seldom know the cause of death of their grandparents and sometimes lose contact with their siblings—Lane-Claypon concentrated on the causes of the parents' death. The results were inconclusive. They seemed to indicate that there were more deaths from malignancies among the mothers of women with breast cancer than among their fathers, but the difference was not significant and its meaning was unclear. Lane-Claypon notes that "this may, perhaps, be in part accounted for by the fact that there are fewer unknown causes of death among mothers than among fathers. It may be also a small though real difference." She is also careful to point out that the limitations of her data are such, that these results, "are not of nature either to prove or to disprove the inheritability of cancer."[19] Well, this is not much different from what is stated in the editorial that you dislike so much in the Journal of the American Medical Association: there is perhaps some "hereditary influence" in cancer, but we are unable to determine what it is exactly and how to measure it.

MM: What about FAP, Familiar Adenomous Polyposis? Is this also a vague "hereditary influence" on cancer? FAP is a condition in which people have numerous polyps of the rectum. As you probably know, in 1925, Mr. Percy Lockhart-Mummery, the surgeon at St Mark's Hospital in London, published three pedigrees of patients with extensive polyposis, which showed that this condition runs in families, and he suggested that the presence of multiple polyps invariably leads to the development of colon cancer.[20] Unlike many of his colleagues, Lockhart-Mummery does not believe that cancer develops as a result of "irritation" or "trauma." He affirms that cancer is always the result of a mutation. His studies of FAP also led him to the conclusion that a second mutation may be needed to transform a simple tumour—in the case of FAP, an adenomatous polyp—into a malignant one.[21] In the end, he established an FAP registry, which records pedigrees of families with this disease.[22] Here we have, beyond any possible doubt, true Mendelian inheritance of cancer!

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17 Alfredo Niceforo and Eugène Pittard. *Considerations Regarding the Possible Relationships of Cancer to Race, Based on Study of Anthropological and Medical Statistics of Certain European Countries*. Geneva: Publications of the League of Nations 1928.

18 Janet Lane-Claypon. *A Further Report on the Cancer of the Breast with Special Reference to Its Associated Antecedent Conditions.* Reports on Public Health and Medical Subjects. N°32. London: Ministry of Health 1926.

19 Lane-Claypon. *A Further Report on the Cancer of the Breast.* pp. 61-62.

20 John Percy Lockhart- Mummery. "Cancer and Heredity." *Lancet.* 1925. i. pp. 427-429.

21 John Percy Lockhart-Mummery. Leaflet. *The Origin of Tumours.* London: John Bale Sons & Danielson 1932; John Percey Lockhart-Mummery, C.E. Dukes & M.D. Edin. "Familiar Adenomatosis of Colon and Rectum." *The Lancet.* 1939. ii. pp. 586-587.

AI: I do not deny that FAP is a truly "Mendelian" condition. But how many people have FAP, compared with the number of people who suffer from non-hereditary cancer of the colon? The FAP story reminds me of Lionel Penrose's investigation of the role of heredity in mental disease. His study, the Colchester Survey, aimed at a quantitative evaluation of the incidence of inherited mental deficiency among the inmate population at the Colchester asylum.[23] The study comprised two parts. First, Penrose examined the inmates, reporting on both their clinical and psychiatric status. Second, Penrose and his co-workers visited the inmates' families, supplementing, whenever possible, the Colchester data with clinical and intelligence testing of the parents. The IQ testing provided a continuous scale, from mild to severe deficiency, while the clinical examination provided data on the prevalence of specific pathologies such as mongolism, Huntington's chorea, dystrophies of endocrine origins, etc. In the final report of the study, Penrose stressed the fact that very few mental disorders, including "mongolism," followed a Mendelian pattern of transmission.[24] Only one condition, phenylketonuria, followed this pattern, but Penrose was aware of the fact that this was a rare disease, a medical curiosity rather than a public-health problem.[25] Even a dedicated student of Mendelian heredity like Penrose has had to acknowledge that while a "pure" Mendelian transmission of pathological traits can be observed in a handful of rare pathologies, for the majority of diseases these traits are hopelessly intermingled with other variables.

In short, we clinicians are not opposed to the idea that some diseases may be transmitted according to a Mendelian pattern. We simply do not believe that the study of such patterns is very relevant to our daily practice. Human diseases are very complex phenomena, and so are the vertical transmission of parental traits and the distribution of diseases among populations. We are quite pleased that scientists study the role of Mendelian factors in laboratory animals and in experimental diseases. It is surely a worthy endeavour that will enhance human knowledge, as do astronomy, botany or Egyptology, but we are not convinced that these studies are very relevant to what we are trying to accomplish at the bedside.

MM: My dear Professor Influence! You are beautifully eloquent, as the members of your profession often are. Your success as a clinician depends as much, and sometimes more, on your rhetoric and bedside manners than on sound science. But, alas, you belong to a dying breed. Medicine is inexorably being transformed into an experimental science. In half a century or so, all diseases will be defined in genetic terms and medical science will be grounded on studies of Mendelian factors.

AI: My dear Miss Mauser! You are entirely wrong. It is your approach that is condemned to become irrelevant, at least in medicine. You and your colleagues will perhaps be able to breed

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22 Paolo Palladino. "Speculations on Cancer-free Babies: Surgery and Genetics at St Mark's Hospital, 1924-1995." In Jean Paul Gaudillière and Ilana Löwy (eds.). *Heredity and Infection. Historical Essays on the Transmission of Human Diseases.* London and New York: Routledge 2001. pp. 285-310.

23 Daniel Kevles. *In the Name of Eugenics*. Berkeley: University of California Press 1985; J-P Gaudillière. "Le syndrome nataliste. Eugénisme, médecine et hérédité en France et en Grande-Bretagne." In J. Gayon (ed.). *L'éternel retour de l'eugénisme*. Paris: PUF 2006.

24 Lionel Penrose. *A Clinical and Genetic Study of 1280 Cases of Mental Defect*. Penrose Papers. University College London 59/2.

25 Lionel Penrose. *Lancet*. 1935. vol. 1, p. 23 and vol. 2, p. 192.

thousands of mice, test their susceptibility to numerous diseases and perhaps even cure some of these animals – but this will not bring you any closer to efficient cures for human diseases. Some day, scientists will move beyond the simplistic concept of Mendelian factors and will find more sophisticated ways of understanding biological and pathological phenomena.

MM: I wish I could live to 2006, when it will surely be obvious which one of us is right today!
AI: I wish I could live to 2006, when it will surely be obvious which one of us is right today!

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Heredity without Mendelism: Theory and Practice of Dairy Cattle Breeding in the Netherlands 1900-1950[1]

Bert Theunissen

Introduction

In the 1940s and 1950s, Dutch geneticists and animal husbandry specialists repeatedly criticised the practices of dairy cattle breeders. The romantic idea that breeding was an art rather than a science seemed ineradicable, the experts lamented. Some breeders might even be accused of breeding for fancy rather than for utility. Particularly the top breeders seemed virtually oblivious of the fact that dairying was an economic activity and that the productivity of dairy cattle should come first.

To bolster their claims, the experts pointed to the dominant role that conformation shows still played in assessing the value of breeding stock, despite the availability of more scientific methods for evaluating the animals' qualities. Herd-book inspectors, breeders and farmers alike still judged the hereditary potential of a young bull on the basis of phenotypic characteristics. Now in pig breeding, for instance, where the objective was the production of pork, judging a boar on the basis of its weight and conformation made sense, for the animal's outward appearance might indeed provide an indication of its economically valuable hereditary qualities. Breeding dairy cows however was a different matter. Although there was a clear difference in conformation between dairy cows and cows bred for beef production, correlation studies had shown that most individual details of conformation in dairy cows were unrelated to their milk yield. In the case of bulls, the breeders' preoccupation with their phenotype was even more questionable. It was not their looks that mattered, but their daughters' milk yield. An objective verdict on the qualities of breeding stock could only be obtained by progeny testing: the best animals, bulls as well as cows, were those that produced the most productive offspring.

What was even worse, the scientists continued, was that many breeders seemed to be on the wrong track altogether in their choice of sires and dams. Despite their claims of being able to 'see' an animal's qualities in its conformation, objective data from the milk recording services showed that milk yields had hardly increased over the last ten to fifteen years. The bulls and cows themselves, however, as the records of the herd-books showed, had definitely changed: they had become smaller, deeper, more short-legged and beefier. True, the Dutch dairy cows were a double purpose breed, producing milk and meat, but the greater part of the profit came from the milk, and the breeders were clearly overemphasizing their animals' disposition for meat production. Considering the many prizes such stocky animals were awarded at shows, it seemed that breeders were unwittingly turning the Dutch dairy cow into a fancy breed unfit for its main economic purpose.

It was high time, the scientists concluded, that fashion and fancy gave way to utility and rationality. Particularly the selection of bulls had to change, since the bull was half the herd, as the

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[1] A more extensive version of this paper will be published in the Journal of the History of Biology.

saying went. Bulls should be subjected to progeny testing, and only proven bulls should be widely used as sires. Only then would breeding become a rational practice.[2]

Frustrated as they may have been about what they perceived as the conservatism of the breeders, the scientific experts knew that, in the 1950s, the tide was already turning and that a reform of breeding in the sense they envisaged was on the way. In the following decades scientists were to acquire a key role in the business of cattle breeding. Progeny testing did indeed become standard practice, and the influence of conformation shows dwindled steadily. Bull shows, once the culminating points of the perpetual competition among the breeders, were eventually even abolished. While breeders began to lose their influence, the involvement of scientists increased. They worked out a system for progeny testing and helped making the plans for its implementation, which involved a drastic reorganisation of the plethora of organisations and institutions in the field of dairy farming and stock breeding. They also developed the statistical means to judge and rank bulls according to merit, and came up with an index for the exact economic profit to be expected from using a given bull as a sire.[3]

The story of how scientists acquired a leading role in dairy cattle breeding is a fascinating one, but my intention in evoking their views of traditional breeding methods was to put a different set of questions in perspective that I would like to explore in this paper. To begin with, Dutch scientists had been claiming already since the beginning of the twentieth century that only progeny testing provided a rational basis for breeding. Why was it that this seemingly simple and sound advice was apparently not heeded by breeders for so long? And what breeding methods did they use then? As indicated, scientists in the 1940s and 1950s disputed the economic effectiveness of breeders' practices. What were the breeders' views in this matter? Why, for instance, would they prefer animals whose conformation seemed to have an adverse effect on their productivity? Finally, Mendelism had been around for more than half a century before Dutch geneticists became seriously involved in practical cattle breeding, which raises the question of what the relation between geneticists and breeders had been in the pre-war period. And what was it that conditioned the change in this relationship after the war?

Questions of this kind, that broadly speaking concern the relation between theory and practice in agriculture, are receiving increasing attention from historians of plant breeding, as a recent thematic issue of the *Journal of the History of Biology* has underlined.[4] Studies by, among others, Barbara Kimmelman, Paolo Palladino, Jonathan Harwood, Christoph Bonneuil and Thomas Wieland have shown that the role of hereditary theory in plant breeding practices in the early twentieth century was much more complex than was suggested by an earlier historiography that described the reception of Mendelism by practical workers in terms of either 'successful

2 Already in 1927 and 1928, dairy adviser C. Zwagerman had published a series of articles that foreshadowed parts of the later critique of breeders' practices. Several other articles appeared in the 1930s, but the criticism only gathered steam in the 1940s. I will mention only a few characteristic examples: Zwagerman (1927, 1928); Hagedoorn (1928); Zwagerman (1934); Bosman (1935); Hagedoorn (1939); Hagedoorn (1941); de Jong (1943); de Jong (1947); van der Plank (1948); van der Plank and Hirschfeld (1950); Hoekstra (1957); de Groot and Bekedam (1957); Hoekstra (1958).

3 General histories of dairy cattle breeding in the Netherlands that describe this development are Strikwerda (1998) and Bieleman (2000).

4 'Special Issue on Biology and Agriculture,' *Journal of the History of Biology* 39/2 (2006), with contributions by Jonathan Harwood, Barbara Kimmelman, Christoph Bonneuil, Thomas Wieland, Karin Matchett and Lloyd T. Ackert.

application' or 'failed assimilation' of its principles.[5] Historical studies of animal breeding are still very scarce.[6] Yet investigations of livestock breeding provide opportunities for instructive comparison, as I hope my analysis of cattle breeding will demonstrate. One of my conclusions will be that Mendelism was, for all practical purposes, irrelevant for pre-war Dutch cattle breeders, and that even scientists in this period agreed with this assessment.[7]

My example here will be the breeding of Friesian black and white dairy cows in the Netherlands. In the course of the twentieth century Dutch Friesians became the principal type of dairy cattle worldwide. The foundational stock of the American Holsteins, some 7500 animals, were imported from The Netherlands in the late nineteenth century as Dutch Friesians.[8] (Their having become known as Holsteins, soon after their arrival, seems to have been due to an inattentive American government official). In the United States and in Canada, the Friesians were valued for their high milk yield, and they were bred as a pure dairy type, mainly producing milk for consumption. In most European countries however the double purpose cow was preferred, producing meat and milk, as farmland was too expensive in Europe for the extensive land use required for raising beef cattle. After the breeding of Friesians in America had gathered steam, the U.S. and Canada on the one hand and several western European countries on the other became competitors on the world market for Friesians. In the end, the post-war trend towards specialisation would give the American pure dairy type a decisive edge: from the late 1960s onwards, a worldwide 'Holsteinisation' took place. Ironically, Dutch farmers nowadays also call their black and whites 'Holsteins.'

Until the middle of the twentieth century, Dutch breeders of Friesians were among the leading promoters of the European double purpose type. They unabashedly marketed their animals as the world's best dairy cows—a somewhat arbitrary qualification since even farmers in different European countries not unusually preferred a slightly different balance between meat and milk production. Still, Dutch dairy cows had an excellent reputation. They had the highest average milk yield in Europe and were valued for their harmonious and uniform conformation as well as for their adaptability to different climates and management regimes. Black and white breeding stock found its way to many countries in Europe, America, Asia, Africa and Australia.[9]

Dutch farmers also did well in terms of the organisation of breeding: participation in herd-book registration and in breeding and milk recording associations was exceptionally high.[10] Developments in other countries were scrutinised in journals issued by the herd-books and in agricultural and dairy industry periodicals. Germany had more scientists working on breeding problems before the war, Scandinavian scientists were quicker to get a grip on practical breeding, and the quantitative genetics underlying the reform of progeny testing after the war was mainly

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5 For references, see the contributions mentioned in note 3.

6 See for instance Russell (1986); Cooke (1997); Wood and Orel (2001); Derry (2003); Orland (2003); Wood and Orel (2005).

7 It should be added, however, that quite different circumstances conditioned poultry and pig breeding practices, for instance, so that more work is required to obtain a general understanding of the impact of Mendelism on animal breeding.

8 For the history of the Dutch black and whites in America, see for instance Prescott and Price (1930); Mansfield (1985).

9 Grothe (1993).

10 Strikwerda (1998: 192).

worked out by American scientists, Jay Lush prominent among them.[11] Yet all in all, it can safely be said that the Dutch case provides an illustrative example of European breeding practices before the advent of systematic progeny testing.

Type and tuberculosis

Returning to the criticism leveled at the Dutch breeders by agricultural experts in the 1940s and 1950s, the first issue I shall address is the change in type that scientists worried about. While it seemed obvious to them that smallness and beefiness were undesirable in a dairy breed, most experts, then and in later years, seemed to have all but forgotten why Friesians had become so small and stocky over the years. For instance it was suggested (without supporting evidence) that smaller cows, while producing less, had been easier to maintain in the years of crisis before the war.[12] Wieger de Jong, professor of animal husbandry at Wageningen Agricultural College (the only institution of its kind in the Netherlands) argued more plausibly that the decrease in size was a side effect of breeding for shows. In terms of procreation, the fate of a bull was decided on at an early age. Animals that matured early, i.e. acquired adult proportions rapidly and fattened easily, were preferred by herd-book inspectors and judges at bull shows, according to de Jong. As it happened, such qualities were more often found in relatively small bulls than in larger ones, which looked rather gawky in their younger years. Since small bulls won the prizes at shows, de Jong concluded, they had been systematically preferred as sires, which in the long run had resulted in a decrease in size of the breed as a whole.[13]

But then, one might ask, why should inspectors and judges prefer stocky animals in the first place, instead of the tall and lean dairy type that had characterised the Friesian breed in the late nineteenth century? Most scientists entertained no doubts about the answer to this question: fashion and fancy breeding must have been responsible.[14] Yet pre-war records show that there was more to the change in type than scientists in the 1950s seemed to remember. Some background information is needed here.

Until the middle of the nineteenth century, most regions in the Netherlands had had their own local type of dairy cows. Friesian black and whites were mainly to be found in the sea provinces in the north and west. Yet by the 1890s, black and whites began to replace the local breeds in regions in the south and east. The main reason for this was an increase in profitability of animal husbandry, which had started after the liberalisation of the export markets in many European countries around the middle of the century. The trend of focussing on animal husbandry was facilitated by the improving means of transportation, and it was reinforced by the sharp drop of grain prices in the 1880s, when American grains flooded the world market. Towards the end of the century, farmers on the many small mixed farms in the east and south of the Netherlands by and large concentrated their activities on the production of milk, meat (beef and pork) and eggs. Their

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11 In the Netherlands, facilities for scientific breeding experiments with cattle would become available only after the war. See de Boer and Strikwerda (1990: 11).
12 Stapel (1988: 42, 67).
13 De Jong (1943: 116); de Jong (1947: 8-10).
14 See note 1.

arable land was mainly used to produce fodder for their animals. Concentrates also became very cheap and were being fed in increasing quantities. Another major stimulus to dairy farming was the establishment of cooperative dairy factories. The creameries lifted a major restraint on the growth of dairy farms in that they solved the farmers' problem of finding an outlet for their milk. While the number of dairy cows had been more or less stationary until the 1880s, their number rose from some 900.000 in 1890 to about 1.3 million in 1930.[15]

Meanwhile, partly as a consequence of the crisis of the 1880s, the government gave up its nineteenth-century *laissez-faire* attitude with regard to agriculture and began to stimulate and support the improvement of breeding practices. Local and regional milk recording and breeding associations were established in quick succession. Engineers from Wageningen Agricultural College were appointed to act as advisers of these associations and to develop educational programs for the farmers. The herd-books expanded their activities from the mere registration of true-bred animals to the improvement of breeding practices. Finally, more and more creameries, following the example set by dairy factories in Friesland, provided an incentive by paying the farmers for their milk on the basis of its butterfat content. The percentage of butterfat turned out to be heritable and less dependent on environmental circumstances than milk yield, thus providing an excellent opportunity for selection.[16]

The pages of agricultural newspapers and weeklies such as *Het Friesch Landbouwblad, Het Landbouw Nieuwsblad, De Veldbode* and *De Veldpost* testify to the growing importance attached to dairy cattle breeding after 1900.[17] Agricultural journalists, academic scientists and government breeding advisers regularly exchanged views on the aims and methods of breeding in such journals, and more and more reports appeared on conformation shows and on the accomplishments of breeding associations and individual breeders. The keen interest taken in the subject by the dairy farmers themselves can be gleaned from the exchanges in the questions and answers section of weeklies such as *De Veldbode* and *De Veldpost*.

As a consequence of these developments, good breeding stock and particularly good bulls were in high demand in the early twentieth century. The most productive black and whites were traditionally to be found on the specialised dairy farms that exploited the vast natural pastures of the northern and western clay provinces, mainly Friesland and North-Holland, so one would expect the breeders in these regions to have experienced a golden age. They did not do quite as well as expected, however.

In the late nineteenth century, the black and whites in Friesland and North Holland were big, gaunt, leggy, sharp-backed, narrow-chested and ewe-necked animals (fig. 1). 'All milk, skin and bone,' as a British commentator put it.[18] They were milking machines indeed and it was precisely for this reason that thousands of Friesians from these provinces were exported as breeding stock in these decades. Most experts and farmers in the Netherlands however were agreed that Friesians

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15 Broekema (1913); Knibbe (1993); van Zanden (1985).

16 For the development of cattle breeding organisations in the Netherlands see for instance Löhnis (1911); Tukker (1924); van Adrichem Boogaert (1970).

17 I will refer mainly to *De Veldbode*, a widely read weekly established in 1903 that continued to appeared during the whole period under investigation and that reported on all important events and dicussions related to cattle breeding. Its full title was *De Veldbode, Geïllustreerd Weekblad voor Land- en Tuinbouw, Pluimvee- en Konijnenfokkerij en Bijenteelt.*

18 Stanford (1956: 61).

could only be profitably exploited on the fertile soils in the sea provinces. These highly productive cows were delicate and demanded high quality food and careful management. This was no new insight. Already in the seventeenth and eighteenth century German buyers, for instance, had learned the hard way that Dutch dairy cattle were difficult to maintain. In the Berlin area the Friesians were for this reason taken care of by Dutch immigrant farmers.[19]

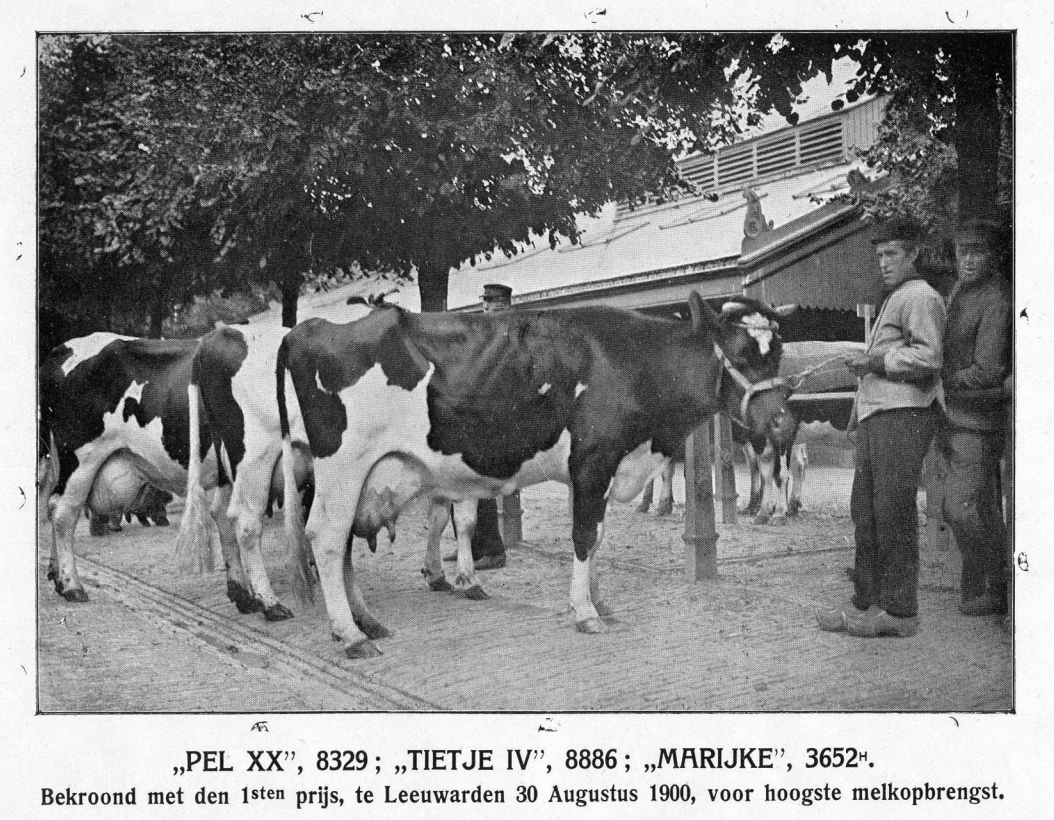

Figure 1. Friesian black and whites of the pure dairy type in 1900. Source: K.N. Kuperus & Zonen, Eenige mededeelingen over den uitvoer van Frieschstamboekvee (Leeuwarden 1912), p. 30.

In the Netherlands, it was contended, the mixed farms on the sandy soils in the east and south provided an environment that was no less 'foreign' to Friesians. Farmers in these regions could not provide the quality foodstuffs required, and they had neither the means nor the time to provide the care the animals needed. Under such less than optimal circumstances Friesian black and whites were said to become weedy. After a few generations, they were no longer better milk producers than the local breed. Friesians had been bred exclusively for production, wrote herd-book-inspector Iman van den Bosch, one of the most respected experts of the time. This had affected their constitution, and thus they demonstrated the wrong-headedness of the much discussed 'Zucht nach Leistung' (selection for production), propagated by the German agriculturist Emil Pott.[20] H.M. Kroon, zootechnical expert of Utrecht Veterinary College, agreed that Friesians ran

[19] Orland (2003: 173-174). Eighteenth-century sheep breeders were also familiar with the problems involved in maintaining foreign breeds; see Wood and Orel (2001: 45-46, *passim*).

the risk of becoming so 'overbred' that their functionality was jeopardised. A government report on the improvement of animal breeding similarly warned against the risks of one-sided breeding for production.[21]

The most damaging allegation of all was that Friesians, if not taken proper care of, were highly susceptible to tuberculosis, a widespread disease among dairy cattle at the time, but one that particularly affected the reputation of the Friesians. A German visitor at a national show remarked that if the conformation of Friesian cattle was not enough to make one suspicious, the constant coughing that could be heard in their stables would not fail to do so.[22] According to veterinarian A. van Leeuwen, German experts even considered Dutch cattle to be the most severely afflicted with tuberculosis word-wide, and Belgian buyers also complained that Friesians were unfit for their soils and often fell victim to the disease.[23] In many regions of the Netherlands black and whites from Friesland came to be held in bad repute too. Seemingly healthy Friesian breeding stock was claimed to 'degenerate' in other provinces and then to succumb to T.B. Veterinarians compared the fine-skinned and weedy dairy type to the tuberculosis-prone 'habitus phthisicus' in humans, characterised by a weak frame and an almost translucent complexion.[24] There was wide agreement that the delicacy and extreme level of performance of the Friesians made them particularly vulnerable.[25]

A considerable group of farmers on the sandy soils therefore preferred dairying with the Dutch red and white cow, the traditional cattle of the regions along the major rivers, the Meuse, Rhine and IJssel, for short called MRIJ-cattle. These red and whites were more robust and sober, and thus better suited for the circumstances on small mixed farms. Their milk yield was not as high as that of the Friesians, yet they were better meat producers: they could be fattened more easily and the quality of their meat was better. Last but not least, they were claimed to be less susceptible to tuberculosis.[26]

A second alternative preferred by farmers outside the MRIJ-regions, was a more robust type of black and whites, to be found in the provinces of Groningen and South Holland, where thanks to the availability of agricultural waste products fattening had traditionally been more important than in Friesland, resulting in a preference for heavier animals. Like MRIJ-cattle, cows of this type were believed to be less susceptible to tuberculosis than Friesians. In the 1910s and 1920s, a group

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20 Van den Bosch (1906). Pott developed his views in reaction to what was then called 'Formalismus,' i.e., selection for phenotypic traits with no demonstrable relation to production; see Pott (1899); Comberg (1984: 122, 336-339).

21 Kroon (1913: 95-99); Löhnis (1911: 28, 46). In the decades after 1900, animal husbandry specialists A.A. ter Haar, A. van Leeuwen and E. van Muilwijk constantly warned readers of *De Veldbode* not to be misled by the high milk yields that Friesian farmers were able to obtain on their rich soils. Wageningen experts concurred with this view; see for instance de Jong and Koenen (1923). Animal husbandry textbooks contained the same message; see for instance Broekema (1913: 16); Kok (1919: 76); Dommerhold (1927: 10, 14-17).

22 Ter Haar (1913).

23 Van Leeuwen (1905); van Leeuwen (1923).

24 Abbo-Tilstra (2002: 27, 146-147, 201).

25 As in the case of their shortcomings in conformation, the susceptibility of Friesians to tuberculosis was pointed out time and again in agricultural journals and handbooks in the early decades of the twentieth century; see for instance Kroon (1913: 97); Bakker c.s. (1914: 133); Timmermans (1923: 12); van Leeuwen (1924); Dommerhold (1927: 10); van Leeuwen (1931).

26 See for instance ter Haar (1919); ter Haar (1923); Kroon (1913: 107).

of breeders of this type in Hoornaar in South Holland offered serious competition to the Friesian breeders of black and whites. The provincial rivalry sparked by this competition can be gleaned from the articles that one of the type's promoters, agricultural journalist E. van Muilwijk, published in *De Veldbode*. He wrote, for example, that breeders in South Holland should beware of breeding with the effeminate aristocratic bulls from Friesland. For within a few generations, tuberculosis-prone, spiky offspring with a miserable constitution would be the result.[27] Animal husbandry adviser Jacq. Timmermans dared his readers to name a single Friesian bull that had done well in the southern province of Limburg. Imported Hoornaar bulls, on the other hand, had almost without exception improved the local breed in this province.[28]

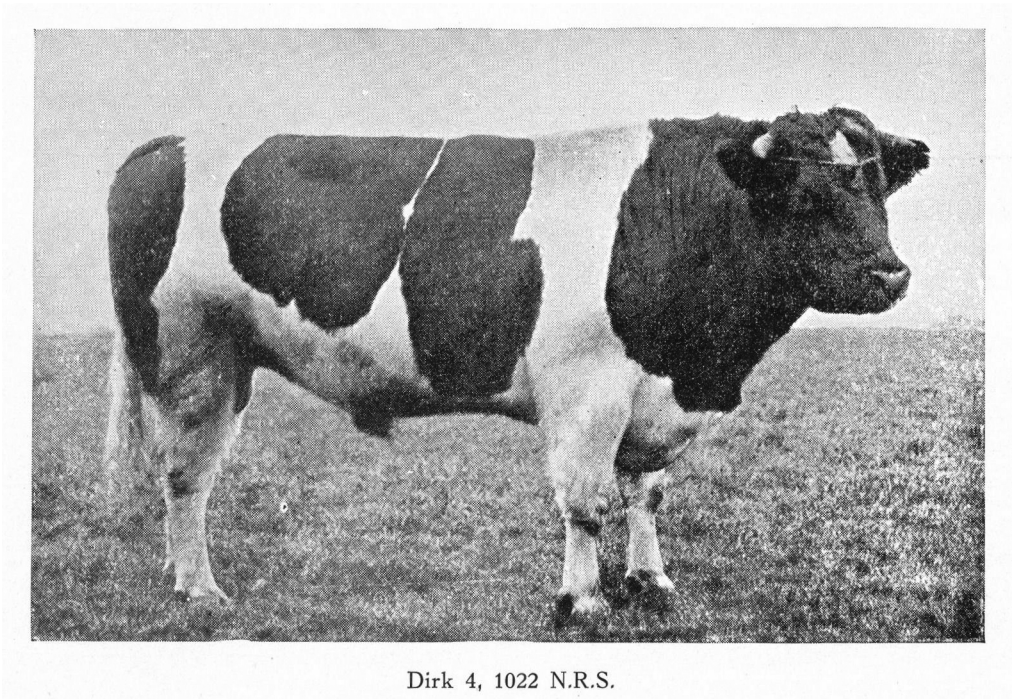

Figure 2. Dirk 4, representative of a more robust type of black and whites. Source: E. van Muilwijk, De preferente zwartbonte N.R.S.-stieren (Den Haag 1937), p. 83.

Figure 2 shows the most famous bull of the Hoornaar type: Dirk IV. For years, particularly in the late 1910s and 1920s, he and his male offspring were considered to represent the ideal type of sire for dairy farmers on the lighter soils. The fact that milk yields were lower than in Friesians was acknowledged but accepted as the price to be paid for a healthy breed. On a more general level herd-book-inspector Iman van den Bosch had argued already in 1906 that it was better to aim for reasonable milk yields with a high butterfat percentage than to strive for record yields of blue milk. Foreigners, he said, preferred milky cows with a sound conformation; cows that literally produced milk like water were undesirable.[29] He had a point: English farmers in the 1910s and 1920s

[27] Van Muilwijk (1919); van Muilwijk (1925). Together with veterinarian A. van Leeuwen, van Muilwijk promoted the Hoornaar type in *De Veldbode* for years.
[28] Timmermans (1919).
[29] Van den Bosch (1906: 597-598).

described the Friesians as an 'irrigation breed' and as 'mere water carts.'[30] And most German breeders, according to C. Kronacher, a leading German expert, preferred animals that were more solidly built than the Friesian black and whites.[31]

Nevertheless, the 'Dirk IV' bloodline became less popular in the 1930s, probably because farmers became dissatisfied with the - by then - even less than mediocre milk yield of this type of cow. The most important reason for its dwindling popularity however was that the Friesian breeders of black and whites made a spectacular comeback in these years. They had taken the criticism of their type to heart and had been working to improve it since the 1900s. In the 1920s, Friesian farmers also began a vigorous campaign to eradicate tuberculosis among their animals. With the help of the Friesian black and white herd-book, the cooperative creameries and other provincial organisations, the first provincial animal health service in the Netherlands was established in Friesland in 1919. Other provinces would follow suit only after World War Two. As a result, the black and whites in Friesland would be the first to be declared free from tuberculosis in 1950.[32]

A culmination point of the Friesian breeders' efforts to improve their black and whites was the bull Adema 197, born in 1934 and bred by the reputed Knol brothers in the hamlet of Hartwerd. In the eyes of the cognoscenti this animal was the most glorious Friesian bull ever bred until then. Adema 197 was claimed to represent a type that adapted more easily to varying circumstances than the original Friesians. He was heavier, deeper, broad- and flat-backed, and more short-legged than his late nineteenth century forebears. Yet contrary to the rather crude Dirk IV, he retained the Friesian dairy type in his more elegant lines, supple skin and fine hair. Moreover, Adema 197 exuded 'nobility,' as the breeders called it, a term borrowed from horse-breeding of which no straightforward definition can be given. It was used by breeders to denote the extra phenotypic quality or beauty, to be appreciated only by the connoisseur, that distinguished the pick of the breed from animals that were merely phenotypically correct according to the standard of the breed. In the fifties, the significance of the term would give rise to extensive discussions in the herd-book journals. Yet whether it was a useful notion or not, no conformation expert would deny that Adema 197 was an icon of nobility.

As to his production qualities, it turned out that Adema 197's daughters' milk yield was 'satisfactory,' while the milk had a high butterfat percentage. All in all, he thus represented the almost perfect bull according to pre-war criteria. As a foundational bull for what came to be called the 'modern Friesian,' he was the most influential Friesian sire for several decades. In the 1950s, there were few true-bred Friesian sires who did not have Adema 197 in their pedigree at least once.[33]

The modern Friesians, with Adema 197 as their harbinger, restored the breeders in Friesland to the leading position they had had at the end of the nineteenth century. In the fifties they even experienced the heyday of their fame, nationally and internationally. The Friesian herd-book flourished, the small circle of top breeders enjoyed an enormous prestige and their animals were much sought after and were sold for high prices. The five-yearly jubilee shows organised by the herd-book were events that attracted an international audience.[34] Foreign buyers were

30 Stanford (1956: 50).
31 Anon. (1928).
32 Abbo-Tilstra (2002: 330).
33 Strikwerda (1998: 96); Strikwerda (1979: 317-333).

particularly impressed by the uniformity of the Friesian black and whites. They knew that the breeders gave priority to quality of conformation: in Holland, 'high milk yields [are] not sought,' a British herd-book official even stated categorically.[35]

Two other factors contributed to the success of the Friesian black and whites. After Friesland had set the example, bovine tuberculosis was eradicated in all Dutch provinces by the mid-1950s.[36] Secondly, the differences in fertility between the heavier and lighter soils in the Netherlands no longer obtained in the 1950s as a consequence of the use of artificial fertilisers and improved pasture management techniques.[37] Thus, the major obstacles to the spread of the Friesian type had been removed.

Still, the constitution of their animals continued to be among the breeders' central concerns in the 1950s. It was their job, they argued, to safeguard the health and adaptability of the breed. To be sure, productivity came first for run-of-the-mill dairy farmers' cows, but a different standard was needed for the breeding stock from which these cows were bred. Trade-offs between milk yield and conformation were inevitable, and to strive for uniform and harmoniously built animals was no mere luxury or fancy. A well-bodied cow was an economic cow, and the nobility that distinguished the best breeding stock was to be seen as an extra guarantee for the quality of their progeny.[38]

Against this background it will come as no surprise that breeders and herd-book officials in these years qualified the growing scientific criticism of their allegedly excessive preoccupation with the phenotypical qualities of their animals as out of place. In the breeders' opinion, the commercial success of their modern Friesians alone may have sufficed to justify their view of the matter. For it was precisely for their conformation and uniformity that the Friesians were sought after. Moreover, details of conformation that lent nobility to an animal, whether functionally significant or not, were definitely important financially speaking. An animal's ranking at shows and its score in the herd-book's point system for conformation had direct consequences for its commercial value.[39] For the breeders, beauty was the hallmark of health and adaptability as well as of marketability. And why change a breed that was so obviously successful? 'This can't go on forever,' one of the Knol brothers is said to have admitted, only to add, however, that 'it is what the farmers want.'[40] The animal husbandry director of the ministry of agriculture remarked that while it was impossible to say whether the modern Friesian represented an advance in terms of efficiency of production, it was an undeniable fact that it sold better than the old type.[41]

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34 Strikwerda (1979: 64, 96-97, 253-257).
35 Stanford (1956: 186-187). This is not to say that the 'modern Friesian' was accepted uncritically by foreign breeders. The hereditary qualities of a group of 57 bulls exported to Great Britain in 1950 gave rise to heated discussions among British breeders; see Anon., 1955.
36 Hofman (1996).
37 Accordingly the N.R.S. decided in 1954 that it was no longer necessary to judge female cattle from different soils in separate categories at shows, as had been customary until then; see Anema and Jepma (1960^{10}: 116).
38 See for instance Jepma (1954); Jepma (1957); Anon. (1955); Anon. (1957a); Anon. (1957b); Jepma (1962).
39 Strikwerda (1979: 255).
40 Kroon (1997: 82).
41 Rijssenbeek (1956).

A middle ground in the discussion over breeding practices was taken by Wieger de Jong of Wageningen Agricultural College. De Jong had risen from the ranks in both practical and scientific circles. The son of a dairy farmer and a Wageningen graduate, he had worked as a regional breeding adviser and herd-book inspector before being appointed as director of the Dutch national cattle herd-book, the N.R.S., which serviced all Dutch provinces except Friesland. In 1947 he became Wageningen professor of animal breeding and chairman of the N.R.S.[42] Thus representing different constituencies, de Jong weighed the arguments from both sides against each other.

De Jong pointed to the difficulties inherent in the notion of constitution.[43] Unquestionably, a healthy constitution was important, yet how were constitution and conformation related? Were short legs stronger, did heaviness indicate longevity, were sturdy animals really healthier? Only empirical studies could decide on such matters, he argued, and these had yet to be undertaken. Nevertheless, de Jong sympathised with breeders who strove for beauty in their animals. Breeding for fancy should not be simply condemned. For many farmers, the joy of breeding and even their happiness in life were bound up with their competitive efforts to create the perfect animal. Conformation shows provided the sporting ground to assess the level of their achievements, and not much would remain of the popularity of breeding without such incentives. While de Jong was undoubtedly correct that, for many farmers, breeding was a labour of love, we might add to his observations that, as Margaret Derry has demonstrated, it is quite impossible to separate the breeders' esthetic ideals and their commercial considerations in shaping the perfect animal. Breeding for perfection and breeding for the market went hand in hand.[44]

While sympathetic towards the breeders' concerns, de Jong was no less worried about the productivity of the black and whites than his scientific colleagues. Already in 1943 he had shown that there was no correlation between the scores for conformation that animals were allotted by herd-book-inspectors and their milk yield.[45] Apparently, the methods that the breeders and the herd-books used to evaluate and improve their animals were not conducive to the improvement of the productivity of the breed. Thus the question arises of what the breeders' methods actually consisted in and what the underlying assumptions were.

Bloodlines and purity

In the late nineteenth century, a growing number of dairy farmers in the Netherlands considered themselves to be not merely dairymen, but also breeders. (While not all dairy farmers were breeders, all breeders were also dairymen. Cows were too costly to raise and maintain merely for breeding purposes; their milk constituted an important part of the breeders' income —the greater part, for most of them.[46]) In western Europe, Dutch cows had been well-known for their dairy

[42] Dekker and Stapel (1976: 315-316).
[43] De Jong (1943); de Jong (1947); de Jong (1957).
[44] Derry (2003: 156-161).
[45] De Jong (1943).
[46] Minderhoud (1935: 126).

qualities for centuries, yet breeding became particularly lucrative in the second half of the nineteenth century, when the fame of the black and whites spread world-wide.

The American cattle traders who in the 1870s and 1880s bought thousands of Friesians provided an incentive for organised breeding in the Netherlands in that they stimulated the establishment of herd-books. An American importer, Holstein pioneer Solomon Hoxie, even acted as adviser of the Friesian herd-book founders, and he and several other American buyers became herd-book members.[47] There is a pattern here, as Derry has shown: the establishment of herd-books indicates a rising international market.[48] The guarantees on paper provided by herd-books were especially important for American buyers. Whereas a Dutch farmer would never buy a cow that he had not inspected himself, New World geographical distances necessitated American farmers to rely on catalogues and certified pedigrees.

What pedigrees had to prove, was 'purity' *(zuiverheid*, in Dutch). In the case of Arabian horses, for instance, purity was ascribed only to animals all of whose ancestors descended from horses that had been bred, literally, 'in the desert.' In Shorthorn cattle, purity referred to descent from the breeding stock of a very limited number of British breeders.[49] Likewise, a pedigreed Friesian could be trusted to have descended from black and white ancestors bred in the Netherlands. The Dutch national herd-book (the N.R.S.) was established in 1874 and it registered animals belonging to what was then called the Dutch lowland breed, mainly comprising the black and white Friesian, the red and white MRIJ and the Groningen whitehead (the *blaarkop)*.[50] To enhance the exclusivity of their black and whites, breeders in the province of Friesland established their own herd-book in 1879, the F.R.S. (*Friesch Rundvee-Stamboek*). From then on, black and whites from bloodlines in other provinces were no longer accepted for registration in the Friesian herd-book, irrespective of their characteristics or qualities.[51]

The concept of purity was an ambiguous and contested one.[52] For instance, the nineteenth century notion of constancy of a pure race ('Konstanztheorie') as propagated by the German horse expert Johann Justinus was based on the conviction that purity resided in an inborn potential of a true race to consistently and unchangingly pass on its defining characteristics through the generations, irrespective of the circumstances under which the animals were kept.[53] Many nineteenth-century practical breeders however knew from experience that the purity of their breeds could not be defined in such a strict sense, and Friesian breeders are a case in point. They were only too well aware that the 'purity' of their black and whites needed maintenance even under stable environmental circumstances. This was convincingly demonstrated by the irregular occurrence of red and white calves born from black and white parents. In its early years the Friesian herd-book made no bones about registering such calves and other off-coloured animals.

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47 Strikwerda (1979: 81-86); see also van der Wiel and Zijlstra (2001: 32-35).
48 Derry (2003: 156-161, *passim*). Conversely, around 1900, when the German, English and American markets were being closed for live cattle , the herd-books experienced a serious crisis; see Löhnis (1901).
49 Derry (2003), chapter 2.
50 For a history of the N.R.S., see Dekker and Stapel (1976).
51 Still, although this was later denied by F.R.S. officials, there were a few isolated cases of Friesians born outside Friesland that had, in the early years of the F.R.S., been registered by the herd-book (Strikwerda 1979, 144). For histories of the F.R.S., see Zwart (1960); Strikwerda (1979).
52 Derry (2003: 9, *passim*).
53 Berge (1961: 131-134); Comberg (1984: 106ff); Wood and Orel (2001: 244-246, 264-266).

They would soon be relegated to separate registers, however, to please the American buyers for whom a pure Friesian should be black and white.[54]

Meanwhile, Friesian breeders did believe that their black and whites represented a very old race that had been native to Friesland since prehistoric times.[55] Crossing of different breeds, which was still common in other provinces at the time, was supposed to have been rather the exception in Friesland, and a 'pure' core of Friesians was supposed to have been preserved through the ages. Accordingly, the most stringent requirement for a Friesian to be accepted for registration concerned geographical provenance: the animal should descend from ancestors bred by Friesian breeders. In this way, the notion of purity functioned exactly as intended, namely to protect the interests of breeders in Friesland and their buyers.

As we shall see, geneticists would translate purity into Mendelian terms after 1900, yet the purity concept had connotations of exclusivity and quality that Mendelism could not capture. An example is provided by a veritable *cause célèbre* in Dutch cattle breeding, the so called coloured spots question (*vlekjeskwestie*). In the middle decades of the nineteenth century a number of Shorthorn bulls were imported in the Netherlands from the U.K. Some agricultural experts believed that they might improve the beef quality of Dutch cows. The experiment was soon terminated however, because the milk yields of cross-breds turned out to be disappointingly low. Traces of Shorthorn influence remained visible for some time in the colouration of some herds, but these progressively disappeared when the cross-breds were bred up to the original Dutch type for several generations. The idea took hold, however, among breeders and their customers alike, that isolated coloured spots on the lower legs were an indication of lingering Shorthorn influence and for this reason highly undesirable. Animals with spots on the phalanges were in the 1920s even excluded from registration by the F.R.S.[56]

Until far into the twentieth century agricultural experts and scientists would spill gallons of ink trying to convince the herd-books that excellent animals were for no good reason kept out of breeding programmes in this way. In their view there was no evidence whatsoever that the spots derived from Shorthorns, while, more importantly, a cow's productivity was in no way affected by the presence of such spots.[57] It was to no avail, however. In 1912 the well-known breeder A.D. Groneman conceded that the experts might well be right, yet that breeders had different concerns: buyers, especially foreign traders, wanted pure black and whites, and pure black and whites were not supposed to have spots.[58] The herd-books acted accordingly and did not change their policy. Clearly, purity referred to a breed standard that could not be compromised, irrespective of whether a deviation from the standard was genetically or functionally significant or not. At issue here was not a genotype but a commercial 'brand.'[59]

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54 Strikwerda (1979: 31-36). See also Dekker and Stapel (1976: 256-267).
55 Bakker (1909) contested this view and argued that the original Friesians had been red and whites, the black and whites having been imported from Denmark after the onslaughts of the rinderpest in the eighteenth century.
56 See for instance Strikwerda (1979: 109-116).
57 A. von Leeuwen, for instance, campaigned for years on end against the exclusion of animals with spotted legs in *De Veldbode*. See for instance van Leeuwen (1914).
58 Groneman (1912).
59 Dog and horse breeding provide similar examples; see Derry (2003: 158, *passim*).

In order to maintain the desirable qualities in their herds, breeders employed methods that, as Roger Wood and Vítešlav Orel have recently underlined, had been common practice among experienced breeders since the eighteenth century.[60] Breeders knew that the best strategy to maintain the desirable qualities in their stock was to breed the animals among themselves. In its most strict form, this amounted to inbreeding, which was indeed practised intensively by all experienced breeders of Friesians.[61] Even parent-offspring and sibling matings were not shunned. Adema 197, to give but one example, was the product of a mating between siblings; he had only one grandfather while his grandmothers were related as aunt and niece.[62] Meanwhile, the risks of inbreeding were well-known. Offspring had to be selected carefully and some outbreeding might be unavoidable once in a while. Still, the ideal of uniformity, in the breeders' opinion, could only be reached by close inbreeding. The best breeders created their own 'bloodlines' in this way, and these were considered to buttress the quality of the breed as a whole.[63]

An additional advantage of breeding in bloodlines was that the herds of the top breeders were not only very uniform, but also slightly different between them, as a consequence of minor variations in conformation in each herd that were consolidated through inbreeding. This subtle distinctiveness was a commercial asset, as it enabled the breeders and their customers to recognise the animals from the better herds. For instance, buyers knew that breeders in North Holland produced black and whites of a slightly larger and milkier type than those in Friesland, while breeders in North Holland liked some of the Friesian bloodlines but not others.[64]

An new method for assessing the quality of dairy cows was introduced in the 1890s, after the example of Danish dairy farmers, namely the systematic recording of milk production. Friesland led the way and would remain the province with the highest participation in milk recording. By carefully weighing a cow's milk yield on a regular basis its yearly production could be estimated, and the figures thus obtained could also be used to assess the hereditary quality of the cows' sires. Milk recording included measuring the milk's butterfat content. After Friesian creameries had, again, set the example, farmers in more and more regions of the Netherlands were paid for their milk on the basis of butterfat content. Selection for butterfat content became the primary focus of selection for the breeders in Friesland in particular.[65]

An instrument to raise the interest in the improvement of breeding methods that had been introduced around the middle of the nineteenth century yet that acquired a much more prominent role in the twentieth century, was the organisation of agricultural exhibitions and conformation shows. The increasing number of local, regional and national shows that breeders associations, agricultural organisations and the herd-books organised after 1900 testify to the growing popularity of the breeding of purebreds as well as to the commercial interests behind it. For as already indicated, show prizes earned breeders money: after a successful show, sales of their stock would immediately pick up.

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60 Wood and Orel (2001) chapters 3 and 4.
61 See for instance Hoogland (1921).
62 Strikwerda (1979: 317).
63 Some famous bloodlines were described in monographs; see for instance van Muilwijk (1935).
64 For the history of cattle breeding in North Holland see Kroon (1979); van der Wiel and Zijlstra (2001).
65 Strikwerda (1979: 65-80).

There were several other tools that were employed by breeding organisations and the government to rationalise the farmers' methods to improve their stock. We shall take these in stride in the analysis of the impact of Mendelism on breeding practices.

Mendelism

For Amsterdam botanist Hugo de Vries, one of the 'rediscovers' of the Mendelian theory of heredity, the improvement of plant breeding and agriculture had been the principal motive for investigating hereditary phenomena, and he considered Mendel's laws to be directly relevant for the breeding of agricultural varieties.[66] While the possible implications of Mendelism for agriculture were thus pointed out from the start, Dutch animal husbandry experts were more hesitant in confronting Mendelian genetics with their field. The subject began to receive serious consideration only in the 1910s, when Mendel's rules were explained in several monographs and articles.[67] Even then, the authors took most of their examples from botany. Examples from livestock breeding only involved very simple Mendelian phenomena, mainly relating to coat colour in farm animals.

For example, veterinarian A. van Leeuwen, the stock breeding expert of *De Veldbode*, after having expressed his reservations about the general validity of the theory, inquired among his readership whether anyone had ever bred a black-and-white cow from red-and-white parents. A group of farmers responded that they had never come across such a combination; only a single farmer believed that he had. Van Leeuwen concluded that alternative explanations could not be ruled out, yet that there was indeed support for interpreting the red colour as a Mendelian recessive trait.[68] The presence or absence of horns appeared to fall into the same category, and before long, the more difficult example of coat colour in horses also turned out to be amenable to a Mendelian explanation.

In 1910 geneticist Arend L. Hagedoorn, a pupil of Hugo de Vries and Jacques Loeb, was invited by the Dutch Agricultural Society to assist in designing breeding strategies for the improvement of Texel sheep.[69] Breeders had been hybridising this breed with English races such as the Lincoln and the Wensleydale for several decades. Aiming for a uniform new type, they were struggling to get rid of unwanted fleece, head and nose colours. Hagedoorn helped them by devising breeding schemes along Mendelian lines. Although his efforts were not unsuccessful, the project was discontinued after some time because of the complexity - and consequently the rising costs - of test-mating and culling.[70]

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66 On de Vries, see for instance Stamhuis, Meijer and Zevenhuizen (1999). For the motives underlying his research, see Theunissen (1994).

67 See for instance Hagedoorn (1912); Waardenburg (1913); Giltay (1914); Lotsy (1915); Reimers (1916).

68 Van Leeuwen (1912).

69 Arend Lourens Hagedoorn (1885-1953), animal geneticist and evolutionary theorist, deserves more attention from historians than he has received until now. Basic information on his life and work (in Dutch) can be found in a commemorative issue, published shortly after his death, of the journal of the Dutch Genetics Society, *Erfelijkheid in Praktijk* (1954).

70 Hagedoorn (1911); Kroon (1917: 43).

This example illustrates the problems inherent in the application of a Mendelian approach to livestock breeding as opposed to plant breeding. As Wageningen animal husbandry specialist J. Reimers pointed out in 1916, experimenting with plants was easier because they could be self-fertilised, and seeds and plants were cheap and could easily be obtained as well as dispensed with in large quantities. Individual animals, on the other hand, especially the larger farm animals, represented a significant economic value and produced far less progeny, and therefore the costs of experiments with animals quickly became prohibitive.[71] Deliberately trying to produce even a single—undesirable—red and white calf, for instance, was not something a breeder of Friesians would readily do for experimental reasons, let alone that he could be induced to experiment with several detrimental recessive factors.

Moreover, we have only been discussing qualitative characters so far. The economically most important characters of livestock however, such as milk and meat production, are of the quantitative kind. Even experts who were convinced that such characters could also be explained in Mendelian terms, had to admit that in this case the practical application of Mendelian theory was virtually impossible. According to Reimers a quantitative character such as milk yield might be accounted for by assuming that a group of similar Mendelian factors was responsible for the trait. Yet even if a Mendelian breeding scheme, based on this assumption, could be devised to improve milk yields, the complexity and costs of such a programme presented great difficulties. Hagedoorn remarked that breeders of farm animals, contrary to plant breeders, would learn nothing of practical use from a visit to the Svalöf experiment station in Sweden.[72]

Accordingly, while Hagedoorn would become a well-known expert in animal genetics, he conducted his experiments with small laboratory animals such as mice. As to the economically important animals, he confined his investigations to animals that were inexpensive, could be kept in relatively large numbers and produced reasonable numbers of offspring, such as chicken and, occasionally, rabbits. Hagedoorn entertained no doubts that the rationality or irrationality of traditional cattle breeding methods could be decided on in Mendelian terms. He was well aware however that a Mendelian reform of breeding strategies was an entirely different matter. Little was known about the genetics of quantitative characters, but there were definitely too many genes involved to be handled by simple Mendelian crossing procedures. Consequently, traditional breeding methods would be indispensable for a long time to come. In 1927 Hagedoorn stated that the influence of genetic theory on cattle breeding practices had been negligible, and in his well-known *Animal Breeding* of 1939 he even wrote that the influence had rather been the other way round: geneticists had learned a lot from the best breeders. What geneticists had to offer to the breeders of large farm animals was of a different nature: 'The geneticists' main contribution to animal breeding is not an analysis of genes, but an analysis of breeding methods.[73] This view was widely shared among Dutch animal husbandry experts at the time.[74]

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71 Reimers (1916: 2, 27); see also Hagedoorn (1912: 5-6).
72 Reimers (1916: 27, 37-38, 78); Hagedoorn (1912: 83).
73 Hagedoorn (1927); Hagedoorn (1939: 19).
74 Broekema (1913); van Leeuwen (1923); *Compte-rendu* (1923: 53-58); van Muilwijk (1928); Overbosch and van der Plank (1931). See Derry (2003: 12-13) for a similar assessment with respect to the role of classical genetics in horse and dog breeding.

What did the assistance that geneticists might give according to Hagedoorn consist in? To begin with, geneticists and agricultural experts concurred with the breeders that inbreeding was a rational strategy. The haphazard crossing of breeds that had been customary among small farmers until the late nineteenth century had resulted in motley collections of animals with unpredictable and widely varying qualities.[75] No improvement was possible in this way, and the national herd-book had been right, in 1906, to have formally subdivided the 'Dutch lowland race' into three clearly delineated breeds, the black and white Friesian, the red and white MRIJ and the Groningen whitehead.[76] But even stock improvement within clearly defined breeds remained something of a lottery as long as bulls of different provenance were used every few years. It was much better, the scientists agreed with the top breeders, to start from a group of excellent animals and to consolidate their qualities in a closely inbred herd. Purity, translated into Mendelian terms, meant homozygosity, and inbreeding increased the degree of homozygosity. Therefore, inbreeding was a rational strategy of breed improvement, provided it was accompanied by scrupulous selection against unwanted recessive traits. Experts explicitly advised against needless outbreeding with unrelated animals. Animals imported from other regions might not adapt well to local circumstances —as the example of Friesians deteriorating on poor soil discussed above illustrated. Moreover, a bull from a unrelated herd with a long history of its own was bound to be different, genetically speaking, in many characters. Recombination would bring these differences to the surface in the second generation, and thus the achievements of years of careful inbreeding and selecting might be undone.[77]

At the same time, however, experts also warned breeders not to overestimate the value of pedigrees. Obviously, the productivity of his ancestors should play a role in the choice of a bull. Yet it was of little use to study more than a few generations of an animal's ancestry. From a Mendelian perspective, it was more instructive to look at a bull's brothers and sisters, since they provided more reliable insights into his genetic strengths and weaknesses than remote ancestors whose contributions to his genes was insignificant.[78]

It is difficult to say whether practical breeders took heed of this advice. Yet a cursory survey of herd-book journals and histories of cattle breeding suffices to conclude that where the market for breeding stock was concerned, the preoccupation with pedigrees continued at least as long as inbreeding remained the principal breeding method and as long as a breeder's reputation was inseparably bound up with the reputation of his bloodlines. For instance, until well after World War II items on individual breeders in herd-book-journals invariably included detailed information on the pedigrees of the foundational animals of their herds. The national herd-book published several illustrated genealogies of the most prestigious bloodlines, and a detailed description of bloodlines constituted the *pièce de résistance* of herd-book histories.[79] Knol Bros. even had the history of their stock-farm and bloodlines privately published.[80] Again, pedigree, like

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75 Kroon (1913: 71, 121); Kroon (1917: 24).
76 Van den Bosch (1906).
77 Kroon (1913: 102); Hagedoorn (1912: 57-64); Lotsy (1915: 15-17, 33); Reimers (1916: 95); Bakker (1926); Hagedoorn (1927: 54, 87-95).
78 Reimers (1916: 89); Hagedoorn (1912: 47-48); van der Plank (1940).
79 See notes 46, 49 and 50.
80 Van Popta (1965).

purity, was not merely about genes. Famous ancestors, however remote, continued to lend prestige to their bloodline. In a herd's history resided its quality and distinction. There is an obvious contrast here with the Mendelian interpretation of purity: as soon as a breed becomes pure in Mendelian terms, i.e. homozygous, its history becomes irrelevant. Mendelian breeders may in a sense be said to aim for the elimination of a herd's history.

Another scientific critique of breeders' practices that could frequently be heard, was that the herd-books were more attuned to the breeders' commercial interests than to cattle improvement. Herd-books, it was argued, might serve as invaluable tools. Much might be learned, for instance, about hereditary diseases, if only the herd-books would register all descendants of pedigreed animals and would also record their genetic peculiarities.[81] It takes no stretch of the imagination, however, to realise that breeders could muster up no enthusiasm for such suggestions. Firstly, they were charged for registration of their animals, so they offered only the best ones for inspection.[82] Secondly, for obvious reasons most breeders preferred malformed progeny from their prize-winning animals to disappear without a trace. The herd-books would lose all their members if complete registration became compulsory, an expert admitted.[83] Thus in the pre-war period at least, the-herd books did not develop into the instruments for rational breeding that the scientists would have liked them to become.

By far the most often-heard advice that scientific experts tried to press upon farmers was that rational breeding should be based on progeny testing. Conformation and pedigrees were helpful to find a promising young bull, yet ultimately, it was the performance of his daughters as dairy cows that determined the true value of a sire. Therefore, rational breed improvement required the systematic use of older, tested bulls. From the early years of the twentieth century onwards, experts and animal husbandry advisers tried to drive this message home to the readers of agricultural weeklies and farmers' handbooks. Hagedoorn relentlessly repeated the message in his scientific and popular publications. Ideally, he added, promising bulls should be tested on a limited number of cows first, and only the best ones should then be widely used as sires.[84]

In this case, there is no evidence that the breeders disagreed in principle. Yet again, meeting this demand for rational breeding in practice was a different matter. The ideal situation as sketched by Hagedoorn was impracticable in every respect in the pre-war period. Farms in the Netherlands were small and few farmers milked more than ten cows. For instance, in 1920 the 953 organised farmers in the province of Limburg owned 2990 cows; in the Netherlands as a whole, an average number of ten cows per farm would only be reached in the 1950s.[85] Bulls were costly to maintain, and bull-calves only increased in value until their second or third year. Therefore farmers who could afford a bull of their own as a rule bought a young bull-calf, used it for a year or two and then sold it for slaughtering.[86] Thus by the time their daughters began to give milk and their real worth became apparent, most bulls were dead.

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81 Reimers (1916: 81, 93); Hagedoorn (1912: 48); Hagedoorn (1927: 130-137).
82 In 1940, for instance, the registration costs of an animal were five guilders; a farm hand at the time earned about fifteen guilders a week (Kroon, 1998: 118).
83 *Compte-rendu* (1923: 51-53). See also Wibbens (1923: 306-330).
84 Hagedoorn (1912: 47-48; 86, 88); Hagedoorn (1927: 63). For the early decades of the twentieth century see also, for instance, Reimers (1916: 79, 92-93); Kroon (1913: 99); van Krimpen (1905: 13).
85 Timmermans (1920: 615-616); Strikwerda (1998: 67).
86 See for instance van Leeuwen (1904); Wibbens (1907); Löhnis (1911: 46).

Farmers might also use a sire owned by a breeder for their cows. Yet if distance and the difficulty of transportation did not preclude such an option, it was, more often than not, the prices that breeders charged for insemination that put farmers off. Around 1910, prices varied between 25 cents and 20 guilders, and the reputed breeder F.A.F. Groneman experienced that small farmers were not prepared to pay the 2 guilders he charged for an insemination by his service-bull.[87]

Since the late eighteenth century small farmers in many regions of the Netherlands had traditionally shared a bull purchased with municipal support. There were fine animals among them, yet many poor ones too.[88] After 1890, more and more farmers began to organise themselves in breeding associations which enabled them to buy better bulls. Government premiums helped them to keep the good ones for a longer period.[89] While some of these associations managed to improve their stock in this way, others fared less well and were discontinued after a number of years. There were indeed many obstacles to be overcome: farmers had to agree on the type of bull to be purchased; after several years of use, father-daughter inbreeding became unavoidable; a shared bull might spread venereal diseases; older bulls might become dangerous or too fat to perform; and the progeny of even an expensive bull could turn out to be disappointing.[90] On the other hand, once a breeding association had acquired a certain reputation, farmers might be tempted to buy their own bull and start their own stock-farm to get a share in the breeding market.[91]

Besides such complications, the number of cows serviced by a bull exploited by a breeding association was still relatively small, and a reliable assessment of his productive qualities was in most cases only possible after his death. Most bulls that, after a thorough investigation of their offspring, earned the much-coveted title of *preferentschap*, indicating proven hereditary excellence, were no longer around to receive the honours or were at best near the end of their period of service.[92] The ideal situation as envisaged by Hagedoorn and his scientific colleagues, in which a number of young bulls was tested before the best of them—by that time having reached the age of at least five or six—seriously began their tour of duty, was beyond the means, financially and practically, of even the most prosperous breeding associations. In 1941, after Hagedoorn had in a lecture once again underlined the importance of systematic progeny testing, N.R.S. chairman H.W. Kuhn responded that Hagedoorn was apparently ignorant of practical cattle breeding: breeders could not possibly implement such a system, for both practical and economic reasons.[93] And animal husbandry adviser R.G. Anema predicted that current practices would probably not change for a hundred years to come.[94]

Kuhn's was a correct assessment of the pre-war situation, yet as to the future he and Anema soon turned out to have been too pessimistic. Progeny testing would become feasible within a few years, after the introduction of artificial insemination in the early 1940s. Interestingly, AI was initially developed to fight venereal diseases causing infertility and spontaneous abortions, which

87 Löhnis (1911: 46); Groneman (1956: 37).
88 Van der Wiel en Zijlstra (2001: 57-61).
89 Löhnis (1911: 3); van Adrichem Boogaert (1970: 303-305).
90 Nobel (1912: 10-11); van der Wiel en Zijlstra (2001: 99-109, 145-146).
91 This happened in North Holland, for instance; see Van der Wiel en Zijlstra (2001: 146).
92 Strikwerda (1998: 114).
93 Hagedoorn (1941); Kuhn (1941).
94 Anon. (1941).

were rampant in the inter-war years, but scientists were quick to realize the potential of AI as an enabling technology for progeny testing. AI opened up the possibility to test a young bull on hundreds of cows at the same time. Years were thus taken off the time formerly needed to assess his hereditary qualities. Further, AI enabled the use of proven sires on an unprecedented scale, and consequently far less bulls were needed than before. This implied a switch from breeding in bloodlines to breeding in populations, which in turn required drastic changes in the organisational structure of dairy cattle breeding. In the process, scientists were to take the lead in breeding matters, while the breeders were slowly but surely relegated to the side-line.[95]

This transformation did not take place overnight—it took several decades. In the 1950s, when the 'modern Friesian' was at the height of its popularity, the breeders, particularly those in Friesland, held on to their breeding methods and to their convictions about the ideal Friesian type. This was not merely because of the obvious threat that AI posed to the market for bulls, but also, as indicated, because breeders opposed the exclusive focus on milk yield that in their view was part and parcel of the scientists' pleas for systematic progeny testing. In due course, however, postwar economic pressures forced farmers to scale up, intensify and specialise their farms, and as a consequence the traditional double purpose cow lost more and more ground to the specialised dairy type.[96] This played into the scientists' hands, since the changeover to the pure dairy type favoured bulls that had been tested for high yields. Eventually, in the 1970s and 1980s, the trend towards specialisation would even lead to the demise of the Friesian black and whites and their replacement by their American relatives, the Holsteins, which had been bred purely for production since the 1880s and had left their European ancestors far behind in terms of milk yield.

The details of these postwar developments are beyond the scope of this paper. Here I have merely mentioned them to indicate the context of the scientists' criticism of breeding practices in the 1950s. Circumstances were changing rapidly in those years, and in their campaign for a new approach to cattle breeding scientists all but ignored the conditions on which breeding methods up till then had been predicated. We can now draw some conclusions with respect to what these pre-war methods entailed and how they related to Mendelian theory.

Discussion and conclusions

By and large, breeders and animal husbandry experts in the pre-war years entertained comparable views on the best methods for breeding dairy cattle, even though some experts became increasingly critical about the relative weight breeders attached to conformation and pedigrees. Where their opinions diverged, commercial considerations on the breeders' part were often involved: market demands were not always 'rational' from the experts' point of view. For instance, while some details of conformation might not be demonstrably relevant for milk yield, they did make a difference on the market for breeding stock. Breeders and experts further agreed that selecting animals purely for production was unwise, since Friesians of the extreme dairy type were difficult to maintain and less resistant to disease, particularly tuberculosis.

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95 On the development of AI in the Netherlands, see Strikwerda (2007).

96 On these postwar economic pressures, see for instance van der Molen and Douw (1975: 9-35).

The breeders' principal method, which consisted in striving for purity by mains of inbreeding and breeding in bloodlines, was deemed perfectly rational by the experts. Progeny testing and the use of proven sires were propagated widely as indispensable for rational breeding, yet most experts were well aware of the limitations that practical realities set to the implementation of this advice. Geneticists generally considered the breeders' methods to be consistent with Mendelian theory. The theory confirmed the rationality of aiming for purity and of inbreeding. At the same time however the experts readily admitted that the Mendelian insights into heredity added little of practical value to what breeders already knew.

The importance of progeny testing was recognised long before the war. It might be added that the basic idea of progeny testing was not a new insight. It was hinted at already in the biblical phrase that 'the tree is known from its fruit,' and some breeders in antiquity were definitely aware that the value of breeding stock was to be gauged from its offspring, as Nicholas Russell has shown.[97] The work of eighteenth century sheep breeders such as Bakewell also reflects this principle. This is not to say that systematic and controlled tests were developed already before the twentieth century; there is no convincing evidence for this, not even in the case of Bakewell and his followers.[98]

On a wide scale, systematic progeny testing became feasible only after the introduction of AI. Mendelism had nothing to do with this. In fact, progeny testing is not predicated on any specific theory of heredity. Besides the availability of AI, its successful implementation after the war rather asked for sophisticated statistical methods than for specific theoretical knowledge about genes or chromosomes and their behaviour. From the late 1950s onwards, breeding methods began to change from breeding in bloodlines to breeding in populations. Accordingly, breeding experts in the Netherlands began to call themselves population geneticists. They should rather have called themselves quantitative geneticists however, since nothing was as yet known of the genes involved in milk production, nor was such knowledge needed for their statistical analyses of milk production through the generations. While these scientists could rightly claim they had taken over the leading role in breeding from the breeders and had turned breeding into a scientific enterprise, the history of classical genetics is of little help in explaining how this came about.

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97 Russell (1986: 25).
98 Russell (1986: 204-205, 211).

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Innovation and Ownership in Living Products: Animals and Fruits in the United States, the 1870s to 1930

Daniel J. Kevles

The best known form of intellectual property (IP) protection is the common utility patent, whose requirements include the stipulations that the invention must be man-made and useful. What is patentable in the United States according to statute dates back to the patent law of 1793, which declared, in language written by Thomas Jefferson, that patents could be obtained for "any new and useful art, machine, manufacture, or composition of matter, or any new or useful improvement thereof."[1] The code said nothing about whether an innovation's being alive or not has any bearing on its patentability. However, in the nineteenth century living organisms were taken to be unpatentable. In the United States, only one living organism was patented—a form of yeast that Louis Pasteur claimed as an "article of manufacture."[2] That was the exception that proved the rule. Plants and animals were not machines or manufactures. Improvements upon them were not identifiable new compositions of matter. And how could one define the utility of an ornamental plant—say, a rose exhibiting a new fragrance or hue?

Under the circumstances, through most of the nineteenth century plant and animal improvers did not seek patents on their products, but this is not to say that they were indifferent to intellectual property protection. While they did not speak of "intellectual property"—the phrase was coined in a Massachusetts court case, in 1845[3]—they were alive to the concept. Indeed, plant and animal improvers were no less profit-minded and imaginative than contemporary biotechnologists, and they devised a variety of property-protection arrangements outside the patent system to achieve protection of the IP in their living innovations. The story of their efforts lies at a rich and relatively unexplored historiographical site—the intersection of pre-Mendelian craft knowledge of plant and animal improvement with law and economics.

In establishing their arrangements, the improvers recognized, at least tacitly, that they had to deal with several difficulties. No property right is worth the paper it is written on that can not be enforced. The requirements for enforcement of any property right include the ability to specify and warrant the identity of the property. This was easily accomplished with a tract of land by

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1 Jefferson's phrasing remains at the core of the U.S. patent code, except for the eighteenth-century word "art," which was replaced in a 1952 Congressional overhaul of patent law by the word "process." Bruce W. Bugbee. *Genesis of American Patent and Copyright Law.* Washington, D.C.: Public Affairs Press 1967. p. 152; Fritz Machlup. "Patents." *International Encyclopedia of the social Sciences.* David L. Sills (ed.). New York: Macmillan 1968. XI, 461-64. I am grateful to the Andrew W. Mellon Foundation for support of the research from which this article is drawn and to Karin Matchett for indispensable assistance.

2 Pasteur's patent, no. 141,072, was issued in 1873. Graham Dutfield *Intellectual Property Rights and the Life Science Industries. A Twentieth Century History.* London: Ashgate Publishing Co. 2003. p. 151.

3 The judge declared, upholding the broad patent of an inventor of cotton spinning machinery: "Only . . . in this way can we protect intellectual property, the labors of the mind, productions and interests as much a man's own, and as much the fruit of his honest industry, as the wheat he cultivates, or the flocks he rears." Catherine Fisk. "The History of Intellectual Property Comes of Age." Key Note Address, Wisconsin Legal History Symposium, University of Wisconsin Law School, November 13, 2004. p. 6, unpublished, copy in author's possession.

surveying and recording its meets and bounds. In contrast, specifying the identity of a living organism—for example, a Shorthorn bull or a Concord grape—was problematic, given that defining biological knowledge such as blood types or DNA sequences was unavailable.

The establishment of *intellectual* property also entails reliable reproduction of the product, including its valuable characters. Absent such reproduction, the IP would be worthless. Faithful reproduction of an organism depends on practical and/or theoretical knowledge of heredity. But the achievement of reproductive fidelity posed a problem for plant and animal improvers that the innovators of, say, mechanical reapers did not face. Unlike reapers, living organisms reproduce themselves. If an improved plant or animal reproduced itself faithfully—or could be made so to reproduce itself—the original improver potentially faced competition from the purchaser that in the absence of patents could not be easily forestalled.

In the nineteenth century, identification of a living organism could take the form of a written description, a drawing, or a photograph, but such descriptions were by no means exact or adequate for the purposes of IP disputes. The ability to identify and reproduce a plant or animal depended on the improver's craft knowledge of biology, heredity, and breeding practices.[4] The history of IP in living organisms during the nineteenth century—and, indeed, even long after the rediscovery of Mendel's laws, in 1900—thus concerns the interplay among such craft knowledge on the one side and the arrangements at that this body of knowledge and skills permitted.

In the United States, IP protection in law for living products found its way onto the agenda of plant and animal improvers during the latter third of the nineteenth century. Before then, markets in agricultural stock were largely local, and the seed, nursery, and animal breeding industries were only incipient.[5] It is likely that the warrant for the identity and character of what was offered for sale rested on the purchaser's knowledge of the purveyor and his reputation. How subsequent competition from buyers was handled is largely unknown, but it may not have been an issue if only because in this period the large majority of new animal breeds as well as plant species and varieties were not the product of effort and investment by improvers. They were imported to the United States, usually at the cost and with the encouragement of the federal government.[6] If breeders did invest in improvements, they likely commanded the local market enough to disregard or shame copycat competitors or they may have considered their efforts a pro bono service to the community, finding reward enough in the admiration of the local agricultural society.

Attention to IP protection for plants and animals loomed larger after the Civil War, for several likely reasons. Regional and national agricultural markets emerged with the construction of the railroads and amid increasing urban demand for meats, fruits, and vegetables, as well as ornamental plants, trees, flowers, and shrubs.[7] The number of animal breeders, orchardists, and

4 The *locus classicus* for information on craft knowledge and practices in plant and animal breeding in the later nineteenth century is, of course, Charles Darwin. *Variation in Plants and Animals under Domestication.* 2 vols.; London: John Murray 1868. Available on January 29, 2006 at *The Writings of Charles Darwin on the Web* (http://pages.britishlibrary.net/charles.darwin/texts/variation/variation_fm1.html).

5 Cary Fowler. "The Plant Patent Act of 1930: A Sociological History of Its Creation." *Journal of the Patent and Trademark Office Society* 82 (September 2000): pp. 622-23.

6 *Ibid.;* Jack R. Kloppenburg, Jr.. *First the Seed. The Political Economy of Plant Biotechnology.* 2nd ed.; Madison: University of Wisconsin Press 2004. pp. 50-57; Margaret Derry. *Bred for Perfection. Shorthorn Cattle, Collies, and Arabian Horses since 1800.* Baltimore: The Johns Hopkins University Press 2003. *passim.*

nurserymen was growing. Eager to be competitive, the proprietors of these enterprises felt the need to offer new and superior breeds or varieties as often as possible. While many such products continued to come from importation, an increasing number were generated by breeders and, in the plant world, by variants and sports found in the fields. Whether generated by hybridization or chance finds, the improved variants usually required effort and investment to turn them into marketable products, a condition that made improvers more attentive to capturing financial returns on the IP they had created. But doing business across vast, impersonal distances, animal and plant improvers could rely much less on reputation to warrant the identity and quality of their products. And the distance as well as the impersonality of the buyer-seller relationships made it all the easier for purchasers to propagate an improver's innovation and sell it as her own.

During the nineteenth century, breeders of pure-bred Shorthorn cattle devised a system for protecting the IP in their animals responsive to these circumstances. Drawing on the methods pioneered by the English breeder Robert Bakewell in the late eighteenth century, they bred through pedigree, selecting for valuable characters and intensifying their embodiment in the animals through inbreeding.[8] The resulting purebreds likely tended to possess an essential feature of IP licensing—intergenerational reliability, which is to say that the products of their stud service were likely to resemble them.

Warranting the identity of the animals was achieved by registering the pedigrees in publicly available stud-books. The books, originally imported from England, along with the breed, were developed by private entrepreneurs in different states, and by the late nineteenth century they were increasingly characterized by non-uniformity in standards, sloppiness in the records, and general unreliability. As warrants of identity, they left a good deal to be desired. To solve that problem, the Shorthorn breeders moved in 1876 to regulate their market to a degree by forming the American Shorthorn Association. The Association bought the existing registry books and amalgamated them into one. The arrangement thus advantaged genuine Shorthorn breeders and protected buyers against fraudulent sellers—that is, purveyors of putative Shorthorns whose animals were unregistered with the Association.[9]

This system for the protection of IP in Shorthorns likely exemplified the systems developed for other farm animals and, with some variation, for pets and race horses.[10] It did not firmly protect the IP developed by individual breeders, but it protected very well the collective IP of the cartel of breeders represented by the breed association. In 1891, Liberty Hyde Bailey, the prominent plant scientist and a professor at Cornell University, noted the value of the system: "There is no law to compel one to register an animal, but every breeder knows that it is only through registration that he can advertise, sell and protect blooded stock. And there is no intelligent purchaser who would

7 Fowler. "The Plant Patent Act." pp. 623-24.

8 On Bakewell, see Harriet Ritvo. "Possessing Mother Nature. Genetic Capital in Eighteenth Century Britain." In John Brewer and Susan Staves. (eds.) *Early Modern Conceptions of Property.* London and New York: Routledge 1995. pp. 413-26. See also H. Cecil Pawson. *Robert Bakewell. Pioneer Livestock Breeder* London: Crosby Lockwoon & Son 1957.

9 Derry. *Bred for Perfection.* pp. 15, 20-29, 34-36. For a more extensive discussion of the history of IP in animal breeding, see Daniel J. Kevles. "Breeding, Biotechnology, and Agriculture. The Establishment and Protection of Intellectual Property in Animals Since the Late Eighteenth Century." In *Preprint 310, Workshop, History and Epistemology of Molecular Biology and Beyond: Problems and Perspectives.* Berlin: Max-Planck-Institut für Wissenschaftsgeschichte 2006. pp. 69-80.

10 Ibid., passim.

think of negotiating for such stock without having obtained the testimony of the herd-book."[11] In all, the breed association-stud book system provided the degree and type of protection consistent with what could be done in the then-current state of biological and breeding knowledge to specify the animal's hereditary essence, warrant its hereditary prowess, and transmit that hereditary essence to succeeding generations. Still, it remains an open historical question whether and how the purveyors of pure-bred animals or stud services managed to discourage purchasers from competing against them with the offspring of their animals.

The principal IP-related problem for improvers of plants that were reproduced sexually—for example, corn, the grains, most vegetables, and flowers—was that they did not ordinarily breed true. Sellers of their seed thus could not guarantee the quality and character of any given crop. J. M. Thorburn & Co., a prominent nursery in New York, warned buyers that they gave "no warranty, express or implied, as to description, quality, productiveness, or any other matter of any seeds, bulbs or plants they send out." Among the reasons was "*the well-known tendency of many vegetables to revert to their original types, notwithstanding the care of the seed-grower*."[12] Then, too, farmers could save seed from their crops, and then either plant them, sell them, or both, thus undercutting the improver's control of his IP in the plant. Under the circumstances, the nascent private seed industry paid little attention to IP protection. It was content to rely for new varieties on importation and on the innovations produced by the state agricultural experiment stations established by the Hatch Act, in 1887. Of far greater concern than IP was the competition the seed trade faced from the federal government. Beginning in the 1830s, the U.S. Patent Office and then the U.S. Department of Agriculture distributed seed gratis to farmers—more than ten million packets annually in the 1890s—via members of Congress and their franking privilege. What the seed industry wanted from the policy arena was not IP protection but an end to the seed distribution program, a campaign that succeeded in 1924.[13]

Innovations and improvements in asexually reproducible plants and trees—the foundation of the horticultural industry—came partly from the hybridizing work of breeders like Luther Burbank but in the overwhelming main from chance finds in the field and orchard.[14] The finds arose from bud sports or fortunate sexual pollinations, but once found they could be reproduced virtually identically by the nurturing of grafts or cuttings. Commercial nurseries acquired such finds, tested them for such characteristics as sturdiness and fruit-bearing qualities, then put them on the market. Stark Brothers Nursery and Orchards, based in Louisiana, Missouri, was one of the oldest and perhaps the largest such enterprise in the country. It sponsored an annual fair that encouraged farmers to submit their good fruits, including those of chance finds, for competitive judgment. In 1893, through this means, the firm learned about an apple tree that produced a luscious red fruit. The next year, it brought the tree with all propagation rights—which is to say all

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[11] Liberty Hyde Bailey. Report. "Protection to the Originator of Varieties." read at the meeting of the American Association of Nurserymen, June 4, 1891. In *Transactions of the American Association [of Nurserymen]*. June 3-13, 1891. pp. 88-91.

[12] J. M. Thorburn & Co.. Catalogue [1908]. Copy in New York Botanical Gardens Archives, Catalogue Collection, Box. 538. Italics in the original.

[13] Fowler. "The Plant Patent Act." pp. 622-23; Kloppenburg. *First the Seed*. pp. 61-65.

[14] Bailey. Report. "Protection to the Originator of Varieties." pp. 88-89.

its IP—from its owner, a farmer in Iowa, named the fruit the "Delicious" apple, and proceeded to market the tree to the world.[15]

Nurserymen and orchardists could be confident that the young trees they sold would bear fruit very much like the fruit on the trees from which they had been derived. The question for the purchaser was whether the quality of the tree—for example, its bearing abundance—and of its fruit would live up to its billing. The reputation of a well-known seller—for example, Burbank or Stark Brothers—counted for something, but in the impersonalized setting of the national market nurserymen relied increasingly on advertising, placing ads in horticultural and gardening journals and distributing catalogues across the country. The ads tended to include what amounted to warrants of their products' quality and identity in the form of farmers' testimonials about the merits of their fruit trees, shrubs, and flowers.

Yet the ease with which, say, valuable fruit trees could be easily reproduced virtually identically, through grafting, and thus numerously multiplied facilitated theft of the developer's IP. Competitors could purchase the trees, or take cuttings of them from someone's nursery in the dead of night, then propagate and sell them. Burbank tried to protect himself against such thieves by telling buyers that the way to judge novel fruits was to *"look to their source*, and also *if possible purchase direct from the originator."* He also charged high prices for his innovations – say, $3,000 for a new plum tree, including all "stock and control"—thus attempting to gain in the first sale revenue that would cover his costs and return a reasonable profit.[16] The pricing strategy was intended to capture what economists call all the downstream revenues of which thieves might deprive him, since he would be unable to control the reproduction of the tree once he had sold it. Trouble was that the high first-sale pricing did not work very effectively to compensate horticultural innovators for the loss of IP in their new fruit trees. Nurserymen repeatedly complained that they failed to receive just returns for all their investment of time and money. Burbank fulminated to the readers of *Green's Fruit Grower* that he had "been robbed and swindled out of my best work by name thieves, plant thieves and in various ways too well known to the originator. . . . A plant which has cost thousands of dollars in coin and years of intensest [sic] labor and care and which is of priceless value to humanity may now be stolen with perfect impunity by any sneaking rascal. . . . Many times have I named a new fruit or flower and before a stock could be produced some horticultural pirate had either appropriated the name, using it on some old, well-known or inferior variety or stealing the plant and introducing it as their own, or offering a big stock as soon as the originator commences to advertise the new variety." [17]

Burbank as an innovator was largely in the business of selling to nurseries and orchardists, middlemen who would propagate his trees and sell them to gardeners, farmers, and other

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15 Dickson Terry. *The Stark Story: Stark Nurseries' 150th Anniversary.* Columbus, Mo: Missouri Historical Society 1966. pp. 38-40.

16 Catalogue. *New Creations in Fruits and Flowers, June 1893.* Santa Rosa, CA: Burbank's Experimental Grounds 1893. p. 12; Catalogue. *Twentieth Century Fruits, 1911-1912.* Santa Rosa, CA: Burbanks' Experiment Farms. 1911. p. 1. Copies in Luther Burbank Papers, Library of Congress, Box 14. Bolded print in the source.

17 Burbank to Jacob Moore. May 4, 1898. In *Green's Fruit Grower.* June 1898, clipping in Luther Burbank Papers, Luther Burbank Home and Gardens, Archives, Santa Rosa, CA. Scrapbooks. Vol. 2. p. 45. See also Jacob Moore to Chas. A. Green, April 20, 1898; "Protection for Fruit Evolvers."Editorial. *California Fruit Grower.* n.d.; and Moore to Peter Gideon. n.d.. *Green's Fruit Grower. ibid.* Scrapbooks. Vol. 2. pp. 44, 47, 115.

consumers. Stark Brothers, which did not breed new fruit trees but only acquired them, was in the business of mass marketing. Realizing the value of their IP by charging high prices would have been counterproductive to their business plan. To protect the IP in their fruit trees, the Starks trademarked them, using the trademark law that Congress passed in 1881. In the 1890s, the Stark catalogues included gorgeous paintings of their named fruits with a small banner beneath each declaring that it was covered by a Trade Mark or, in the case of the Gold Plum, that it was "Trademark Pat[ente]d. Feb. 25, 1895." [18] The trademark, however, would not prevent someone from obtaining the tree or cuttings from it, propagating the wood, and then selling the tree under a different name.

Under the circumstances, beginning in the 1880s and with mounting insistence in the 1890s, American nurserymen began urging the establishment of legal protection for what they called the rights of "originators." Some of the agitation recommended the expansion of the patent system to include coverage for innovations in plants and trees. Mindful of their exclusion from the patent system, nurserymen wondered why, as the *California Fruit Grower* put it, "the writer of a book, the composer of a song, the designer of a drawing or the originator of a mechanical device should be protected in their productions, while the originator of an improved flower or fruit is denied the same privilege." [19]

The move to patentability was blocked, however, when, in 1889, in *Ex parte Latimer,* the U.S. Commissioner of Patents rejected an application for a patent to cover a fiber identified in the needles of a pine tree, declaring that it would be "unreasonable and impossible" to allow patents upon the trees of the forest and the plants of the earth."[20] The commissioner's ruling formed the basis for what came to be known as the "product-of-nature" doctrine—that while processes devised to extract what is found in nature can be patented, objects discovered there or bred from there can not be patented. In a report to the American Association of Nurserymen in 1891, Liberty Hyde Bailey rejected the horticulturalists' patenting initiative as in any case unwarranted. New varieties were not inventions, he noted, precisely because they were accidents found in the fields, adding, "When the time comes that men breed plants upon definite laws, and produce new and valuable kinds with the certainty and forethought with which the inventor constructs a new machine, or an author writes a book, plant patents may possibly become practicable."[21]

Bailey held that plant originators should nevertheless be protected, though he doubted that any new legislation would do the job. "It is evident that after a variety is put upon the retail trade it becomes public property, and no statute could further protect it," he observed. He proposed that the nurserymen draw on existing trademark law to obtain protection through a national register of plants administered by the Department of Agriculture. The originator would send the department "a specimen, description and perhaps picture of his novelty," and the department would issue a certificate, a type of trademark insuring him "inviolable rights" in his innovation.

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18 Copy in Scrapbooks. Vol. 1, p. 141. Burbank Home and Gardens, Archives.

19 "Protection for Fruit Evolvers." Editorial. *California Fruit Grower.* quoted in Luther Burbank, Burbank's Experiment Farms. *The 1899 Supplement to New Creations in Fruits and Flowers.* Luther Burbank Papers, Library of Congress, Washington, D.C., Box 14.

20 Daniel J. Kevles. "Ananda Chakrabarty Wins a Patent. Biotechnology, Law, and Society, 1972-1980." HSPS. *Historical Studies in the Physical and Biological Sciences* 25: 1 (1994), 111.

21 Bailey. Report. "Protection to the Originator of Varieties." pp. 88-89.

He acknowledged that thieves could sell the variety under a different name, but he thought that "tricksters" would be discovered and in consequence commercially disadvantaged. The public would soon learn to buy only from originators who possessed a registration certificate, just as they had learned to purchase only animals registered with the breed associations.[22]

Bailey, like the Stark Brothers with their trademarked fruits, tacitly assumed that the certificates would not only protect the name of the innovation but also secure to the originator the exclusive right to the plant or tree and to its propagation. But that assumption was severely undercut in 1895 by the ruling of a federal appeals court in the case of *Hoyt et al v. J. T. Lovett Co.* James Hoyt and Edwin Hoyt, nurserymen in Connecticut, had sued the J. T. Lovett Nursery, in New Jersey, for selling a grape that had been found in the Green Mountains in Vermont. The Hoyts believed they had bought the grape wood with exclusive rights and they had trademarked it as the "Green Mountain Grape." The court found against the Hoyts partly on grounds that certain facts in the case contradicted the tenets of trademark law as it had been judicially interpreted. But its decision also addressed the scope of trademark protection for living products.[23]

Apparently Lovett's lawyer had raised the issue, contending, in the words of the court, "that the protection of a trade-mark cannot be obtained for an organic article which, by the law of its nature, is reproductive, and derives its chief value from its innate vital powers, independently of the care, management, or ingenuity of man." The court, while noting that the question was "novel and unprecedented," agreed, writing: "The Hoyts did not make the Green Mountain vine, nor, strictly speaking, did they produce it. It grew out of the earth, was fashioned by nature, and endowed with powers and qualities which no human ingenuity or skill could create or imitate. If such protection as that now claimed by the complainants was allowed, a breeder of cattle could with equal propriety and reason demand like protection for the natural increase of his herd. In every aspect such claims would seem to be impracticable and inequitable."[24]

Meanwhile, Liberty Hyde Bailey had evidently persuaded the nation's nurserymen to discard their ambitions for patent protection in favor of establishing trademark protection through a national registry. But the ruling in *Hoyt et al* had nullified Bailey's contention that to accomplish their purpose the nurserymen needed only administrative action by the Department of Agriculture. Legislation was necessary, and during the next decade the leading nurseries, including Burbank and Stark Brothers, moved to obtain it, engaging a lawyer in Washington, D.C. named F.T.F. Johnson. In 1906, a bill, perhaps drafted by Johnson, was introduced in the House that would amend the trademark act by authorizing the commissioner of patents to register an originator's new variety of plant, bush, shrub, tree, or vine. Registration of the name would constitute a trade mark and would include for twenty years the "exclusive right to propagate for sale and vend such variety of horticultural product under the same so registered."[25]

The bill enjoyed broad support from nurserymen, a number of whom wrote letters to Johnson that were introduced at hearings on the bill before the House Committee on Patents, in March

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22 *Ibid.* pp. 89-90.
23 *Hoyt et al v. J.T. Lovett Co.,* Circuit Court of Appeals, Third Circuit, 71 F. 173; Dec. 3, 1895.
24 *Ibid.*
25 U.S. Congress, House of Representatives, Committee on Patents, Arguments before the Committee . . . on H.R.113570, Authorizing the Registration of the Names of Horticultural Products and to Protect the Same, March 28, 1906, 59th Cong., Washington, D.C.:GPO 1906. pp. 3-5, 12-13.

1906. M. Crawford, who lived in Cuyahoga Falls, Ohio and who had given the world the Crawford peach, explained the principal reason behind the desire for protection: "An originator may work ten or twenty years to produce a variety worth naming and introducing. If he attempts to introduce it himself he will hardly get enough out of it the first year—the only year he controls it—to pay the printer. The second year he is undersold by competitors, many of whom never saw the real thing."[26]

Several committee members expressed sympathy for protecting the rights of the originators, but the committee leadership found the bill before it constitutionally dubious. For one thing, by trying to protect rights in the product by protecting rights to its name, it sought to combine the exclusivity of a patent with the coverage of a trademark. More important, constitutional authority for the granting of federal trademarks rested on congress' power to regulate interstate commerce. The bill allowed for trademark protection of plants even if they were not sold in interstate commerce, and under prevailing interpretation of the commerce clause it was unconstitutional for congress to regulate intrastate trade. Congressman Frank D. Currier, of New Hampshire, the chairman of the Patents Committee, summarily declared: "The proposition is as clearly unconstitutional as anything can be."[27]

Although an immediate failure, the 1906 venture did lead to the formation of a lobbying group, the National Committee on Plant Patents under the American Association of Nurserymen. In 1929, Paul Stark, of Stark Brothers, became chair of the committee. Along with other nurseries, Stark Brothers had been trying to protect its propagation rights in new fruits by imposing contractual obligations upon the purchaser—for example, an agreement that he would neither sell nor give away scions, cuttings, or buds. Liberty Hyde Bailey had suggested in 1891 that nurserymen use such contractual arrangements and the court in *Hoyt et al* had in passing noted their acceptability. However, the contracts were some times difficult to enforce, which helped energize Stark's eagerness for the stronger IP protection that a patent would provide, and in 1930, not least because of Stark's lobbying effort, Congress passed the Plant Patent Act. [28]

The act covered only asexually reproduced organisms, and it authorized a patent to anyone who "has invented or discovered and asexually reproduced any distinct and new variety of plant, other than a tuber-propagated plant. . . ."[29] Given its requirement of distinctiveness rather than usefulness, it was not a utility patent law. Moreover, it did not establish the conventional legal bargain that granted the inventor a monopoly right in exchange for public knowledge of how the invention was produced so that others could innovate beyond it. In most cases, there was no such knowledge to be disclosed. Liberty Hyde Bailey may have predicted that patent protection would accompany the discovery of the laws of inheritance, but the rise of Mendelian genetics played little or no role in the work of the nurserymen who were the Act's principal advocates. Even in 1930,

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26 Crawford to Johnson, March 19, 1906, in *ibid.,* p. 10.
27 *Ibid.,* pp. 4-5, 9.
28 Bailey. Report. "Protection to the Originator of Varieties." p. 90; *Hoyt et al v. J.T. Lovett Co.,* 71 F. 173; Dec. 3, 1895; Fowler. "The Plant Patent Act." pp. 630-42; Glen E. Bugos and Daniel J. Kevles. "Plants as Intellectual Property. American Practice, Law, and Policy in World Context." *Osiris.* 2nd Series. Vol. 7, *Science After '40* (1992): 81-88.
29 Quoted in Fowler. "The Plant Patent Act." p. 641.

the innovations in fruits that were their stock in trade continued to arise from chance variations in the field rather than breeding on Mendelian principles.[30]

In all, the Plant Patent Act harkened back to the seventeenth century, when patents were granted as privileges in the market—royal dispensations to encourage commerce in new technologies, often from abroad, or to reward favorites. Indeed, the Plant Patent Act might well have been called the Stark Horticultural Privilege Act, not only because of Stark's role in its passage but because it granted a privilege of intellectual property protection that was tailored to the practices and needs of horticultural innovators.[31] Still, for all its simultaneous restrictiveness and looseness, the act was the first statute passed anywhere in the world that extended patent coverage to living organisms. It helped pave the way for the legal protection of IP in sexually reproducing plants, which Congress authorized in 1970, and for the extension of utility patents to all living organisms other than human beings after 1980, when in the emerging age of biotechnology the U.S. Supreme Court ruled that whether an innovation is alive or not is irrelevant to its patentability.[32]

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30 The rise of Mendelian genetics similarly changed breeding practices and the system of IP protection for animals very little. No doubt one of the reasons was the small number of offspring produced by animals, which makes difficult conventional genetic analysis. In 1925, one farm expert noted, "Up to the present time, the new knowledge of genetics has contributed little" to advances in animal breeding, adding, "Animal breeding proceeds in much the same way as it [did] four thousand years ago." Derry. *Bred for Perfection.* pp. 12-14.

31 I am indebted to Mario Biagioli for the analogy of the Plant Patent Act to the earlier practice of awarding patents as privileges. On patents as privileges, see Miller and Davis. *Intellectual Property.* p.5; and Jessica He. "'Hail to the Patents!' The Ethics, Politics, and Economics of the Early Modern Patent System in England." Senior Essay, Ethics, Politics, and Economics, Yale University 2005. pp. 2-27.

32 For these developments, see Bugos and Kevles. "Plants as Intellectual Property."; Kevles. "Ananda Chakrabarty Wins a Patent."; and Daniel J. Kevles. "The Advent of Animal Patents: Innovation and Controversy in the Engineeering And Ownership of Life." In Scott Newman and Max Rothschild. (eds.) *Intellectual Property Rights and Patenting in Animal Breeding and Genetics.* New York: CABI Publishing 2002. pp. 18-30.

Coalition and Opposition: Heredity, Culture, and the Boundaries of Anthropology in the Work of Alfred L. Kroeber

Maria E. Kronfeldner

Introduction

"If there is nothing beyond the organic, let us quit our false and vain business and turn biologists…."[1] This is what anthropologist Alfred L. Kroeber (1876-1960) said in 1916—a time when ideas about heredity changed a lot, when genetics established itself as an experimental science, when hereditarian thinking was gaining wide acceptance in the US, and—last but not least—when American anthropology emancipated itself from being a museum-based profession and became an academic discipline. In face of all this, Kroeber, student of Franz Boas (1858-1942), was fighting for the boundaries and the autonomy of the new academic discipline. And this struggle included a severe opposition to certain kinds of hereditarian thinking.

Kroeber tried to accomplish his boundary work by focusing on a concept of culture that not only saves man from being 'just another animal' but gives anthropology a distinctive phenomenon for study. According to him, culture is defined as not only *opposed* but also *analogous* to biological heredity. In addition, he stressed that the rise of a Weismannian, non-Lamarckian concept of inheritance, today often called 'hard inheritance,' and the correspondent denial of 'soft inheritance' was *necessary* for the historical development of such a concept of culture.[2]

Some historians have acknowledged Kroeber's point about inheritance of acquired characteristics.[3] Yet, they did not concentrate on the consequences of his case for an historical account of the *impact of the concept of hard inheritance*.[4]

In *part 1*, I will say a little bit more on the shifting boundaries of anthropology at the beginning of the 20th century. This makes clear why Kroeber needed an opposition to hereditarian thinking.

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1 Kroeber (1916b: 296).

2 Kroeber himself did not use the terms 'hard' or 'soft' inheritance and today these terms are not necessarily used in the same way by different authors. I will use them in the following sense: hard inheritance is what Weismann's concept of inheritance implied, which will be specified later in this paper. Soft inheritance is the exact opposite, implying that the hereditary material is malleable at any time, as for instance in Lamarckian inheritance. The term 'Lamarckian' is today used in unison for the idea of inheritance of acquired characteristics, even though Lamarck was by far not the only one referring to this kind of inheritance. It was common knowledge of his time and even Darwin believed in it. See Zirkle (1946) on the history of the idea from the Greeks to Darwin. Ernst Mayr (1982) is often quoted as the one who introduced the terms of 'soft' and 'hard' inheritance. Cyril Darlington, however, used the term "hard heredity" already in 1959, as I learned from Jonathan Hodge during the workshop. Yet, Darlington used the terms with a slightly different meaning (see Darlington 1959: 14, 54-56, Appendix, and compare Mayr 1982: 687).

3 See for instance Stocking (1968: 250-269); Harris (1968: 121); Peel (1971: 143-146); Freeman (1983: 34-50); Degler (1991: 96-100).

4 Thus, it is not surprising that Kroeber has been ignored in accounts of the impact of the concept of hard inheritance (as for instance in Paul 1995: 40-49) or in historical accounts of the history of hereditarian thoughts in general, as for instance in Ludmerer (1972). He is briefly mentioned by Kevles (1985). In turn, it is not surprising that a standard history of anthropology, such as Patterson (2001), can ignore Kroeber's reference to the concept of hard inheritance as important for his concept of culture.

I will then analyze in *part 2* how Kroeber used a Weismannian or non-Lamarckian concept of hard inheritance to secure the boundaries of anthropology. This shows why he wanted geneticists to enter into a *coalition* with him. I will end, in *part 3*, with some systematic notes on the concept of culture, with remarks on why Kroeber's case is important for contemporary debates on evolution, and on why his case is important for writing a cultural history of heredity.

1. The shifting boundaries of anthropology at the beginning of the 20th century

That sciences are organized into disciplines means that conceptual boundaries are constantly built and rebuilt: the space of ideas gets delineated into areas of autonomy and exclusive authority over problems. Since ages, anthropology has conventionally been defined as 'the science of man.' At the beginning of the 20th century in the US, anthropology was thought to comprise four parts: physical anthropology, ethnology (which was later called cultural anthropology), linguistics, and archaeology. At the same time, it stopped being a mere museum based profession and became an academic discipline, with the usual outward signs this has: curricula, degrees, journals, disciplinary associations etc.[5] Naturally, there was a need to define the boundaries of anthropology in the face of other academic disciplines and areas of research, such as psychology, biology in general, and genetics in particular. And this need was also a need to define the internal relationship between physical and cultural anthropology.

Marginalizing physical anthropology

Franz Boas regarded physical anthropology as central to understanding the behavioural differences between groups of people: heredity, a phenomenon considered as part of physical anthropology, was for him one of *several* factors an anthropologist has to take into account in order to understand the development and behaviour of individuals.

His student Alfred L. Kroeber was more radical. He tried to marginalize the field of physical anthropology. Kroeber grew up in a German-Jewish-American intellectual context in New York and received Columbia's first PhD in anthropology in 1901, the ninth in the whole US. Immediately afterwards, he got a permanent position. His job was to build up a department of anthropology at the University of California, Berkeley. By 1907 he was an important figure in the discipline and counts until today as the most influential figure in the establishment of American anthropology after Boas.[6]

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5 For more on the history of anthropology before it became a scientific discipline and how it developed since then in general see: Hinsley (1981), Darnell (1998), Patterson (2001).

6 See Bidney (1965) for a short review of his life and work, Steward (1973) for a book length one, containing a summary of the biography written by Kroeber's wife Theodora Kroeber (1970); see also Thoresen (1975) on the establishment, financing, and development of academic anthropology in California.

Figure 1. Anthropologist Alfred L. Kroeber, who strongly believed in culture as important to explain similarities and differences, and Ishi, famous last member of the Yahi tribe, 1911. Photo credit: UC Berkeley, Phoebe Hearst Museum of Anthropology.

For Kroeber, cultural anthropology was at the centre of the discipline, while "the other parts were secondary and marginal and owed their significance to their contribution towards an understanding of cultural history," as the anthropologist David Bidney says in a review on Kroeber's impact.[7] Consequently, Kroeber never contributed anything to physical anthropology. At the same time, others, geneticists such as Davenport and other anthropologists, pulled in the exact opposite direction: they tried to marginalize *cultural* anthropology. The following example from the arena of the politics of science will show that anthropologists such as Kroeber had quite concrete reasons to be afraid of losing their jobs. In other words, there was a practical or pragmatic pressure to secure the boundaries of anthropology by marginalizing physical anthropology and by opposing hereditarianism.

Representation in the scientific bureaucracy

Between 1916 and 1918, Boas and his students fought for their representation in America's scientific bureaucracy. At issue were the posts for the *National Research Council*'s Committee on Anthropology. For historians of anthropology the story is well known. George E. Hale, the Director of the National Research Council, asked William H. Holmes (1846-1933), important figure in American anthropology and defender of a racial interpretation of cultural differences, to organize the Committee on Anthropology. He chose Aleš Hrdlička (1869-1943), who was a defender of physical anthropology as an independent discipline, to take the lead. The goal was to prevent that Boas and his students get control over the committee, i.e. to prevent cultural anthropology from becoming too influential. Yet they could not totally ignore Boas. Holmes thus put Hrdlička, Boas, and Charles B. Davenport (1866-1944), a geneticist and the leader of the

7 Bidney (1965: 268).

American eugenicist movement, on the list for the committee. Yet, Hale dropped Boas from the committee because of Boas' anti-war activism. In April 1917, Madison Grant (1865-1938), a wealthy racist propagandist, who published his best-selling book on the "Passing of the Great Race" in 1916, offered money for the committee's work in exchange of membership in it. In the end, the committee consisted of Holmes, Hrdlička, Grant, and Davenport. And it was Davenport, who had been selected by Hale in February 1918, who was to represent the interests of the Committee on Anthropology to the National Research Council's Division of Medicine and Related Sciences. In a nutshell, a geneticist, who defended eugenic doctrines, came to represent anthropology in the scientific bureaucracy of the National Research Council. And this was at a time when there were already *trained* anthropologists to do so. [8]

Besides this struggle for representation, there was the emancipation from the older generation of anthropologists such as Holmes, which were not trained as anthropologists and predominantly oriented towards a racial hereditarianism, and the general dominance of racism and eugenics in the US at that time. These are the three main contexts in which cultural anthropologists in the US formed a clear professional identity as *cultural* anthropologists.

That Kroeber perceived a danger (and wanted others to perceive such a danger) in the various developments just mentioned is also evident from the language of war and territory that he used: according to him, biology is a discipline that "forged its weapons, taught itself their use, conquered a territory, and stands forth a young giant of prowess," in order to "annex the antiquated realm of history that lay adjacent."[9]

Now, it was Kroeber who used the *biologist's own concept of hard inheritance* to keep up the two oppositions: against the institutional hegemony of biologists and against the scientific hegemony of hereditarianism. According to Stocking, he was the *only one* among social scientists, who realized that the concept of soft inheritance (i.e. inheritance of acquired characteristics) prevented the autonomy of anthropology and other social sciences.[10]

2. Alfred L. Kroeber's boundary work: culture and/as inheritance

Kroeber's boundary work for anthropology found its first peak with a couple of papers between 1915 and 1917, ending with his famous article on "The superorganic" (1917), which established cultural determinism as his major doctrine.

The psychic unity of man and the superorganic nature of culture

Already in 1910, Kroeber laid down the basic frame of his point of view on culture, heredity, and anthropology. His example was morality: according to him, morality is governed by an innate, instinctual moral sense. Yet, variations in moral behaviour between "civilized" and "uncivilized people" are due to different cultural influences and not due to innate differences in the alleged moral sense. In other words, *behavioural* differences do not imply that there are essential inborn

8 For more on this and the history of the Committee on Anthropology see in particular: Stocking (1968: 270-308), Cravens (1978: 89-120); Patterson (2001: 55-60).
9 Kroeber (1916a: 34).
10 Stocking (1968: 259).

mental differences between groups of people: to the contrary, one should assume a *psychic unity of mankind* and explain the behavioural differences by the influence of what Kroeber called *civilization, history*, or *culture*. [11]

From this assumption, Kroeber went on to describe culture as "outside of race and independent of the human body."[12] This means that culture influences culture (via behaviour), but it does not influence the body, at least not the innate racial basis of the respective behaviour, and vice versa. That culture influences and thus explains culture means that culture is for Kroeber a system or process *sui generis*. Culture is "superorganic"[13]—'*on top*', so to say, of organic matters, relying on "social inheritance or cultural transmission" instead of biological inheritance.[14]

To understand his position clearly, the following points have to be taken into account: in his 1915 paper "Eighteen professions," arguing for the autonomy of anthropology as a distinct discipline, Kroeber assured that the psychic unity of man is not a proven or disproven fact, but a necessary assumption for the "historian," i.e., the anthropologist, since otherwise "his work becomes a vitiated mixture of history and biology."[15] Yet, at the same time, he acknowledges that history and biology are intertwined and that the degree of their contribution in the development of individuals cannot be tested.[16] Yet, the two statements are not contradictory. On the contrary, the argument that culture is a process in its own right is compatible with Kroeber's claim that the behaviour of *individuals* and their development is caused by multiple factors, culture being merely one of them. If, however, we look at *culture itself*, then we see that culture is independent of nature, i.e., a phenomenon that can only be explained by reference to pre-existing culture. It is from this inter-individual *phylogenetic* perspective so to say, that culture always derives from previous culture, as a cell always derives from previous cells.

The last issue that might cause misunderstanding is the issue about holism: Kroeber's paper on culture as superorganic is often treated as defending a strong holistic conception of culture.[17] Even though I cannot decide this issue here, the following two points should be taken into account. (i) Although Kroeber believes that culture is maintained via individual mental states or individual actions, he also believes that "[c]ivilization is not mental action itself," but rather "a body or stream of products of mental exercise."[18] This is not pointing to an ontologically dubious *whole*; it is pointing to a causal inter-individual *lineage* of the effects of mental acts. (ii) In addition, although he sometimes wrote in 1917 and in 1919 as if individuals are mere *passive* bearers of culture (implying that their properties do not determine culture and vice versa, i.e., culture does

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11 This psychic unity does not exclude individual differences. It is an "identity of average" as he makes most clear in Kroeber (1917: 194-203).

12 Kroeber (1910: 446).

13 Kroeber (1916b, 1917). Kroeber took the term superorganic from Spencer, who used it in the sense of exo-somatic or artificial as secondary *environment* of organisms, as Kroeber makes clear in the re-edition of papers from him (Kroeber 1952: 4). Kroeber, on the other hand, uses it for an autonomous *system of change and stability*, i.e. inheritance.

14 Kroeber (1916c: 368).

15 Kroeber (1915: 285).

16 Kroeber (1915: 285).

17 For a critique of the concept of the superorganic understood in a holistic manner, see Bidney (1944), Herskovits (1948) and the discussion of the issue in Kaplan (1965) that shows that the actual issue is methodological and epistemological, but not ontological; it is an issue about the distinctive subject-matter of anthropology.

18 Kroeber (1917: 189 and 192).

not determine the properties of individuals) and as if culture is a special ontological substance, he recanted from this in 1952: he admitted that culture as a whole is not a peculiar emergent entity or substance and that individuals are more important than he put it in 1917. His goal in 1917, he himself says in 1952, was to establish the recognition of culture as an "autonomous" system, independent of "biological explanation."[19] Consequently, if the context of an opposition to hereditarianism is ignored, Kroeber's claim about the superorganic nature (and its genesis) cannot properly be understood.[20] And it was this opposition that correlates with a denial of the Lamarckian principle of the *inheritance of acquired characteristics.*

Inheritance of acquired characteristics

In 1916, in a paper called "Inheritance by magic," published in the *American Anthropologist*, Kroeber moved the denial of inheritance of acquired characteristics to the centre of his account. In order to do so, he referred to three important aspects of August Weismann's (1834-1914) ideas on inheritance: first, that experiments failed to produce positive evidence for the inheritance of acquired characteristics; second, that all cases of evolution are explainable without reference to inheritance of acquired characteristics; third, that inheritance is 'hard': that the hereditary material is *not produced* by the organism, but *present* from the start, *continuously existing*, and *protected* against changes that occur in the somatic tissue. Acquired changes, i.e., changes to the somatic tissue of the organisms, are not heritable on this basis. In Kroeber's words, Weismann's "basic idea" was "that the hereditary substance is totally distinct from the organic body, and that therefore the fate of the individual cannot affect the race."[21] In addition, Weismann's concept of heredity meant that the germ plasm exists over time *independently of individuals*. The germ plasm is thus sub-individual and inter-individual at the same time—almost as superorganic, i.e., independent of individuals, as Kroeber assumed culture to be. Kroeber also referred to Mendelism, the "new branch of biological science," as providing a corroboration of this concept of hard inheritance. Kroeber states that "if Mendelism rests on anything at all, it rests on the doctrine of the utter separateness of what it calls gamete and zygote. This separateness may be purely conceptual, but it is the only concept which it has yet been possible for anyone to think out that will explain and hold together the looming mass of facts heaped up by genetic observation and experiment." Kroeber also mentions that although Mendelians perceive themselves as opposed to

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19 Kroeber (1952: 7, 22-3). Compare Kroeber & Kluckhohn (1952: 49), but without reference to Kroeber's papers between 1916-7, or Bidney (1965: 273).

20 A point I originally took from Kuklick (2004). I thus depart from the conclusions drawn by anthropologists such as Bidney (1965), who derive from the failure of a total independence of culture from individuals that the concept of the superorganic did not make any sense. It did make sense, but only in a very specific way: namely, in the sense of a separate system of change and inheritance. Note that I use the term "system" or "process" to follow Kroeber with his late assertion that he does *not* regard culture as a "substance" (1952: 4, 22). With this I do not want to decide whether the ontological status of 'culture' has to be interpreted in a realistic or nominalistic manner. Do beauty or culture exist *in themselves* or do they merely exist in concrete beautiful things and culture bearing individuals? Either way one can ascertain that culture exists as an inter-individual process or system, a system of change and heredity. In a similar sense, we can say that evolution is a process or system of change that exists, even though individual organisms vanish, without regarding evolution as a specific substance, an extra entity existing in addition to and in the same sense as the evolving entities.

21 Kroeber (1916a: 26).

Darwinism, "one of their fundamental achievements has been the involuntary confirmation by real knowledge of an idea first clearly grasped by a Darwinian theorist."[22]

Despite Weismann and despite Mendelism, the principle of the inheritance of acquired characteristics was still quite popular in the first 20 years of the 20th century. Because of this, Kroeber called his paper "Inheritance by magic," since "if found in the minds of uncivilized people," the belief in the inheritance of acquired characteristics "would be described as belief in sympathetic magic."[23] As one might expect from a trained cultural anthropologist of that time, Kroeber wants to know *why* the people had such an 'irrational' belief—'irrational' from his point of view.

He cites two motivations for the belief in the inheritance of acquired characters: first, Lamarckian palaeontologists (as well as Mendelians) maintain that Darwinism cannot explain the origin of variation. Thus, in order to account for the origin of variation some scientists call the inheritance of acquired characteristics to the rescue. Yet, Kroeber believes that this is not a viable route for Mendelians, since if they move back to Lamarckian inheritance, they run into a severe tension: the "absolute distinction between gamete and zygote which is the kernel and essence of all the new unit heredity seems contradictory of any possible understanding of use inheritance as a process, and leaves it an empty name."[24] Second, the general public and the social scientists stick to inheritance of acquired characteristics for another reason, as Kroeber states: they stick to it since they still do not distinguish between culture and race (synchronic perspective) and between cultural change and biological evolution (diachronic perspective) in a "*consistent*" manner. They confuse culture and nature. [25]

According to Kroeber, this confusion is caused by the assumption that cultural change, i.e. civilization, is *evidence for* and is *causally linked to* biological evolution. In Kroeber's words, it arises from the assumption that "the acquisition of greater wealth or learning or skill by one group is evidence of a superior faculty for such acquisition inborn in that group through organic heredity."[26] This is what Kroeber calls the "fallacy that the social is organic."[27] Those who "nominally" employ culture but regard it nonetheless as "ultimately, and in general directly, resolvable into organic factors," are subject to this fallacy.[28] And the cause for this fallacy is the belief in Lamarckian inheritance.

And it is true that for instance Herbert Spencer (1855), the most influential Lamarckian with respect to mental traits, assumed that civilization is correlated with biological evolution. According to Spencer, civilization can *only* be explained by reference to Lamarckian inheritance, where 'nurture' becomes 'nature' in each generation, leading to innate differences between races.[29] New behavioural patterns become habits, which become instincts—via inheritance of

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22 Kroeber (1916a: 27).
23 Kroeber (1916a: 38).
24 Kroeber (1916a: 30).
25 Kroeber (1916a: 31). Compare Kroeber (1916b: 295; 1916c: 370; 1917: 163).
26 Kroeber (1916a: 33).
27 Kroeber (1916a: 36).
28 Kroeber (1916a: 37). —The influence of Boas is evident, since it was Boas who first stressed that culture, language, and race (i.e., the genetic endowment of people) do not covary. See Boas (1894), or Boas (1911).
29 See Richards (1987) and Gissis (2005) on Spencer.

acquired characteristics; these then play a role in the genesis of new behavioural patterns, which become habits, which then in turn become instincts, and so on. The explanation of the evolution of such mental abilities like intelligence, moral sense, or musical sense, is one of the reasons why Spencer opposed Weismann's claims about the all-sufficiency of natural selection, which totally excluded inheritance of acquired characteristics.

Yet, as part of the well-known debate about the all-sufficiency of selection, Weismann had already answered that Spencer ignores that tradition is an alternative to his Lamarckian explanation. In an essay on music in animals and man, Weismann (1892) claimed that we *do not* need Lamarckian inheritance to explain the evolution of man's capacities and achievements, if we admit that there is tradition. According to Weismann, Spencer and others confused *achievements* (culture or cultural change) with innate *abilities* (nature or biological evolution). They thus ignore that the first can change without the latter. Weismann illustrated his point with the following thought example: is it possible that there was a Mozart in Samoa, a person with a musical sense or innate ability equal to Mozart's? According to Weismann, it would indeed be possible. But since the hypothetical "Samoaner Mozart" could not build on already accumulated musical traditions and the corresponding culturally transmitted abilities, it was not possible that the Samoaner Mozart expressed his high musical sense the way the real Mozart did. Kroeber acknowledged Weismann's essay and heavily relied on it, but regarded it as "a brilliant miss," since in the end, Weismann "hastened to the inconsequent conclusion that faculties are probably different after all."[30]

The relationship between inorganic, organic and superorganic change

It follows from Kroeber's account that cultural evolution can proceed independently from biological evolution. Kroeber expressed this claim most clearly in the following figure 2:

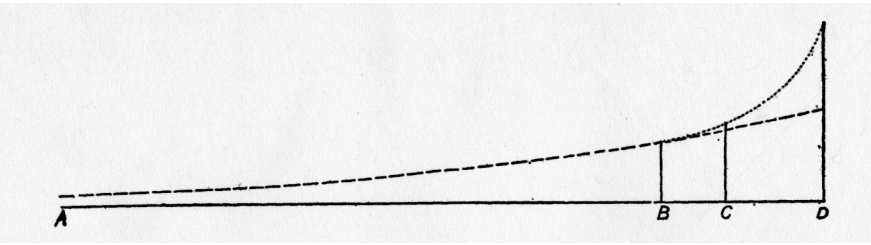

Figure 2. The relationship between inorganic, organic and superorganic change. Source: Kroeber (1917) p. 211. The continuous line denotes the inorganic, the broken line the organic, and the dotted line the superorganic.

Kroeber presents the graph in order to stress that the lines, representing the three different systems of change (inorganic, organic, and superorganic) develop independently from each other. The important point is B, the first human that was able to learn socially from others; C would be the 'primitive' man and D the present moment.[31]

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[30] Kroeber (1916a: 37).

With this, Kroeber opposed what I would like to call *racist hereditarianism*.[32] The latter regarded the synchronic and diachronic behavioural differences between groups of people as being *correlated with* and mainly *caused by* innate differences in ability to produce these cultural differences. Thus, greater wealth and power of one group of people is due to higher innate intelligence. In a diachronic perspective, every cultural change (civilization) is then accompanied by a change in innate endowment. This is what Kroeber denies.[33] But note that, by assuming an inborn faculty of man for civilization and by assuming innate individual differences, Kroeber accepted the hereditarianism of his time. He merely rejected its racist version.[34]

In addition, by looking at culture in this manner, cultural inheritance—symbolized by the dotted line—emerges as the very process that makes culture '*super*organic'. If civilization and biological evolution are as decoupled as Kroeber assumes, then culture becomes clearly visible as a separate, second *system of inheritance and change*. In the end, culture is conceived as being *opposed* to biological heredity (culture as *super*organic) and, at the same time, it is conceived *as* heredity of another sort.

The joining of hands across the gulf

Given that we can replace Lamarckian inheritance of acquired characteristics with social or cultural inheritance, Kroeber assumes that "[b]iology and history can join hands in alliance across the gulf that separates them."[35] From a close intertwining interaction of culture and nature in the concept of Lamarckian inheritance of acquired characteristics, we moved with Kroeber to a strict *separation of nature and culture* on the basis of the concept of hard inheritance. For Kroeber, this conceptual separation is linked to a disciplinary one: biologists should limit their study to biological heredity and the respective organic mental faculties and should leave the explanation of the superorganic culture to the historically working anthropologists. To return, where we started:

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31 Kroeber defined "[h]eight above the base" as "degree of *advancement*, whether that be complexity, heterogeneity, degree of coordination, or anything else" (Kroeber 1917: 211; Emph. added). A page later, he refers to the increase in number of cultural items and complexity of social organization as the things that distinguish us from the Neandertal people as example of the primitive man. The terms advancement or progress pop up here and there in 1917 and also in other papers. Despite these progressivistic wording, Kroeber tries to distance himself from progressivism by stressing: that "[n]othing is more erroneous than the wide-spread idea and oft-repeated statement that the savage is only a child" (Kroeber 1910: 445), a statement that directly leads to a critique of Darwin and like-minded thinkers who claim that the "savage is in a stage intermediate between the higher animals and ourselves." (ibid.) Kroeber also stresses that "[a]ll men are totally civilized" (Kroeber 1915: 286) and that he does not use the term civilization for "high" civilization, since for him it makes perfectly sense to talk about "Apache civilization" (Kroeber 1918: 355), which includes their language, their kinship systems, habits, religion, diet etc.—The just cited examples give a mixed message for the question whether Kroeber was still progressivist and less radical in terms of cultural relativism than his teacher Boas. A precise answer is, however, not central for the issues raised here, even if it is important in its own right; it has to wait for another occasion.

32 Kroeber also opposed eugenics, for instance, in Kroeber (1916a: 34-37; 1916c: 370; 1917: 188-9). If eugenics is understood as Kroeber did, that is, in a narrow way as assuming that progress *cannot* be achieved by social reform (hereditarian eugenics), then it also ignores the possibility of long-term human betterment by cultural inheritance. If eugenics is understood to include Lamarckian points of view, then it reduces culture to environmental influence that is projected into the next generation via biological inheritance. Cooke (1998) suggests that eugenics was Lamarckian (kind of soft eugenics) before 1915 and was predominantly hereditarian afterwards.

33 Kroeber does not say that he can empirically prove that he is right. He merely states that the others cannot prove that they are right. See for instance Kroeber (1916a: 34).

if there is something superorganic, anthropologists do not have to turn into biologists. Instead, biologists are invited to "join them in a cooperative effort to establish the exact nature and the precise limits of the organic and the superorganic."[36]

In the end, Kroeber's plea for a coalition became true, for instance, when Thomas H. Morgan indeed joined in. Already in 1924, in a paper called "Human Inheritance," and again in his "The Scientific Basis of Evolution," he presents social evolution and its peculiar process of "inheritance" as *Ersatz* for Lamarckian inheritance of acquired characteristics, for which he sees no experimental evidence.[37] Social inheritance can be such an *Ersatz* precisely because it leads to the same effects, i.e. because it is functionally equivalent: efforts to change or to learn during one's lifetime are heritable and thus not pointless from an inter-generational, evolutionary point of view. Consequently, Morgan advocates the same interdisciplinary division of labour between geneticists and anthropologists Kroeber asked for.

3. Consequences for the concept of culture and the history of hereditarian thinking

Even if the concept of culture is still subject to controversial debates, not much has changed with respect to Kroeber's claim that culture is a system of change that is maintained via a distinctive inter-individual, trans-generational process of cultural inheritance. *In this sense* culture is even today conceived as a thing *sui generis, as autonomous.* Let me illustrate this last point in a systematic way by distinguishing between three theoretical roles the concept of culture has played up to the time of Kroeber's boundary work.

Three theoretical roles of the concept of culture

Without much further historical argument, I want to claim that up to the 1920s, with respect to the dichotomy between culture and nature, there have been three major theoretical roles the anthropological concept of culture played in the explanation of behaviour:

(C 1) Culture has often been understood as an explanandum: something that is to be explained, by nature or nurture or both of them. I count Tylor's classic anthropological definition of culture as an exemplar of this category: "Culture or Civilization, taken in its wide ethnographic

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[34] Kroeber (1916a: 35). In Kroeber (1916a: 36 and 1917: 189-192) he therefore refers to Galton as being right in claiming that "between individuals mental faculties are inherited in the same ration and degree, and therefore presumably in the same manner, as physical traits […] But it is an entirely uncompelling inference when he then proceeds to explain the diversity between the attainments of social groups such as ancient Athenians, modern Englishmen, Africans, and Australian natives, as due to differences between the average inherited faculties of the bodies of men carrying the civilizations of these social groups" (Kroeber 1916a: 35). "That heredity operates in the domain of mind as well as that of the body, is one thing; that therefore heredity is the mainspring of civilization, is an entirely different proposition, without any necessary connection, and certainly without any established connection, with the former conclusion" (Kroeber 1917: 192).

[35] Kroeber (1916a: 39).

[36] Kroeber (1916b: 295).

[37] Morgan (1932: 187-217)

sense, is that complex whole which includes knowledge, belief, art, morals, law, custom, and other capabilities and habits acquired by man as a member of a society."[38]

(C 2) Franz Boas is well known to have initiated a change to culture as a more-or-less important factor in the generation of behaviour of individuals. Culture has become an explanans: culture helps explaining behaviour, but has to be distinguished from other factors, like race, in such an explanation of behaviour. [39]

(C 3) Kroeber went a decisive step further. He explicitly took *culture as a system of change and inheritance in its own right*, one that relies on social heritage. Culture thus became again an *explanandum*, but a new one. And although the early Kroeber thought that culture is also the only explanans for culture as explanandum (only culture explains culture), the late Kroeber admitted that many factors are involved in bringing about the inter-individual system of change and inheritance he called culture.[40]

It is this last step that I wanted to stress, since it is usually ignored, e.g. even by Stocking, who is well-known for his work on the history of anthropology (especially on Boas, Kroeber, Lamarckism in social science, and the culture concept) and by Cravens and Degler, who are well known for their work on the history of hereditarian thought. Although Stocking, for instance, realizes that Kroeber radicalised Boas approach and further developed the concept of culture, he looks at the concept of culture through a Boasian lens and does not clearly distinguish the second and third way of using the concept of culture. He writes for instance that Boas' and Kroeber's concept of culture provided "a functionally equivalent substitute for the older idea of 'race temperament'. It explained all the same phenomena, but it did so in strictly non-biological terms, and indeed its full efficacy as an explanatory concept depended on the rejection of the inheritance of acquired characters."[41] This is misleading. Boas and Kroeber, first of all, did not have the same concept of culture, since in Kroeber's hands culture became a system of change and inheritance in its own right. Secondly, Kroeber's concept did not simply *explain the same phenomena*, since the concept of culture changed its theoretical role—from an explanans to an explanandum.[42]

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[38] Tylor (1871: 1). As far as I know, the 'acquired' in Tylor's definition bears no systematic role in his account and it is not evident—without further analysis—that it means cultural inheritance in the sense Kroeber means it. Nonetheless, it should be mentioned that Tylor, as does Kroeber, says that he considers questions of race as practically irrelevant for his goals (Tylor 1871: 7).

[39] See Stocking (1968: 212-220). My point holds even if Boas sometimes pointed to social learning as part of culture, since he also did not put an emphasis on it as a central aspect. He predominantly regards culture as a special kind of *environment*, a social environment that influences individual development. This might be the reason why Stocking uses the term "cultural determinism" synonymous to "behavioural determinism" or the "cultural determination of behavior," i.e., in the sense of 'culture explains behavior' and not in the more radical sense 'culture explains culture'.

[40] Nonetheless, Kroeber uses culture in the other two ways vis-a-vis the one he added. This is most evident in Kroeber (1918).

[41] Stocking (1968: 265). Cravens (1978) and Degler (1991) also use the term culture mainly for an environmental factor in the development of individuals, even though Degler comes close to my point, when he writes that Kroeber demanded "more than a mere change in assumptions as Boas had done; he was insisting upon a new mode of explanation for human behavior" (Degler 1991: 94). Freeman (1983) probably comes closest to my point of view, but without distinguishing between different roles of the culture concept.

CONTEMPORARY DEBATES AND A FOURTH ROLE FOR CULTURE

The distinction between the three theoretical roles of the culture concept is not only helpful to revise the history of the concept of culture. It is even helpful to understand contemporary debates about the relationship between culture and nature. First, Boas concept is the one that still dominates nature-nurture-debates in psychology and behavioural genetics. Kroeber's concept, however, is the one that is used in debates about man's place in nature and in those about the interaction between biological evolution and cultural change. In other words, the first is used in developmental contexts, the second in evolutionary contexts. Both contexts involve different questions of interactions.

In addition, there are people who still ignore Kroeber's concept. Evolutionary psychologists, for instance, reduce culture to a mere triggering condition of innately specified behavioural patterns. Cosmides and Tooby, thus, define culture as "any mental, behavioural, or material commonalities shared across individuals […] regardless of why these commonalities exist."[43] Culture is here the explanandum, the specific attributes of a group of a people. It is not a *factor* in the explanation of what people do; it is the explanandum, the phenomenon to explain. At the same time, it is not an *explanandum in Kroeber's sense*. On the contrary, it is considered as merely 'evoked' through experience in the world. Thus, culture (mental, behavioural, or material commonalities) is basically innate. It can be reduced to the decisive influence of innately specified characteristics of mind. The influences of the natural and social *environment* are mere triggering conditions.

Yet, the social environment is what others, dual-or-multiple-inheritance-theorists[44] as well as 'standard social scientists,' as evolutionary psychologists like to say, call culture: a distinctive factor in the explanation of behaviour, that is, an explanans, and a special explanandum at the same time, namely a separate second system of inheritance of ideational units that can and needs to be studied in its own right. And this is exactly what Kroeber wanted to say—with the help of Weismann's concept of hard inheritance. And this is why I regard his case as historically and systematically important. In a way, Kroeber's case and the three different usages of the concept of culture offered above show that evolutionary psychology falls back to the 19th century concept of culture: used by Tylor and long ago abandoned in anthropology. Note that what I have said so far holds even though—from our contemporary perspective—we might question whether a *psychic* unity of man is justified, since mind (or mental abilities) is itself a developmental product of nature and nurture.[45] No child is born with a ready-made mind. Culture would then start off from a mere *genetic* unity of mankind.

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42 That Kroeber wants to distinguish his concept of culture from Boas' is also evident from Kroeber & Kluckhohn (1952), a review of various definitions and concepts of culture, for which they became famous later on. In this they put Boas together with Tylor into the category of "descriptive" definitions using enumerations and Kroeber into this and into a second category of "historical" definitions: definitions with "emphasis on social heritage," even though the early papers of Kroeber at centre here are ignored in this review.

43 Cosmides & Tooby (1992: 117).

44 Such as Cavalli-Sforza & Feldman (1981), Boyd & Richerson (1985), Durham (1991), Richerson & Boyd (2005), or Jablonka & Lamb (2005) and the niche construction theory (Odling-Smee, Laland & Feldman 2003).

45 This has been stressed by John Dupré (2004, 1993).

With dual-or-multiple-inheritance-theorists the last argument (that evolutionary psychologists ignore that culture is a second system of inheritance) can even be taken further since these approaches claim that culture interacts with the biological system of inheritance, at an ontogenetic as well as at a phylogenetic level, influencing thereby the distribution of genes in subsequent generations. With this, these approaches actually introduce a *fourth theoretical role of the culture concept*:

(C 4) Culture becomes a factor not only in the ontogenetic development of individuals but a factor in the phylogenetic process of culture and nature interacting in the evolution of organisms that have a body, a mind and a culture. James M. Baldwin (1861-1934), and others at the beginning of the 20th century, made a similar usage of culture as a factor in the evolution of organisms.[46]

The historical impact of the concept of hard inheritance

I will now explicitly drive home the main point of this essay with respect to the cultural history of heredity. What was the historical impact of Weismann's concept of hard inheritance on how the relationship between nature and culture was conceived? I want to defend the following three claims:

(H 1) First, inheritance of acquired characteristics or soft inheritance in general allowed for *soft hereditarianism*. On the basis of soft inheritance, one could be a hereditarian and give culture a significant role to play in the evolutionary process, since the hereditary material itself was considered as being soft, that is, malleable by cultural or environmental influences. Culture, and that includes education and social reform, could play a role without the need to refer to social or cultural inheritance.

(H 2) Given Weismann's concept of hard inheritance, this possibility was gone. *As long as cultural inheritance is ignored*, hard inheritance leads to a hard hereditarianism, a picture where cultural and environmental influences cannot exert any influence on the evolutionary process. One could reduce everything to biological inheritance by combining the continuity of the germ plasm with the view that the germ plasm is the sole hereditary material transferred down the generations of individuals. (It was the latter, that has often wrongly been attributed to Weismann as I have shown above).

Both of these claims are more or less part of the received view on the impact of soft and hard inheritance. Yet the received view also takes it for granted that the concept of hard inheritance was therefore partly responsible for the vogue of *hard hereditarianism*—a view where nurture (natural environment and culture) does not play any explanatory role anymore. And indeed, at least until the end of World War I, geneticists as well as the general public predominantly believed in the

[46] The relationship between Baldwin, Boas and Kroeber would deserve close investigation here but has to wait for another occasion. Consult Simpson (1953) or Weber & Depew (2003) for more on the 'Baldwin effect'.

power of biological inheritance to explain behavioural differences (within and between groups). At least, they usually did not say anything to the contrary.[47] This is why Bowler, for instance, writes that the "social consequences of biological determinism" are not a product of social Darwinism or Darwinism as such, but a product of the rise of genetics, which "represents the collapse of a pre-Darwinian 'developmental' view of nature with consequences that were at least as profound as those associated with the initial conversion to evolutionism."[48] I depart from this received view by claiming that:

(H 3) Since nothing in the concept of hard inheritance prevented one from acknowledging cultural inheritance, the connection between the concept of hard inheritance and biological determinism (or hard hereditarianism, choose your term) is neither necessary nor historically true, as the examples of Weismann and Kroeber show.

The concept of hard inheritance was thus not exclusively linked to hereditarianism, or, to put it in other words, the concept of hard inheritance did not have an unambiguous, unidirectional historical influence. To the contrary, it had an *important* historical impact on the rise of the concept of culture as a superorganic, separate *system of change and inheritance*: a concept of culture that led to the break of the hereditarian consensus in the US of the early 20th century, and that thereby helped establish the boundaries of anthropology. This culture concept flourishes until today, at least in anthropology.

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47 See Ludmerer (1972), Kevles (1985), Barker (1989), Paul (1995: 40-49). The concept of hard inheritance surely was not the only reason for the dominance of hereditarianism, but it is usually taken as one of the reasons. Part of the hereditarian bias might have been due to the growing scientific success of genetics as an experimental science in explaining biological heredity. Part of it might have been due to socio-political views, part of it due to institutional developments, as Cravens (1978) suggests. Usually, Johannsen is cited as an early exception to the rule of 'geneticists were hereditarians', and Morgan and Jennings as exceptions of the 20s, e.g. in Paul (1995: 115-117).

48 Bowler (2003: 24).

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Comments on Daniel Kevles' and Maria Kronfeldner's papers

Edna Suárez

Within the context of our workshop, the papers of Dan Kevles and Maria Kronfeldner could not be more different than they are. One deals with plants, the other with man; one deals with property rights and the other with the institutionalization of disciplines and the history of concepts. One extends along a Braudelian mid-term durée (the realm of general economic trends), and the other along the trajectory of an individual and an academic discipline.

Thus, I hope you are not expecting me to find relations among them, though the title of this session, "Contexts of Heredity" may provide me, at the end, with some common questions to both exponents.

I am going to begin with Dan Kevles' paper. His reconstruction of the many ways in which animal and plant improvers sought protection to what they saw as their "intellectual property," offers us an explanatory framework for the pre-history of the patents of living beings in the United States. As Chakrabarty won the Supreme Court case in 1980, to be warranted a patent for his genetically modified bacterium, many in the United States and around the world wondered not only if the US Congress should have been involved in a new patent legislation, but even more, what historical, economic and even ethical or moral transformations had allowed the Supreme Court judges to take that narrow decision.

As the Century of the Gene closed with a mixture of good and bad news for the genetic engineering industry, the growing number of patents of living beings or their parts, or even the patent of bio-macromolecules by US firms, universities and governmental agencies, stands still as a highly controversial issue around the world. What I would like to stress is an outsider's view of the history of the US, that is, its *exceptionality* regarding the patentability of life and, more generally, the importance of granting intellectual property rights since more than a century ago.

Trademarks and some kinds of property rights developed in different ways across the industrialized countries during the XIXth Century. When I speak of the exceptionality of the US condition regarding the patentability of life and, more broadly, the history of intellectual property rights, I attempt to redirect our attention to what might be seen as an almost "natural" search for financial return by part of the breeders and improvers of animals and plants in XIXth century United States. Clearly, it was not a *natural* right, as is manifested in the confrontation of values implicated in the "products of nature doctrine." It is an historical phenomenon, a general economic trend, but also a question of values that came together with the transformation of the American market, and which needs an explanatory framework. I think Daniel Kevles is particularly well situated to give us that framework and that is what I would like to ask of his recent research in what is part of the pre-history of patents.

Dan gives us some clues to the exceptionality of the US condition. He argues that before the Civil War "markets in agricultural stock were largely local, and the seed, nursery, and animal breeding industries were only incipient" (p. 3), thus the protection of intellectual property found its way only during the latter third part of the century, as "(r)egional and national agricultural

markets emerged with the construction of railroads and amid increasing urban demands for meats, fruits, and vegetables, as well as ornamental plants" (p. 4). It is in the context of the competition for markets after the Civil War, of the need to capture financial returns and do business at long distances, that the animal and plant breeders, orchardists and nurserymen, began to seek the "protection of their rights."

The old-regime system of prestige, reliability and admiration of products by the local community, were not sufficient any more. But the succeeding of the advocates of property, of course, did not take place without enforcement measures and even casualties. Dan refers an important triumph of the seed industry in 1924, when they succeeded in their campaign to ban the distribution of free seed to farmers by the US Department of Agriculture and the US Patent Office.

My questions to Dan do not have the intention to deviate our analysis to the economic history of the US. Rather, they point to the need of awareness of the historical specificity of these changes. Moreover, I think this issue has something important to tell us about the cultural history of heredity. It is convincing that the development in regulations of intellectual property of plants had almost nothing to do with the rise of Mendelism, since many of the claims of the agricultural industry had to do more with crafts and with the chance finding of mutations and sports in the American fields. But, along the history of the reification of heredity, as Carlos Lopez has called it, a central phenomenon seems to have taken place when heredity began to be considered a *commodity*, a tendency that has not expired today. Could we say more about the "commodification" of heredity as part of the long-durée history of heredity? I hope that the nature of my comments will make clear that we are not expecting for general answers, but more modest attempts to deal with the specificity of cultural—including of course values—and economic contexts.

Maria Kronfeldner's paper looks in another direction. The context, although also referring to the United States, points to the academic scene and the construction of concepts as part of the boundary work developed by cultural anthropologists in the first part of the XXth century. Here, however, we have the heavy load of hereditarianism of several kinds (including of course eugenics and racism) as a more explicit factor of her historical and conceptual analysis. I find Maria's distinction of three theoretical roles of the concept of culture illuminating for understanding recent—and not so recent—developments in the intersection of evolution and development. The connection between the concept of culture used by evolutionary psychology and the early concept of Tylor, accounts for the impression that a somewhat old-fashioned concept of culture is at play in this approach.

Even more fruitful is her critique of the received view, namely, that hard heredity—that is, the rise of genetics—is responsible for the collapse of the developmental view of nature and for the expulsion of nurture. Maria's argument, instead, tries to direct our attention to the fact that linked to the idea of hard heredity, in Kroeber's later work, cultural or social inheritance were certainly expelled from evolutionary accounts. On the developmental level, however, hard inheritance provided the framework of coalition and opposition that anthropology needed in order to distinguish itself from biology and in particular genetics. Cultural inheritance, even if it is embodied in biological individuals, is autonomous from hard genetic inheritance. Heredity was

always more than genetics. In this particular case the "hardening" of inheritance and its restriction to genetics dialectically provided a space for cultural anthropology to flourish in the academic scene.

Maria's analysis is convincing, in part because it give us a framework to account for the differences between so many versions of hereditarianism in the XXth century, and to clarify some terms in the nature-nurture debate. Though I should confess that I am deeply ignorant of the history of anthropology and I imagine her views might be contested by those who have interpreted the superorganic nature of culture in different terms. My questions, instead, refer again to the context of these developments in American Anthropology. The drawing of disciplinary boundaries, and their changes, can tell us a lot about the actor´s views of themselves. But I long for a more detailed account of the relations of Kroeber and his contemporaries and, more importantly for a comprehension of the century of the gene, I would like to have more details of the connections between the rise of cultural anthropology in the United States and the prevalence, for instance, of dual-inheritance-theorists in contemporary debates.

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Producing Identity, Industrializing Purity: Elements for a Cultural History of Genetics

Christophe Bonneuil

In December 1910, just one year after the coining of the terms "gene," "genotype" and "phenotype" by Wilhelm Johannsen in his *Elemente der exakten Erblichkeitslehre* (Johannsen, 1909), a symposium on the "Genotype Hypothesis" was one of the key attractions of the meeting of the American Society of Naturalists at Cornell. Leading figures of genetics and plant breeding[1] discussed the various aspects of Johannsen's "principle of pure lines, as a true analytical implement, as an indispensable method of research in heredity" (Johannsen, 1911, 143). Even more so than "unit factors" or "genes," "types," "permanency," "stability" and "purity" were the buzzwords of this meeting. Almost everybody endorsed then the idea proposed a few years earlier that "the study of the behavior of pure lines is the basis of the science of heredity" (Johannsen, 1903, 9). The papers of this session, published in American Naturalist were continued by follow up discussions in Science (Jennings, 1911b; Shull, 1912a and 1912b).[2] This stream of papers enthusiastically used, promoted and extended Johannsen's concepts of pure line and genotype. Jennings, who had experimented on the effects of selection on pure cultures of *Paramecium*,[3] explained that "we need badly a term that will include 'genotypically identical' series of forms" (Jennings, 1911b, 842). This is why he turned Johannsen's 'structural' genotype concept round to a 'populational' one ("a concrete, visible group of organisms" having "the same combination of hereditary characters" and proposed an extended definition of pure lines:

(1) in case of vegetative reproduction [of unicellular or pluricellular organisms],
(2) in at least some cases of parthenogenesis (where no reduction division occurs),
(3) in case of self-fertilization of homozygotic organisms [pure lines stricto sensu in Johannsen's sense],
(4) in case of inbreeding of a group of genotypically identical homozygotic organisms (Jennings 1911b, 841).

As early as 1904, Shull had also extended Johannsen's stricto sensu definition of "pure lines" to any "population relating through budding or other method of vegetative reproduction" (Shull, 1905 quoted in Shull, 1912a, 27), for which the USDA agricultural scientists O. F. Cook and Herbert J. Webber had recently coined the term "clon" soon to become "clone" (Webber, 1903). As a young scientist willing to play a role at the frontier of genetics, Shull verified Johannsen's claim that F1 hybrids from homozygotic parents show no more variability than pure lines do. As a breeder, he also hoped to command and control the homogeneity and vigour of F1 hybrids (as compared to populations) and to capture heterozygosis in stable, mass-produced and profitable

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1 The speakers were: W. Johannsen, Herbert S. Jennings, George H. Shull, Edward East, Raymond Pearl, J. Arthur Harris and Thomas Hunt Morgan.
2 I thank Christina Brandt for making me aware of several of these papers.
3 See J. Schloegel, this volume.

life forms. For these reasons, Shull was no less attracted than Jennings by the search for general conceptualisations for genetically identical groups and he joined in spreading the gospel of "clone," "biotype" and "genotype" concepts. He undertook to extend the validity of Johannsen's genotype concept to cross-breeding populations (Shull, 1908 and 1911). He also introduced the notion of "clonal varieties" to label under one and the same category not only potatoes and *Paramecium*, but also perfectly standard and homogeneous heterozygots such as his F1 hybrid corns from two pure lines, since "in the 'clone', it is possible to retain as a permanent feature of the group any purely heterozygous character, as for instance the vigorous constitution dependent upon the stimulation of heterozygosis" (Shull, 1912a, 28).

The practices of grafting, budding and other vegetative reproduction techniques were common practices, some being as old as agriculture. What was then the rationale behind the creation of new scientific terms in the first years of the XXth century, that related "pure lines," "clones" and heterozygous F1 hybrid clone-like varieties? And how can we account for the considerable amount of efforts displayed by geneticists, through hard experimental and statistical work on beans, protozoa or chicken, to separate "fluctuation" as what is caused by the environment from what lies in "genotypical constitution?" Why so much work to construct an "intrinsic" genetic identity of organisms, that could be separated from the influence of time and place and could circulate unaltered in new kinds of scientific and economic networks. In other words, what were the specific historical conditions of this period to call for so huge efforts to engineer and conceptualize genetic sameness, genetic stability and genetic purity?

In *Purity and Danger*, an essay dedicated to cultural attitudes toward "impurities" and "pollutions," Mary Douglas stated: "I consider as partial any explanation of ritual pollution that would limit itself to only one kind of impurity or only one kind of context" (Douglas, 2001 [1966], 21). Following Douglas' methodological commandment, this article sketches a cultural history of early XXth century genetics that relates new conceptualizations of the identity and connectivity of organisms that postulated the stability of "types" and of hereditary constituents, the rise of quantity production of new life forms (in biological laboratories, agricultural experiment, fields, hospitals and markets), and new cultural attitudes towards time, space, purity, efficiency and fairness. I will argue that the new framings of heredity and these new life forms were designed in and for a new space of flows, a new matrix of practice and meaning that structured both apparently esoteric scientific investigations on *Paramecium* or *Drosophila*, and industrial culture of rationalisation and control. The first section will discuss some of the concepts and analytic tools of this paper: Müller-Wille and Rheinberger's "epistemic space" and Phillip Thurtle "space of flow," and Boltanski and Thévenot's "orders of worth" and how I relate them in my attempts towards a cultural history. The second section analyses the shift from a Darwinian space-time of organic fluxes to an experimental-industrial space-time. The third section documents the quest for purity that pervaded late 19th century and early 20th century biological research.

1. "Epistemic space," "space of flow" and "worlds of worth"

The advent of modern genetics has often been described as the advent of the gene as the unit of explanation and the victory of hard heredity over soft heredity conceptions (Mayr, 1982; Fox-

Keller, 2000). Its heroic advent is still often narrated as the victory of Mendelians over Biometricians, old school breeders, and Neo-Lamarckists (Provine, 1971; MacKenzie and Barnes, 1979; Buican, 1984). But this focus on Mendelism has obscured the complex relations between mendelian hybridisation research programs on the one side, and "pure line research" programs—associated with a more typological than combinatory thought—developed by De Vries and Johannsen. More generally, the Mendelism-centered view of the sciences of heredity in the first half of the 20th century generated a great numbers of anomalies and generated stories of reluctances, exceptions and intellectual speciations: "rediscoverers" like De Vries seeing isolation and mutation as more important driving forces for evolution than hybridization and more powerful tools for plant breeding (Meijer, 1985), Johannsen having little interest in mendelian crosses as a research strategy (Müller-Wille, 2007), interest in cytoplasmic inheritance and non-Mendelian heredity (Sapp, 1987), reluctance to Mendelism based on a physiological and Pasteurian thinking that would turn to be very productive a few decades later in the birth of molecular biology in France (Burian and al., 1988), plurality of breeding strategies (beyond the traditional view of breeding revolutionized by Mendelism, or being an application of it) until the mid 20th century, all of them being perfectly rational when considered as technological paradigms which co-evolved with differentiated bio-socio-economic contexts (Palladino, 1994; Harwood, 1997; Wieland, 2005; Bonneuil, 2006).

This paper does not aim at analysing the whole zoo of non-Mendelian (or superficially Mendelian) research schools in early 20th century genetics and breeding and weighting the contribution of each in the progress of genetic knowledge (which clearly did not proceed along a single line). What I rather want to explore, is what the various traditions of research on heredity after 1900 (which profoundly disagreed on the role of genes, cytoplasm and the environment in heredity, on the role of mutations and hybridization in evolution, on the value of Mendel's laws for practical breeding, etc.) deeply shared at more profound levels. If there is a revolution in the study and mastering of heredity at the turn of the 19th and 20th century, and if this revolution cannot be reduced to the diffusion of Mendelism, I will frame this revolution, on the basis of numerous studies from many scholars, as a shift in the "epistemic space," the "knowledge regime" and the "worlds of worth" in which heredity was thought and manipulated.

Staffan Müller-Wille and Hans-Jörg Rheinberger (2004) have called for the need of a cultural approach to understand wide shifts in "knowledge regimes" on heredity. Such shifts, they argue, cannot be reduced to "'epistemic things'—in the sense of being determined within individual experimental settings"—or to a paradigm, but rather "depended on a vast, spatial configuration of distributed technologies and institutions connected by a system of exchange: botanical gardens, hospitals, chemical and physiological laboratories, genealogical and statistical archives" (Müller-Wille and Rheinberger, 2004, 23). To make sense of such wide shifts, Müller-Wille and Rheinberger have coined the term epistemic space, a more "regional" concept than Foucault's episteme. This concept seems very fruitful because it provides a lens to map the continent drifts between, say, common traits exhibited by the various "epistemic cultures"[4] of heredity in the early 19th century and common traits exhibited by the various epistemic cultures of heredity in the mid 20th century. These authors have exemplified their "epistemic space" approach with the shift they

[4] On "epistemic cultures," see Knorr-Cetina, 1999.

see around the middle of the XIXth century when heredity became not only a genealogical (vertical) notion but also a spatial (horizontal) one, i.e the cytological space of hereditary germs in the gametes and fertilized egg. Such a shift was made possible by the development of cell theory, by the assumption of an essential fluidity between all organisation levels of organic life from hereditary elements to species and of the existence of similar mechanisms to account for their transformations, and by a focus of the biological gaze towards the search for "patterns and processes that structure life on the intra-specific level" (Müller-Wille and Rheinberger, 2004, 13). They also argue that the epistemic space of heredity "resided in the heart of capitalist institutions from its very inception" (ibid., 23) and that "the emergence of heredity as a research attractor, as a discursive center, occurred in a knowledge regime that started to unfold when people, objects, and relationships among them were set into motion" (ibid., 13).

From a different starting point, Philip Thurtle has come to see a similar connection between changing rationality in thinking about heredity and late 19th century's wide scale circulation of goods and people. His work understands "the history of the science of heredity as a mutation in cultural practices for dealing with space and time" (Thurtle, 2008).[5] From this perspective,

> Genetics is a science of mass culture in much the same way that the modern newspaper is a communication medium of mass culture or the urban train station is a transportation medium of mass culture. They all are reliant on the same technologies of transportation and communication, they all create a new conceptual space that denies the importance of place in human interactions, and they all support new ways of folding experiences that will lead to modern conceptions of information. Some would even claim they all privilege a lowest common denominator in order to describe human connectedness over new geographic distances and over radically long periods of time. (Thurtle, 2008)

More precisely, Thurtle explores the cultural conditions of possibilities of what he calls "genetic rationality," one major aspect of which is the quest for a "genetic identity, the unchanging core of heritable material sealed off from the influence of time and place" (Thurtle, 1996, 2007, 2008). Thurtle goes further in showing how different research programs in genetics and breeding, such as Burbank's and De Vries', inhabit (and contribute to make emerge) different types of spaces, and document the emergence of a "new type of space at the turn of the century, a space built on the exchange of manufactured commodities, managed by a host of new informational practices" (Thurtle, 2007). The second industrial revolution allowed for increased profits by exploiting economies of scale and increased circulation of goods, and called for a host of new innovations the way information was collected, stored and processed. This, according to James Beniger was the hallmark of the "control revolution," which took place from the last decades of the 19th century on, in order to increase production efficiency, ensure the safe distribution of standard goods and raise product awareness among consumers (Beniger, 1986). These developments, argues Thurtle, opened up a new type of space, which he calls (after Manuel Castells) the "space of flows," a space in which objects circulate intensely from one location to another and are designed to be used in a wide number of places; a space in which the values upheld by exchange came to be promoted at the expense of the values of the specific locations. (Thurtle, 2007). Seen from this wide cultural

[5] I thank Philip Thurtle for sending me pieces of his forthcoming book.

perspective, the shift documented by Jean Gayon (2000), from force to organisation in views about heredity at the turn of the century shows striking homologies with a global shift form energy and speed (the industrial revolution) to control (the control revolution) in the same period.

A third strand of scholarly work that seems to me particularly useful for a cultural history of genetics is provided by Luc Boltanski and Laurent Thevenot "sociology of worth" (Boltanski & Thévenot, 1999 and 2006; Boltanski & Chiapello, 2006). From a wide range of situations where people are led to justify their actions, these social theorists have abstracted a plurality of logics of justifications ("worlds of worth" or, in French "cité"), each being exemplified by a classic author: civic (Rousseau), market (Smith), industrial (Saint-Simon), domestic (Bossuet), inspiration (Augustine), fame (Hobbes), and connexionism (a new order of worth they found in late capitalism's neomanagement discourse). These seven "orders of worth" are based upon a "convention of equivalence" that brings together different sets of people and objects and creates a certain kind of commensurability that allows judging them and weighting their worth, but the underlying principles of order differ from one another. For instance in the domestic world of worth (*cité domestique*), "worth depends on a hierarchy of trust based on a chain of personal dependencies. The political link between beings is seen as a generalization of kinship (…). The person, cannot, in this world, be separated from his/her belonging to a body, a family, a lineage, an estate" (Boltanski & Thévenot, 1999, 370). On the other side, in the industrial world of worth (*cité industrielle*), worth is based on efficiency for a specific function and the relations between persons (and objects) "can be said to be harmonious when organized, measurable, functional, standardized" (ibid, 373). Notwithstanding its weakness of seeming quite fixed and a-historical grammar, the "worlds of worth" perspective can provide a fresh standpoint on many findings of scholars in the history of heredity. As we shall see, the call for purity, pervading the *longue durée* history of ideas on heredity, can take quite different forms in different worlds of worth. In a *cité domestique*, purity might refer to kinship, to a trustworthy keeping of pedigree books whereas in a *cité industrielle*, purity might be redefined by a particular assay (a measurement of performance or a back-cross). Rather than a structural property (say, a homozygotic constitution) whose value is associated with the possibility of its replication, of its mass-production in a stable state, purity was in the mid 19th century dominated by a mix of domestic, inspiration and fame worlds of worth, and hence valued as something particularly rare and unstable, that needs constant care to be maintained.

2. Out of Darwinism's space-time: erasing time and space, disciplining organic fluxes, controlling variation

Peter Bowler has written about "The eclipse of Darwinism" (Bowler, 1983). More than a mere shift in evolutionary thinking around 1900, this "eclipse" also refers to a wider change in biology's knowledge regime, from an evolutionary space-time to an experimental-combinatory space-time. Mid 19th century biology, eroding the previous dichotomy of individuals and species, saw life as a property extending both downwards (to the cells and molecules) and upwards (to the species, societies and colonies). Biologists of the generation of Darwin, Haeckel, Galton or Weissmann imagined extensive organic traffics, linking the macro and the micro levels of organisation, linking

organisms and the environment and linking organisms from different species (cell theory, pangene theory, evolution, interspecific hybridization, acquired heredity, symbiosis, etc.). Natural processes and human activities were seen as similar in nature and interconnected so that the observation of one realm would greatly improve the understanding of the other. 19th century biology's emphasis was on continuous change, exchange and admixture—rather than on stability, fixity, isolation and purity—as fundamendal properties of life and as driving forces of evolution. Darwin's pangenesis theory, Quatrefage's "tourbillon vital," for instance, "nicely demonstrate the degree to which, by the late nineteenth century, individuals had been resolved in an underlying system of circulating, sub-microscopic entities only to re-emerge as ephemeral and contingent results from the interaction of such entities, both with one another, and with their respective environments" (Müller-Wille, 2007).

Early 20th century biologists, on the contrary, put the emphasis on isolation as the driving force of speciation (synthetic theory of evolution) and ceased to view naturally occurring hybridisation and gene flow as a major research object, sought for new typological units reinforcing stability and fixity as an underlying principle of life and turned organisms into purified reagents that experimental strategies put in reaction with one another. While 19th century had framed reproduction as a system of circulating and ever changing elementary entities such as "gemmules," "pangenes," "organic units," and so on (Müller-Wille, 2007), it seems as if 20th century biology had—symbolically and practically—disciplined these circulations, fixed these entities into invariant units (stable genotypes and immutable genes, safe at low mutation frequencies,), and had grasped and redefined heredity, as well as many other biological functions, in terms of predictability of effect in controlled biological reactions.

Out of history

In mid 19th century, Coleman has shown, "embryology, natural history, evolution theory, even cellular anatomy, were historical disciplines," and one may add plant and animal breeding and human biometry to this list (Coleman, 1977, 162). But in a few decades, the rise of an experimentalist way of knowing in late 19th century (Pickstone 2000; Rheinberger and Hagner, 1993) was associated with a leaving behind of the ideal of historical explanation in biology. This move was particularly strong in the understanding of heredity, from time and vertical transmission to a timeless combinatory structure keeping its permanency though space. Even if they chronologically overlapped, refracted by the diversity of biologists' individual trajectories, we may distinguish analytically a few steps in this move.

A first step, the shift from heredity as historical force to heredity as structure has nicely been analysed by Jean Gayon. "Heredity was not the sum total of ancestral influences; it was a question of structure in a given generation. What happened to the progeny did not depend on what happened to the ancestors of its parents, but only on the genetic makeup of its parents" (Gayon, 2000, p. 77). Indeed, most mid 19th century breeders, physicians and biologists saw heredity as a kind of force whose effect would be stronger and more robust when accumulated over many generations ("atavism"). This view could explain the sudden apparition at one generation of ancestral characters which had 'skipped' several earlier generations. Although such a view was still held around 1900 by most breeders and was behind Biometricians' law of ancestral heredity, Jean

Gayon has shown that this move to think heredity as a particular constellation of particulate elements rather than a force was taken in the 1860's and 1870's by Darwin (1868) and by Galton (1876) himself. Darwin's pangenesis theory (1868) postulated material particules (the gemmules) gathering in the gametes from throughout the body of the parents so as to be passed to the next generation. This idea of independent organic particles of heredity[6] stemmed from the more general view of the "independent life of each element of the body" (Darwin, 1868 [1990], 119) promoted by Claude Bernard and Rudolf Virchow. In 1876, Francis Galton, in "A theory of heredity," argued that the basic locus of heredity was not so much a line of transmission from parents to descendants, but rather a cytological space, "the newly fertilized ovum" filled with the "germs or gemmules, or whatever they may be called." He compared this structural space to a "post office" where mail bags full of letters (the "organic units" of heredity) are processed to be distributed to their recipients:

> Ova and their content are, to biologist looking at them through microscopes, much what mail bags and the heaps of letters poured into them are to those who gaze through the glass window of a post office. Such persons may draw various valuable conclusions as to the postal communications generally, but they cannot read a single word of what the letters contain. (Galton 1876, 331)

This metaphor is one of the earliest occurrences of the idea of heredity as text and of the idea (if not the word) of heredity as information that has to be stored, processed and redistributed. It is striking that such new conceptions of heredity had been drawn from a comparison with the processing of information in postal services, one of the key technological and bureaucratic activities that boomed during the control revolution of late 19th century.

Another metaphor used by Galton to describe the hereditary units of the "stirp," is the political metaphor of the "nation," within which some individuals compete to be elected and serve as representatives in the fully developed body (Galton 1876). Whereas Darwin had developed analogies with breeder's practices (which were still cottage industry and craftmen practices connoting a kind of stewardship over animals and crops that was essentially similar to the shepherd in Plato's Republic, hence situating heredity in a domestic world of worth), Galton preferred industrial/bureaucratic and political metaphors to make sense of heredity.

A second step was the 'sanctuarisation' of the particles of heredity into a specific place, "deeply buried in the body" as François Jacob put it, separated from the experience of the organism in its environment.[7] Heredity shifted from infinite universe to closed world. Heredity became a matter of inwardness rather than of interactivity. The great American fruit breeder Luther Burbank viewed heredity as "stored environment" and he saw hybridization as a powerful tool precisely because it put into contact two plants originating from different places (Thurtle, 2007). Heredity was bonded to a place. But this bond was cut by new visions of the units of heredity being isolated

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6 Each particle or "gemmule" was for Darwin a precursor for a cell, rather than for a character, as assumed by De Vries in his 1889 intracellular pangenesis. But Darwin did himself a move in this direction when he wrote that "a certain number of gemmules is necessary for the development of each character…" (Darwin, 1868 [1990], 157).

7 "A higher order structure has to exist, still more hidden, more deeply buried in the body. It is in a third order structure that the memory of heredity is located" (Jacob, 1993, 207).

from both the environment and the particular experience of the organism. By the turn of the century, the organic units of heredity were not anymore going out in the whole body and then back to the gametes: their circulation was disciplined and they came to be confined in the "stirp" (Galton, 1876), the "germinal plasma" (Weissmann, 1883, 1892) and/or in the nucleus (De Vries, 1889). One could think about a specific place of storage separated from the contingencies of the organism. A division of labor, a specialisation of function had been sought for the storage of hereditary information.[8] Therefore, as Galton (1889) and Johannsen stressed it, no transmission of hereditary traits did occur from parents to children; but from germinal lines to gametes and from gametes to somatic and germinal lines : "Heredity may then be defined as the presence or absence of identical genes in ancestors and their descendants" (Johannsen, 1911, 159). This was a major reordering of how organisms connected with each other in time and place: the space-time of origins and bonds was replaced by the "deeply buried" cytological space-time.[9]

Much related to this second move, the third step may be named a "devitalization" or a "stabilisation" of the units of heredity. For Darwin and for Galton until the 1870's, as well as for De Vries in the 1880's, the gemmules (or pangenes) were much more than discrete, independent and particulate bearers: they had their own and rich organoid-like life. Their life history was strongly impacted by their past and was full of events of encounters, repulsion, competition for being "representative." The hereditary units grew, ate and reproduced; they were viewed as assimilating materials, changing from latent to active state and back, from being prolific to being exhausted and sterile and vice versa, etc. Darwin's, Galton's, Weisman's, Spencer's and De Vries' hereditary units had their own family tree, their particular and ever changing history. The micro world of gemmules being analogous to the macro world of organisms in evolution, the particles of heredity were viewed as capable of experiencing differentiation and transformations, increasing in complexity and radically changing in number, state, and fertility.

Galton, for instance postulated in the 1870's that "patent elements" [i.e. the organic units of heredity that were expressed in the parent organisms] were less likely to be transmitted precisely because, having been developed into cells in the parent organism, they were somehow exhausted and less active (less "fertile") or less numerous in the gametes and could not compete with the "latent elements" (Galton, 1876, 339-340). This accounted elegantly for the law of regression, this "steady tendency to deterioration in exceptional peculiarities" that he had observed in the patterns of inheritance of human genius and that was corroborated by "the avowed difficulty, among breeders, of maintaining the high character of any variety that has been produced by accident" (Galton, 1876, 340). For Galton, "existing races are only kept at their present level by the severe action of selection": *performance was not encoded in hard heredity but constantly maintained through a designed environment of selection*. This "nothing is fixed for ever" view of heredity widely

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8 Althought the term "information" in anachronical here, I use it having in mind Galton's metaphor of the post office.

9 This move away from interactivity and bondedness in the definition of the biological self was ultimately extended to man by Sigmund Freud. Whereas early 20th century Biologists searched for the unchanging core of living beings sealed off from any bond in time and place, Freud relocated human identity from a priviledged bond with the environment but rather inward into the ego, "what seems us autonomous, unitary, well separated from anything else" (Freud, 1995, 7). He disqualified what Romain Rolland had called "oceanic feeling," a feeling in which the individual feels bonded with the entire world, as an expansion of the ego typical of infantile narcissism.

held by late 19th century biologists and breeders, even when they started to think of heredity as cytological space rather than a force, was very close to the fin de siècle notions of entropy and fatigue described in Anson Rabinbach's cultural history of the sciences of energy and work in the same period. It is interesting to note that Galton himself explained mental fatigue in quite the same way as heredity. In effect, he concluded that while brilliant and active minds are more subjected by the pathologies of "excess of work," "les personnes à esprit mou protègent leur propre santé cérébrale" (Galton 1889b, 103). This view strongly echoes to his views on heredity and regression, when he hypothesized that elite traits bearing gemmules are less fertile (hence less inherited) precisely because they are extraordinarily so expressed in an individual. The recurrent theme here is the fragility and fatigue of the elite. As Rabinbach showed, the Darwinist's move from "nature's design" to an undecided future made by chance and by endless struggles fuelled a multiform fin de siècle sensitivity for energy dissipation, race degeneration and national decline (Rabinbach, 2004, 49). Rabinbach has shown how much "Helmoltz's cosmos was a cosmos at work" (Rabinbach, 2004, 123). In a similar manner, late 19th century biologists' genome, to use an anachronistic term, was a genome at work, a dynamic space of organic activity and competition rather than a typological concept ("genotype") or a program it would later become in the "century of the gene."

Galton himself made an important move from organoid-like swarming units to stable units of heredity. In Natural Inheritance, he stated that "the stability of type, about which we as yet know very little, must be an important factor in the theory of heredity" (Galton, 1889a, 31). Unlike in his writings from the 1870's, he now viewed the hereditary units as rather immutable entities, and compared gametes formation with a deal in a cards: heredity was more about lottery than about development (Bulmer, 2003, 129). De Vries followed this move and incorporated the statistical approach for the first time in 1894, referring to Quételet's urn with white and black balls to explain the 1:2:1 ratio he would later rediscover in Mendel's work. Finally, in 1903 De Vries, had totally changed his views on pangenes: even if he kept the latent/active dichotomy, he abandoned his earlier view that they could change in their state, number and nature, and he acknowledged that their state was almost invariant (Stamhuis et al, 1999, 247-259).

Mendel and neo-Mendelians, thanks to their use of the simplest symbolism to depict complex physiological characters, led to a further drastic reduction of the relevant properties of a hereditary unit, from a whole array of states (numerous/few, fertile/sterile, fast growing or not, well nourished or not, latent or active, circulating more of less actively in the body, etc.), to only "presence/absence" and "dominant/recessive": the "history" of the units was pointless, their combination was everything.

Finally, Wilhelm Johannsen, who coined the terms gene, genotype, and phenotype (Roll-Hansen, 1989), finished the job of disciplining and stabilizing the units of heredity:

> The concept of the gene as organoid, as small body with its own life and whatnot, is not any more to be taken into consideration by research. The conditions for such a concept are totally absent. A horse nesting in the locomotive as cause of the movement is no less a 'scientific' hypothesis than the doctrine of organoids to 'explain' heredity." (Johannsen, 1909, 485)[10]

In the course of this devitalization of the "hereditary units," they became immutable bearers of elementary traits. The range of possible states they could go through (latent/active, attracted/repulsed, actively growing or not, numerous/few or fertile/sterile) were drastically reduced to being present or absent, dominant or recessive. The production of heredity ("like engenders like") ceased to be a matter of competition, repulsion or growth but became a more deterministic combinatory game in sets of immutable units. Heredity ceased to be the product of organic history (not fully predictable from the nature of elementary units in their initial state) and became the predictable output of a particular constitution. Charles Lenay catches this shift in a vivid way in a thought experiment to imagine how Mendel's contemporaries might have read his work:

> Its reflections on constant differential characters, which like abstract and unalterable qualities, could be distributed in the descendants without being modified or even interact between each other caught the biologists on the wrong foot, who where looking for mechanisms of continuous transformation, materially comprehensible, of characters of the species. (Lenay, 2000, 1058)

Indeed, much more than with mid nineteenth century biology, the new understanding of heredity of the turn of the century, postulating a tuned and predictable machinery of hereditary units, was very much in line with the rising tide of the industrial world of worth.

The stable gene concept, whether viewed as a kind of chemical reaction (Johannsen) or as a material particle (De Vries, Morgan…), was the keystone of the new combinatory, structural and a-historical view of heredity. Once hereditary units had no relevant life history, (natural) historical explanations became irrelevant in the understanding of heredity. For Johannsen "ancestral inheritance" was a mere fiction (Johannsen, 1911, 138). "Ancestry by itself is irrelevant; dispositions are decisive" he stated in his 1905 Textbook (Johannsen, 1905, p. 216, quoted by Müller-Wille, 2007). For W. Johannsen,

> the genotypic constitution of a gamete or a zygote may be parallelized with a complicated chemico-physical structure. This reacts exclusively in consequence of its realized state, but not in consequence of the history of its creation.(…) The genotype conception is thus an 'ahistoric' view of the reactions of living beings – of course only as far as true heredity is concerned. This view is an analog to the chemical view, as already pointed out; chemical compounds have no compromising ante-act, H_2O is always H_2O, and reacts always in the same manner, whatsoever may be the 'history' of its formation or the earlier state of its elements (…). A special genotypical constitution always react in the same manner under identical conditions—as chemical or physical structures must do. (Johannsen 1911, 139 and 146)

Such a "life out of history" view of heredity dominated of course the 20th century, or "century of the gene" as Evelyn Fox Keller puts it. For instance, Salvador Luria opposed two levels in life and two realms in biological research: "life in action" and "life in history" (Luria, 1973). While the latter refers to the understanding of evolution, the former encompassed all other fields of biology,

[10] "Die Auffassung der Gene als Organoide u.dergl. ist aber nicht mehr von der Forschung zu berücksichtigen. Voraussetzungen, welche eine solche Auffassung nötig machen sollten, fehlen gänzlich. Ein Pferd in der Lokomotive steckend als Ursache der Bewegung (…) ist eine ebenso 'wissenschaftliche' Hypothese als die Organoidslehre zur 'Erklärung' der Erblichkeit." (Johannsen 1909, 485).

placed under the leadership of molecular biology, in which biological functions were framed as a programmed machine sealed off from the contingencies of history and stochasticity.

In the early 20th century, most plant, animal, microbe and human geneticists, no matter whether they embraced Mendelism or not (Bonneuil, 2006), developed a new view of heredity that had lost most of its temporal weight, of its historic meaning. This changing relation to time echoed the larger drive to rationalize plant breeding and agriculture as an industrial enterprise, from a cottage industry based on a kind of stewardship on living populations, to quantity production of elite races and varieties. Willet M. Hays, scientist at the USDA, first secretary of the American Breeders Association (ABA) and soon to become undersecretary of agriculture, gospelled this drive:

> The work of breed and variety improvements and of breed and variety formation is now going forward, *but at a pace too slow for these times when the world is advancing with accelerated speed all along the line.* As science, inventive genius, constructive skill, business organization, and great market demands at home and abroad have pushed forward things mechanical, so should ways be found of improving these living things which serve as machines for transforming the substance of soil and air and the force of the sun's rays into valuable commodities.... The energy of the generative cell, and its development into the mature plant or animal, is more abstruse and more profound than the mechanisms of the mightiest locomotive.... As one machine is more efficient than another, so the blood of one generative, or of a small group of generative cells combined into an efficient variety or breed unit, is more valuable than another. (Hays, 1905, my emphasis)

Gaining time was the leitmotiv. This ideal of getting faster elite cultivars and races attracted both the Mendelians and those, like De Vries, Johannsen, Nilsson and Blaringhem, who believed that isolation and mutations would yield stable improved types even faster than hybridisation. De Vries, praised Hays isolation of distinct elementary species of wheat, similar to the one systematized at the Swedish Svalöf station, which he opposed to the slower Darwinian method of population breeding of the German breeder Rimpau:

> The American breeder by one single choice isolated the very best strains and observed them to be constant and pure. The German breeder, on the other hand, by selecting a number of ears, must have gotten an impure race, and needed a long succession of years and a constantly repeated selection to attain, in the end, the same result. (De Vries, 1907, 102)

In other words, breeding methods inspired by Darwin's evolutionary theory were both rejected as scientifically unsound and too time consuming for rational practical breeding. The slow time of evolution had no place in the modern world. As Hays recalled,

> That association [the ABA] (…) has suggested that the scientists in biological lines turn for a time *from the interesting problems of historical evolution to the needs of artificial revolution.* (…) It has thus recognized that the wonderful potencies in what we are wont to call heredity may in greater part be placed under the control and direction of man, as are the greater physical forces of nature. (Hays, 1903, opening address of the ABA, quoted by Castle, 1951, 62, my emphasis)

From "historical evolution" to "artificial revolution," the time had come for living organisms being redesigned along the needs of agro-food world markets and the time-space matrix of the industrial revolution. Emile Schribaux, the first professor at the Paris Institut National Agronomique to teach genetics, gospelled in a similar way for "the improvement of the plant machine" (Schribaux, 1911, 17). William Bateson went even further in the machine-like conception of life when he boasted: "We can pull out the yellowness and plug in greenness, pull out tallness and plug in dwarfness" (quoted by Müller-Wille, this volume).

This new industrial spirit affected the space-time in which living beings came to be understood and manipulated. What connected organisms in time and space was re-attributed to combinations of hereditary units that were a-historical and extracted from the influence of locality. In this new framing,

> A pure race, for a given character, is not, as previously believed, a race that possesses a long lineage of ancestors having this character; it is simply a race in which the character is produced from the union of two gametes of the same kind. (Meunissier, 1910, 13)

Most breeders and geneticists saw the genesis of races, not anymore as the produce of time and vertical transmission but instead of their own proper combinatory engineering. Such an expropriation of the past in the production of relevant life forms opened a wide space for transforming the future with a forward looking, manipulatory, bio-political attitude. Much in line with English and American geneticists and eugenists, Philippe de Vilmorin, head of a major European seed company acknowledged that this new conception of time, space and artifice in the optimisation of living beings, "can have a crucial influence on the future improvement of our species" (Vilmorin, 1910, 12).

Experimentalizing variation

Closely linked to the conjuring away of history, the changing framing of variation is another post-Darwinian turn of early 20th century genetics. Variation was for Darwin a fundamental property of life, a continuous and ongoing process. This view implied that breeders had to continue the selection from generation to generation so as to counter this permanent drift if they wanted to maintain their varieties at the best level. Many historians of early Mendelism and of the Biometricians-Mendelian controversy have shown that the concept of the fixity of the pure line (Johannsen, 1903) came to be a weapon against biometricians' view of heredity as continuous (Roll-Hansen, 1978 and 1989; Provine, 1971). This controversy was only the tip of the iceberg of late 19th-century "new biology"'s systematic attempts to produce—or freeze or orient —variation by all kinds of experimental means.

Trained in a more professionalized and experimentalist context of late 19th century biology, many young biologists departed from Darwinian amateur and "panoramic regime"[11] of knowledge making, and from Darwin's views on biology and on variation. Some, like Hugo De Vries, one of the three "rediscoverers" of Mendel's law in 1900, developed an experimental program to show that big variations, which he called "mutations," rather than small continuous

[11] On panoramic knowledge regimes, see Thurtle, 2008.

ones, could account for speciation and evolution. This idea was held by many scholars of evolution and embryology, including T.H. Morgan. They developed a large array of experimental strategies to produce and track variations in controlled "milieux de culture." The hundreds of mutant strains of *Drosophila* in Morgan's laboratory by 1914 are only one example here (Kohler, 1994). In the course of this experimentalization of biology (Rheinberger and Hagner, 1993), a bunch of new life forms were created and grown up in the laboratories, and variation came to be seen as a process amenable to experimental command and control rather than a "natural" process. As it was possible to "fix" the environment (standard and constant milieu), it was also possible (and sought for) to fix the organism itself through generation by repeated inbreeding or cloning (see discussion below on this new culture of purity and repeatability of life).

The reframing of variation from a natural, historic and continuous phenomena to something that could be experimental, discontinuous, artificially and systematically engineered happened in a period when standards and standardisation were a deep concern (Schaffer, 1994; Wise, 1995). The experimentalisation of life went hand in hand with the industrialisation of life, in the same matrix of practice and meaning. Variation and fixity of biological entities came into existence as biological phenomena because they were a central issue in agricultural, medical and industrial practices in the "control revolution" of the turn of the century. Andrew Mendelsohn has nicely shown how a shift from "soft" to "hard" heredity in microbiology occurred in the context of stabilisation of mass produced vaccines, in which "vaccine safety and efficacy constructed, produced, constituted heredity as fixity and in a new, absolute sense" (Mendelsohn, 2005, 95). For "heredity (at least at the realm of microscopic life) came to be located within and redefined by an enterprise of control and testing, production to an exact standard and reliable distribution" (Mendelsohn, 2005, 85)

In the first decade of the 20th century, it became a commonplace among breeders and geneticists to contempt Darwinian's view on variation for having missed the basic fact that elementary species, pure sorts or pure lines are fixed and show no more variation in which selection can work on. A Canadian scientist visiting Svalöf's station reported that : "the Darwinian idea of the omnipresence of hereditary variation in all life was still held by Nilsson who regarded it as necessary to continue the selection from generation to generation to effect a complete fixation of the characters (…) this idea came to be abandoned" (Newman, 1912, 28). Johannsen as soon as 1898 (Roll-Hansen, 2005) as well as De Vries (1907) condemned Darwin-inspired breeding methods and called attention for pre-Darwinian techniques and concepts such as Vilmorin's "pedigree selection" and the "elementary species," a concept that had been promoted in the 1850's-1870's by the French creationist naturalist Alexis Jordan. For Jordan the species boundaries could be determined with certainty only through experiment, i. e. through cultivation side by side of various forms over several generation, so as to see if their differences bred true. But Jordan's elementary species concept, was discarded as splitting hair by the leading naturalists, such as Darwin's friend Joseph D. Hooker, Georges Bentham and Asa Gray. These leading figures, who headed the great herbaria in Europe and the United States, maintained the armchair study of dried plants fragments, rather than experiment, as the cornerstone of proof-making in taxonomy. They also imposed successfully the broad species concept through the imperial power of standardizing enterprises such as the colonial Floras, Bentham's *Genera Plantarum* and the *Index Kewensis*

(Bonneuil, 2002). Against "species mongers" Hooker and his allies argued that the broad species was more in line both with the study of biogeography and evolution (framing life as a constant flow of variations interconnecting all taxonomic categories) as well as with the imperial project of a commercial unification of the world. It was for instance necessary to attribute a unique technological and commercial value to a species of rubber plant, whether it was collected in different places and named under different ("bad") species names by various travellers. In sharp contrast with this natural historical and imperial metrology, experimental biologists and geneticists of early 20th century rehabilitated "Jordan's classical work" (Johannsen, 1913, 389) and small species concept. While the first metrology was part of a larger drive to rationalize extractive mercantile enterprises, the second kind of metrology, allowing the creation and circulation of new stable and pure forms of life at the subspecific level, which were turned into mass commodities, was constitutive of the space of flow of agro-industrial goods.

More than just a finer grained taxonomy, what was rehabilitated in this move was a typological view and a search for a stable biological type as "the most biological concept in the science of heredity" (Johannsen, 1905 quoted by Roll-Hansen, 1978; but see also Theunissen, 1994 on De Vries typological views, and Mayr, 1973 for a general analysis). Shull, one father of the hybrid corn, posited very vividly this "modern view of heredity" (Johannsen, 1911, 130), in the history of biological ideas:

> The doctrine of evolution had to overthrow the [creationist] conception of permanency of specific types (…). It was Darwin's great triumph (…) to convince the scientific world – and through the scientific world, ultimately the whole world—that everything is in a state of flux, and that there is no such thing as permanency among living things. Owing to the work of De Vries and the other early students of modern genetics, permanency of type again demands serious scientific consideration (…). The old idea of the immutability of specific types was based upon almost total ignorance of genetics, as was likewise the Darwinian conception of fluidity and gradual change (…). The critical work of the past few years has brought a great change and the new idea of permanency is gaining ground with the growth of experimental knowledge. (…) we can definitely say that types are absolutely permanent and do not, at least in some cases, gradually change into something new. (Shull, 1911, 234-35)

If the analysis and production of stable forms of life constituted the heart of the young genetics, at least two strands of approaches of stability were in competition. Some found the basic immutable entities in the "unit factor" or gene (or in the linkage group localised in the chromosome), whereas others, including Johannsen, opposed factorial genetics and saw the genotype[12] as a whole, the elementary species, or its most radical form, the pure line, as the key permanent biological type (Churchill, 1974). This contrast hints to discontinuity between Mendelism and "pure line research" that has been neglected by historians. Indeed, although the two lines of research were convergent, Johannsen (1909, 1911) as well as Shull (1911) and East (1911) presented the "pure line principle" or "pure line theory" as a research programme that was clearly distinct from "hybridisation studies." Although they diverged about the level that displayed at best stability and immutability and where hard heredity could be located, theses two lines of research strongly

[12] Johannsen (1911) stresses the "stability of genotypical constitution" (p. 141) or "fixity of a genotypical constitution" (p. 143), which he viewed as a kind chemical equilibrium (Churchill, 1974).

converged in rejecting 19th-century biology's dissolution of the type in an infinite variability of ever circulating beings (species at the macro level and hereditary units at the micro level), modifying themselves mutually when encountering one another. They agreed on the promotion of authenticity, fixity of the biological self, of a "genetic identity" deeply buried and sealed off from the effects of time and place… but manipulatble by the experimenter.

These timeless, experimental/manipulatory and typological views of life reinforced or created boundaries in the biological world, in the social world, as well as between the natural, the cultural and the social realms:

— It established a great divide between the past and the future, between time consuming empiricism to planned improvement, between cottage industry and mass production of elite organisms.

— Its focus on stability, predictability and standardisation reinforced a great modernist divide between the natural world of landraces and the optimized world of pure strains and high yielding cultivars devised by human scientific genius. Till late in the 20th century, the discourse on crop biodiversity was a discourse about the past and the "origins." Vavilov, for instance, promoting a systematic exploration of "the whole *initial* varietal potentialities of the world" (my emphasis), stated:

> The vast resources of wild species, especially in the tropics, have been practically untouched by investigation (…) An actual mastery of the processes of evolution (…) can be accomplished only through the combined efforts of a strong international association and through the removal of barriers impeding research in those most remarkable regions of the world (1932, 331 and 342).

This is a typical colonial and modernist discourse of discovery and scientific use by civilized/scientific Man, of untapped resources: gene flow was framed as a resource from the past (for the breeding science and industry), rather than an ongoing process in which farmers' knowledge and agency make a difference in future conservation and innovation, as in the recent 'participationist' and 'connexionist' discourse of *in situ* crop diversity conservation (Bonneuil and Demeulenaere, 2007). In this modernist framing, interspecific and intervarietal crosses were seen as a specialized undertaking of the professional geneticists (breeder, cytogeneticist…), gate keepers of the boundaries between (elementary) species. Landraces were redefined as "ecotypes, derived from populations upon which natural selection operated during very numerous generations in the same environment" and hence conjuring away any role of the farmers (Bustarret, 1944, 346).

— Hence a stronger boundary and division of work between farmers and breeders (whose social status was based on their mastering of artificial crosses, large scale screening and pure line breeding). In the following decades, the seed was constituted into an object of public policy that promoted quality standards that reinforced the professionalisation of plant breeding and the making of seed into a commercial "input" (Bonneuil and Thomas, in press).

— Finally a stronger boundary was drawn between academics and practical breeders: in sharp contrast with Darwin's reliance on breeders' testimony, leading figures of the new "genetics," like Johannsen and Shull, considered breeders as not trustworthy in matters of heredity (Johannsen, 1911; Glass, 1980).

Müller-Wille and Rheinberger (2004) have argued that , in the new epistemic space of heredity, biological transmission and cultural transmission, that were in the mid 19th century thought with the same concepts, became strongly separated. I believe that the four modernist divides mentioned above were key elements of this general drive.

3. Industrializing purity

As a prelude to a cultural history of purity in the rise of genetics, this section tells two stories of discovery and two stories of justification of purity. Together, these stories document how purity and stability became both a norm of industrial production, a norm of scientificity in experimental biology and a norm of fairness in social and economic relations.

Vilmorin's pure lines and the problem of control in the seed chain

Both Nilsson, De Vries and Johannsen acknowledged the French breeder Louis de Vilmorin's work as a crucial step toward the notion of pure line. He pioneered the "pedigree breeding" technique of selecting individuals (rather than groups of plants) and documenting "a perfectly correct genealogy of all plants from the beginning of the experiment" (Vilmorin, 1859, 44). In a 1856 work on sugar beet breeding for sugar content, he also noted that the progeny of some individuals was sometimes homogenous and sometimes highly variable, and he proposed that breeding should not only search for high performance types but also for lines with minimum variability (Gayon and Zallen, 1998). Reducing variability, and increasing the predictability of a standard agronomic or technological performance of the seeds was a major goal as the seed trade from improved varieties developed, not only for vegetables and flowers, but also for major crops such as beet, wheat and barley. As grain and seed markets extended, trust networks and standards had to be extended. Inspired by similar regulations on fertilizers trade, seed regulations emerged in different industrializing countries setting minimal purity standards and minimum germination rate. A standard, rather than variable output was expected from improved seeds by the advanced farmers that pioneered their use. Homogeneity was also valued to facilitate the use of harvest machines. The Vilmorin Company employed about 400 employees in 1889 and, as one of the leading seed companies in the World, had to meet the challenge of quality standardization and control to maintain its position. Even before seed trade regulation imposed national standards, Vilmorin conducted both cultivar performance assessment at a multi local scale before release and, in the 1880's, routine seed quality testing (Flavien 1889, 17).

To ensure quality downwards on the seed chain, it was necessary to control quality upward at the seed multiplication level. Ideally, this could be done at Vilmorin's estate near Paris by skilled, disciplined and carefully managed waged manpower. But this method of production of commercial seeds was costly. In order to decrease production costs, seed multiplication was

subcontracted to farmers near the Loire, under the supervision "of a special team of inspectors who checked all farming operations" (Flavien 1889, 14). The assessment of seed purity delivered by these farmers was made easier if the initial purity of the seeds delivered to them for multiplication was perfect, so as to detect adventitious mixtures more easily. A visiting engineer specialised in scientific management of work concluded with admiration:

> In seed production, the division of work adopted at the Company Vilmorin aims at producing, with all the necessary care, seeds of extremely pure races ["de races extrêmement pures"], and multiply them widely in such conditions that, without loosing their purity ["franchise de race"], they can be delivered at the lowest possible price. (Flavien, 1889)

The Vilmorin Company hence combined pedigree selection technique to produce pure lines with a particular quality control for seed production where purity was a key element to ensure standard quality at the lowest production cost. As a perfect example of the "control revolution" documented by James Beniger (1986), purity was here a powerful tool for the Company to keep control along a seed production chain where the work was subcontracted.

Stabilizing beer, barley and beans : from Pasteur to Johannsen

Andrew Mendelsohn has argued that the mass production of attenuated strains of Anthrax as vaccine by Pasteur's laboratory in the 1880's was one moment of shift from heredity as force to heredity as presence or absence of a permanent and transmissible trait (Mendelsohn, 2005, 91). Microbiology and its new zoo of small "corpuscules," each having its agency and its particular chemical or medical action is indeed certainly one of the roots of the particulate and structural view of heredity. Microbiology was also a field of practices and discourses of purity. Pasteur, for instance, in his works on the spontaneous generation, the vinegar, wine and beer fermentations on the 1860's and 1870's, sought for purity not as a quantitative magnitude ("more or less pure") but as "an absolute absence, mathematical if I may say" of any germ other than the studied one (Pasteur 1876, 218). It was a question of yes or no. Pasteur even wondered whether the beer industry could have attained its actual state without having followed his principles of pure culture (Pasteur 1876, 216-17). He noted that the commercial beer contained not only the beer yeast but also undesirable other yeast species (such as *Saccharomyces pastorianus*) and "disease germs" (vinegar and milk bacteria, and various fungi) which were responsible for turning the beer spoiled after some time, and discarded as undrinkable. This problem of conservation of the beer was only partly, and at high cost, solved by the large scale use of refrigeration techniques (ice machines) from 1880 on. The beer demand was highest in warm months but it was easier to produce and keep unspoiled in cold months. While steam boiling, cooling compressors, new energy sources and bottling machinery made mass production possible, "keeping quality" remained the bottle neck in the mass scale production.

J. C. Jacobsen, the founder of the large Carlsberg Breweries in Copenhagen and a great admirer of France came across Pasteur's work just when he was creating a laboratory, then to become a world centre for biochemical research. Emil Christian Hansen head of the physiology department of the Carlsberg Laboratory deepened Pasteur's taxonomy of the micro-organisms present in the beer leaven, and greatly improved its method of "pure culture." To make sure that a strain derived

from a single cell, he used in 1882 the gelatine-substrate technique he had learned during a visit to Robert Koch in Berlin. A first beer production trial was held in 1883 at Carlsberg Brewery, with different pure lines from the good yeast species he had named *Saccharomyces carlsbergensis*, including the one he called "Carlsberg bottom yeast n°1." Large scale production of pure yeast bottom-fermented beer was reached in 1885, and an apparatus for the continuous production of pure culture yeasts was devised (Glamann, 1988). Jacobsen wrote in 1884 that "from now on fermentation in my brewery will wholly be carried out by means of this pure yeast, produced from a single cell! Truly a triumph of scientific research!" (quoted from Teich, 1983, 121). By then Carlsberg controlled almost half of the Danish lager beer market (Boje and Johansen, 1998, 60). Abroad, the "pure yeast" method was heralded among German brewers by beer scientists like M. Delbrück who stated that "the yeast is a working machine" transforming sugar into alcohol, hence amenable to industrial rationalisation (Delbrück 1884 quoted in Sibum, 1998, 48; see also Teich, 2000). Finally in the 1890's, except in Britain, most of the large Breweries in the industrialized world turned to pure yeast technology, an innovation that together with ice machines, train transportation systems, urbanization and changes in alcohol consumption patterns, transformed the brewing industry into one of the most advanced, global, concentrated, capital-intensive and mass-scaled food industry of the time.

Stabilizing beer so that it could flow along the global networks of an expanding beer market, while remaining immutable, had implied a thorough disentanglement of the quality problems that resulted from the production and transportation conditions from those which could be fixed by controlling the "intrinsic" nature of yeasts and standardizing them into pure lines. Barley posed similar issues: its germination kinetics, sugar and protein content were key properties whose optimization and standardisation were required to rationalize the production process and mass-produce standard quality beers. From 1881 to 1887, just by the time when pure yeast was introduced, Wilhelm Johannsen was research assistant at Carlsberg Laboratory and explored Barley's ripening and germination's chemistry and physiology (Teich, 1983). Later, when Johannsen took a position at the Royal Veterinary and Agricultural College in Copenhagen, he engaged in barley breeding for brewing quality in collaboration with Carlsberg. In this research he combined Galton's biometrical and statistical methods and Vilmorin's and Hansen's pure line principle to work with descendents from single individuals through self-fertilization (Roll-Hansen, 2005, 43-47, Johannsen 1899). It is in this context that Johannsen picked up the creed of purity as a norm of proof, efficiency and fairness. The vagaries of uncontrolled and changing environmental conditions and uncertain ancestry had to be erased so as to harness at large scale new forms of life engineered to react in the same way to given conditions. "The study of the behaviour of pure lines is the basis of the science of heredity, even if populations—especially human populations—are not made of pure lines" wrote Johannsen in 1903 in his study on the ineffectiveness of selection in genetically homogenous populations of beans (Johannsen, 1903, 9). Pure lines, and the particular kind of typological thinking that was associated with them, were the cornerstone of the production of both sound knowledge and of large agro-food markets and industries. Louis Blaringhem, lecturer at the Sorbonne Faculty of Science engaged in a Svalöf-like barley breeding program for the brewing industry, and an ardent promoter of De Vries' and Johannsen's views in France, stressed:

> The ideal thing for industry is to operate on products whose nature is well defined and always identical. There exist excellent methods for the purification of inert matter, such as fractioned distillation (…) [but] living matter is complex and the grower, unaware of the value of these methods, cannot provide the guarantee expected by the industrialist, hence a difficulty in economic exchanges. (Blaringhem, 1905, 362)

As pure yeast culture had transformed the beer industry, he heralded that stable and pure lines of crops would revolutionize agriculture and boasted that "the future belongs to pedigree pure sorts" (Blaringhem, 1913, 87).

Purity as fairness in the industrial world of worth

There was actually nothing new in using "types" or traits transcending space and time, stability and purity, to maintain social boundaries (Douglas, 1966). As pointed out by Nicholas Russel in his exploration of early modern animal breeding, "the parallels between the human obsession with title, hereditary position and social caste and animal pedigrees, are too obvious to need emphasis." (Russel, 1986, 19). Russell argues further that the careful keeping of pedigrees, for lack of disentanglement of the effects of environment and heredity, acted mainly as a political tool to legitimate the political power of the aristocracy.

What was new then in the understanding and valuing of purity at the turn of the 19th and 20th century? My argument is that, in the post-Darwinian space-time that we have documented in the preceding section, the search for purity was basically reframed within the "industrial world of worth" (Boltanski and Thevenot, 2006). From 17th to mid 19th century, purity was framed in a mix of "fame," "inspiration" and "domestic" world of worth. Breeding was a search for fashionable conformations (cf Bakewell, "fame" world of worth) and aesthetic criteria ("inspiration" world of worth) rather than purely economic performance; personal knowledge and "breeder's eye" ("inspiration" world of worth) deeply mattered as well as ancestry, stewardship and interpersonal relations ("domestic" world of worth). Purity was viewed as something highly valuable because it was particularly rare and unstable, and needed constant care to be maintained. The key trait was rarity. Genealogies (General Stud Book) acted as tools to organise trust around the genealogical value of English Thoroughbred from Arabian origins in a context of scarcity since new importations of Eastern bloodstock was banned (Russel, 1986, 99). In the same way, the "degeneration" of elite cultivars (including Major Hallet's "pedigree seeds" of late 19th century) acted as incentives for farmers to buy new seeds to the plant breeder.

In a context when breeding was a cottage industry lacking of powerful information and control technologies (including intellectual property rights) necessary to control large trade networks, scarcity and instability of elite breeds was consubstantial with the economics of breeding (Berlan, 2001). There was no need to extend trust in elite breeds further than intellectual property could extend. Purity was hence "sticky." It was altered when races and varieties moved in time and space, and remained dependant on continuous and distinctive practices of the breeder, rather than warranted into an inward timeless constitution of the organisms. As we have seen, this was also much in line with fin de siècle's visions of entropy and fatigue, with Darwin's idea of continuous variation as well as with Galton's view of the "stirp" as a space of (inter)activity and competition.

In a few decades at the turn of the 19th and 20th century, purity was drastically reconceptualized. Of course it remained dependant on adequate skills and practices (from avoiding contaminations in microbiology to careful avoidance of cross breeding to maintain pure lines), but it was made more robust because these practices could be codified and routinized and because living populations were now seen as basically made of intrinsically stable and pure types, which just needed to be sorted out. Purity was not anymore the produce of history, but rather a structural property (homozygocy) that scientists could master across time and space.[13] Purity lost its domestic dimension. Purity was assessed not only "vertically" (through checked genealogies), but also "horizontally" as predictable functional performance (whether a Gauss curve, a replicable biological effect, a safe vaccine or a high strength wheat). Purity lost in the same movement its association with rarity. It became valuable not because it was an unstable and rare state of living being, but on the contrary because it was amenable to quantity production and to replication across time and space.

In the industrial world of worth, fairness in the commercial exchange was associated with the purity and stability of the product. Darwin-inspired population breeding methods and their impure/unstable products, which were previously valued because they created a special role for elite social groups to intervene actively so that the world would not fall apart in chaos, entropy and degeneration, became the stigma of unfair exchange:

> [If continuous selection would be the right way] it means that all the seed destined for sowing should be produced directly [by the breeder] (…) it is easy to see that the gain made by the breeder of a new variety depends, for a large part, on the acceptance of this proposition. (De Vries, 1907, 43)[14]

> Almost all cultivated varieties have been obtained by selection. Only [elementary] species born by mutation deserve agronomists' consideration because they alone are genuinely stable (…)But [with Darwinian selection methods] once the variety is put to the market, (…) it quickly loses its value (…) the fast degeneration of the improved seeds he sells ensures the renewing of his order books (…) [hence] the focus on breeding by selection and the present neglect of cultivating forms born by mutation. Only these are stable from their very birth. (Blaringhem, 1905, 377)[15]

Purer was not only more efficient, it was also fairer. The reframing of purity practices and meaning in the "industrial world of worth" of the control revolution that accompanied the industrialization of the agro-food sector in the last decades of the 19th century, informed not only laboratory and

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[13] Paradoxically, genealogical techniques (book keeping and other inscription devices) became even more important as history was expelled for the framing of heredity. Parentship was important only in so far as it was taken into manipulation, isolation and traceability techniques, but it was not anymore central. Constitution rather than connection was the hallmark of heredity. As Rheinberger would put it, in plant genetics, genealogy became a "technical object" rather than an "epistemic thing."

[14] I thank Jean-Pierre Berlan for attracting my attention towards this book from Hugo de Vries. See Berlan, 2001.

[15] Blaringhem was then a young left wing intellectual, and as a son of a medium farmer, he shared the third Republic's ideological project to free the farmers from the domination of merchants and notables, a project that combined the industrial world of worth and the civic world of worth.

economic practices but also judgement about fairness and about the kind of social order that was desirable.

PURITY AS NORM OF PROOF AND THE MAKING OF BIOLOGY AS AN EXACT SCIENCE

> Der wichtigste Probierstein hier ist aber das kritische Experiment mit genotypisch 'reinem' Material. (Johannsen 1913, iii)

> Es ist in der Geschichte der neueren Biologie auffallend, daß zu einer Zeit, wo man, in Bezug auf Mikroorganismen, durch 'Reinkultur' (durch Kultur mit einer einzigen Zelle als Ausgangspunkt) äußerst wichtige Resultate erhielt, in der Erblichkeitsforschung die Verhältnisse der höheren Organismen fortwährend in weit gröberer, summarischer oder statistischer Weise studiert wurden. Was die Arbeitsmethoden eines Koch oder eines Hansen für das exacte Studium der Mikroorganismen bedeutet haben, dasselbe bedeutet auch für die Erblichkeitsforschung die Reinkultur, d. h. die individuelle Nachkommenbeurteilung, wie sie Vilmorin und Mendel präzisiert haben: Ohne Reinkultur keine klare Einsicht, sonder Konfusion und Irrtum! (Johannsen, 1913, 196)

This new industrial framing of purity informed not only laboratory and economic practices and normative views about the kind of social order to be reached in the 20th century but also the very meaning of how biology should be an exact science. Exactness differed from precision as Bateson stated in 1902: "We have been told of late, more than once, that Biology must become an exact science (…). But exactness is not always attainable by numerical precision" (quoted by par Provine, 1971, 71)[16]. The focus on exactness was not in the title of Johannsen 1905 book in Danish, but was introduced in his 1909 *Elemente der exakten Erblichkeitslehre*, and already discussed in his 1906 talk at the International Conference of Genetics.

His creed for exactness was a weapon against biometricians who, Johannsen thought, measured precisely, but measured the wrong thing. "Exact biological analysis" meant indeed for him "the fundamental distinction of true type differences and fluctuations" (Johannsen, 1907, 110). Ignoring the existence of biotypes, biometricians worked with ill-defined categories. Interestingly, Johannsen illustrated this point with an analogy taken from the industrial world of the second industrial revolution:

> If anybody makes a study as of the speed of the railway-cars, the botanist noted, he will of course regard every train or type of train separately: express train, local trains, goods trains, and so on. (…) But what would be said of an enquirer who, for solving the problem, collected statistics as to the speed of the different carriage-classes (…) and by this method found out that the average speed of the first-class car was much greater than the average speed of the third-class car—for in the express trains (in the continent at least) there are only (…) first and second-class cars, while in the local trains the third-class cars is the majority (…) I must confess that the main part of biometrical work in questions of heredity somewhat resembles such preposterous statistics. (Johannsen, 1907, 99)

[16] This argument soon became a topos. For instance, after Bateson and Johannsen, Jennings stated that "the men who (…) have lectured on the necessity of becoming exact are the strongest opponent of exact experimental and biological analysis—seeming to feel that mathematical treatment renders other kinds of exactness undesirable" (Jennings 1910, 143). See also Johannsen 1913, 154.

In other words, the metaphor stated, biometricians developed a pre-control revolution kind of knowledge, which could not help anybody to understand and manage the modern world.

Pure lines and biotypes offered as well the promise to get out of the vagaries of species delimitation in taxonomy. As H. C. Watson had written to Darwin, "The short truth is, that we have no real proof or test of a species in botany. We may occasionally disprove an alleged species by seeing its descendants become another such species, —or we may unite two by finding a full series of intermediate links." As I showed, the chaos in taxonomy had been avoided by imposing the rather conventional "large species" norm to the naturalists community through the botanical tools of imperial power (Bonneuil, 2002). But the epistemological weakness of such a closure remained. Systematics seemed unable to cope with observer-dependent knowledge and to achieve communicability and accumulation. So the rehabilitation of the small species concept by early 20th century geneticists also offered the promise to establish a "new botany" as an exact experimental science working with new taxonomical units.

Hansen and Pasteur were seen as the founding father of this exact biology because they achieved an "exact analysis of yeast population" (Johannsen, 1907, 104). "Heredity can only be studied in an exact manner by breeding experiments" and, Johannsen added, there are two ways to do it: the "analytical experiment" with pure lines, and the synthetic experiments of "hybridology" (Johannsen, 1907, 103). As proponents of the spontaneous generation in Pasteurs' mouth half a century earlier, Neo-Lamarckians were, for Johannsen, committing the sin of impurity "Most of the "neo-Lamarckian" literature demonstrates the necessity of exact experiments" (Johannsen, 1907, 104). "Contamination," once the stigma of the unskilled microbiologist, became the sin of the bad student of heredity. As Jenning phrased it, Castle's experiment showing effects of selection in rats and guinea pig were of poor value because they "dealt with races of complicated descent; they plunge us at once into all the difficulties due to interweaving, blending and transfer of characters from one genotype to another" (Jennings, 1910, 140). On the contrary, purity was required if one was to turn living forms into elements of experimental systems and measure replicable and constant effects under similar conditions (Rader, 1999; Löwy and Gaudillière, 1998):

> The ideal material for any genetic, biological or agronomical research is of course the pure line; because of its intrinsic stability, in space and time, it makes possible to control the factor 'heterogeneity of the plant material' in the experiments. (Bustarret, 1944, 353)

Conclusion

While biometry inferred a norm from heterogeneous life forms, exact genetics materially produced normal life forms, in creating populations made of strictly standard, identical and highly performant organisms: "pure sorts," "pure lines," "clones," F1 hybrids corns, "inbred lines," all being "isogene individuals" (Jennings, 1910, 152). Singling out "the 'Shakespeares' of the species" was the motto of both sound science of heredity and rationalized industrial mass-production:

> As electrical energy must be harnessed, so these investigations are showing that the peculiar breeding potencies of the rare plant or animal must be singled out and given opportunity to work. Both in practical breeding and in evolutionary studies the individual with exceptional breeding power is gaining respect. . . . The world is learning to seek the 'Shakespeares' of the species with the same avidity that it seeks gold mines. (Hays, 1906 quoted in Boyd, 2001, 654)

Indeed, in the early 1900's, "the climate of biological opinion was favorable to the pure line theory" (Provine, 1971, 108). In his pioneering reading of the communications of the 1910 "Genotype Hypothesis" Cornell symposium mentioned in the introduction of this paper, William Provine depicted how Shull, East, Jennings and Pearl and many geneticists were then riding the tide of "the modern view of heredity." Jennings and Pearl argued, on the basis of the pure line theory, that selection in cross-breeding population was incapable of changing a character beyond the existing limit of variation. East and Shull, deeply sharing the typological belief in "the discreteness, uniformity and permanence of the types" (Shull, 1911, 237), sought to extend the genotype concept to open-pollinated crops and rushed to sort out and amplify the very best genotype of open-pollinated crops such as maize in the same way as this had been done for self-fertilizing crops:

> A (…) demonstration that populations of cross-breeding plants and animals are composed of fundamentally distinct types, intermingled but not changed by panmixia, and capable of being separated by appropriate means and of being shown to possess the discreteness, uniformity and permanence already demonstrated for the genotypes of self-fertilized and clonal races, will add greatly to the importance of the fundamental conception of permanency of types involved in the work of De Vries and Johannsen. (Shull, 1911, 238)

The innovative step was to infer that, if all plants of a corn field resulted from the cross between two parents, or, in other words, from the combinations of two among "numerous elementary species," then "the fundamental problem in breeding this plant is the development and maintenance of that hybrid combination which possesses the greatest vigor," i.e. to mass produce the one best cross (Shull, 1908, 300, my emphasis). A difficulty was the depression caused by inbreeding to get fixed pure lines as parents to be crossed. But Shull did not loose hope because, together with this depression, he obtained in his pure lines "the gradual lessening of variability," which Vilmorin had searched for half a century earlier and which Johannsen had predicted on the basis of his "pure line theory" (Shull, 1911, 244; Johannsen 1907).

William Provine argued that, at the 1910 symposium, Johannsen's "pure line theory seemed so obvious that most outstanding geneticists accepted it without adequate proofs" (Provine, 1971, 108). Similarly, Ernst Mayr has criticised the limitations of the typological view of the species

promoted by De Vries' and Johannsen's work. For instance, De Vries' typological views led him to postulate the genetic homogeneity of natural populations due to strong natural selection pressure. For him, the normal situation in nature was that interbreeding individuals were of identical genetic composition (hence the need for mutations to make a difference in evolution) (Theunissen 1994, 243-44). He also, as we have seen, dismissed mass selection as leading less efficiently (longer time, more impurities) "in the end, [to] the same result" than pedigree pure line selection (De Vries, 1907, 102). While reasoning in this way however, De Vries overlooked the possible productivity of gene recombination in interbreeding individuals under lower selection pressure, a productivity that was acknowledged later in the evolutionary synthesis, and harnessed in "recurrent selection" breeding schemes from the 1940's on.[17] Similarly, when Jennings dismissed selection in cross-breeding populations for being incapable of changing a character beyond the existing limits of variation or when East and Shull discarded the value of breeding strategies based on pure lines rather than on populations, they conjured away the importance of recombination that was key to the practical success of breeding and that would later become central in quantitative genetics and population genetics (Provine, 1971, 122).[18]

The point in mentioning the discontents of genetic purity is not here to blame geneticists, from a "histoire jugée" perspective, for having missed or delayed new and fruitful scientific avenues in the 1900's. My point is rather twofold. A first observation is that Hardy-Weinberg's 1908 law and the study of allele frequencies in mixed populations can be seen as more "Mendelian" than the hybrid corn innovation. In many ways, East and Shull's work towards hybrid corn, rather than a Mendelian innovation in plant breeding, as often depicted by geneticists and historians of genetics, resulted from the kind of typological view of the species that E. Mayr and W. Provine criticized. This can help historians to avoid the plot of the hybrid corn as a Mendelian success story (Bonneuil, 2006) and sharpens the analytical distinction made earlier in this paper between two ways of stressing stability and permanency in biology and heredity by 1900: one taking the hereditary unit or gene as the immutable unit, and one taking the biotype as the immutable unit. These were in fact two "stabilisation" strategies that both emerged from the wider drive to reshape life in a new industrial time-space of flows. We have developed this argument in detail in this paper as far as the "biotype" or "clone" strategy is concerned. But the second strategy of singling out and stabilising immutable genes for valuable traits (disease resistance, productivity, chemical composition adapted to industrial transformation, etc.) has done a similar and complementary job: it has allowed to put "hereditary units" in circulation within a global scientific-economic network of plant breeding, where they were reassembled into

[17] Population and quantitative geneticists have later argued that in fact the two strategies presented by De Vries in 1907 do not only differ in their rapidity, but also that they don't lead to the same result on the long run. The isolation or pedigree method, corresponding to a maximum of selection pressure, impedes any further recombinations and leads to a plateau in genetic improvement. This plateau can be overcome only by an alternance of slow selection pressure cycles allowing recombinations to happen (close to mass breeding) and pure line breeding cycles to extract parent lines foir the hybrids. This principle is the basis of "recurrent selection" breeding techniques (Jenkins, 1940).

[18] Two years before the Cornell meeting, G. H. Hardy and W. Weinberg came in 1908 to new ways of understanding genes flows in natural populations, that concluded for the existence of regularities in the proportions of alleles in mixed populations without supposing that theses populations would quickly tend to homogeneity.

new placeless products, such as the Green Revolution cultivars that were made insensitive to photoperiods and grown worldwide (Bonneuil and Demeulenaere, 2007).

Hence my second point: to understand why "the climate of biological opinion was favourable to the pure line theory," and why natural selection seemed so unimportant as compared to stability of the type,[19] historians of genetics need to acknowledge how deeply the quest for purity and stability in early genetics and plant breeding has been shaped within a larger drive to rationalize the agro-food sector and mass-produce the one best. As Mary Douglas demonstrates in her cultural understanding of attitudes toward "impurities" and "pollutions," we cannot understand early genetics' obsession for purity and stability by just looking at genetics:

> Defilement is never an isolated event. It cannot occur except in view of a systematic ordering of ideas. . . . The only way in which pollution ideas make sense is in reference to a total structure of thought whose key-stone, boundaries, margins and internal lines are held in relation by rituals of separation. (Douglas, 1966, 42)

From the few rituals of separation documented in this paper, it clearly appears that early 20th century genetics emerged in a larger scientific/economic/cultural matrix of practice and meaning that reframed how organisms were connected together in time and space and with their environment (Thurtle 2007). In this wide cultural shift, a deep and intrinsic genetic identity was constructed for living organisms, separated from the influence of the place and the environment. New "pure" and stable life forms were mass-produced in laboratories and industries, which could circulate without alterations through extending "space of flows," be they inter-laboratory networks (the most famous being the circulation of strains within the *Drosophila* community) or larger scientific/economic/medical/cultural hybrid networks of the control revolution.

Finally, I must confess a major hole in this article: the material practices have only been superficially discussed here, even though they should be documented in any comprehensive cultural history of the birth of genetics. Although the geneticists of the turn of the century promoted stability and purity as a constitutional and intrinsic property of life (typological conception of biotypes and structural view of purity as homozygoty), they knew, as well as historians know, that the production and maintenance of these pure forms of life necessitated hard work, industrial scale observation and treatment of minute differences, and standardisation activities. As shown by Kohler (1994) with the production of the standard drosophila, with a stable rate of crossing over in every part of the chromosomes, the coming into being of pure life forms rested upon labor-intensive and capital intensive "networks of purity," being elements of the control revolution. So an entire aspect that should have been addressed in a more comprehensive essay on the cultural history of early 20th century genetics is the question of the transformations of the material practices of observation, recording, book-keeping, processing and manipulating that were associated with the shifts we have described. Although we have a few good pioneering works (Kohler, 1994; Rader, 1999; Löwy and Gaudillière, 1998; Müller-Wille, 2005), at hand,

[19] De Vries, for instance, argued in his *Mutationstheorie* that natural populations were genetically homogenous, because selection would quickly wipe out any new form that was less vigorous or replace the whole population by a beneficial new mutant. So the normal situation in nature was that interbreeding individuals were of identical genetic composition and only mutations made a difference in evolution (Theunissen 1994, 243-44).

much remains to be done to explore the "industrial" scale and organisation of the work and use of sorting machines in a breeding station like Svalöf (that established the standards for many others), the role of bureaucratic microtechniques (standardized forms for observations; inscription devices such as maps, registers, fieldbooks; management of information flows, etc.), the disciplining of bodies associated with the production of pure life forms and controlled experimental environments. Only with this additional work on the mundane microtechniques of genetics, will it be possible to grasp fully the intimate relations between norms of objectivity, exactness and precision, visions of life, bureaucratisation, mass-production and large-markets at the turn of the century.

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Mendelism and Agriculture in the First Decades of the XXth Century in Mexico

Ana Barahona

Introduction

History and philosophy of science have played a fundamental role in the comprehension of science in modern culture and society. Studies about history of science in Latin America began during the last four decades of the 20th century, developed under the model of European sciences and their influence. Many of these projects were based upon the diffusion model proposed by George Basalla in 1967,[1] since it offered a historic, comparative and transcultural analysis, including epistemological and sociological considerations. However, despite being one of the first contributions to the field of social studies of science, the application of this model meant paying too much attention to the development of science within metropolitan areas without considering the local complexities, i.e. without considering the local characters of the so called "peripheral" countries, such as Mexico.[2]

Current studies in the sociology of science, philosophy of science and scientific literature have validated the comparative and local vision of historical work. These studies have identified central elements in the process of diffusion and have developed more precise ways to deal with its complexity.[3]

It is necessary to carry out historical studies that take in consideration the generated interactions after the first contact between imported scientific novelties and their result in local contexts. For example, how the introduction of scientific disciplines or techniques in different countries in Latin America has had different impacts in scientists' status and their interaction in local political structures.[4] This new vision demands the study of local organizations and scientific institutions focusing on the scientific and technical elites, which at different times and in different countries, have identified problems and offered solutions at the same time that they have given a series of beliefs, objectives and ideals to the scientific community. In this sense, the study of the "periphery" becomes a local study, ant its narrative depends in contextual aspects and not on general standars.

Therefore, the introduction of genetics in Mexico will be treated as a social history of science and practices in a local context, and not as a result of "difusion" or imperialist/colonial imposition. This does not mean that the role played by the import of practices and techniques, resources and ideas, can be ignored; these elements will be treated as part of the conditions that allow us to explain the particular manner in which genetics was introduced in Mexico.

During the 19th century plant and animal breeding relied basically on hybridization, massive selection and individual selection techniques, which where continuously modified according to

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1 Basalla, 1967.
2 Chambers, 1993.
3 Latour, 1987, and Vessuri, 1994.
4 Home and Kohlstedt, 1991; Petitjean, 1992; McClellan, 1992, Palladino and Worboys, 1993, and Vessuri, 1994.

the place and organism in which they where utilized.[5] In México, as in general in Mesoamerica, this kind of practices had deep cultural roots in the selection of maize varieties by peasants, that lead to the "creation" of the vast amount of biodiversity that characterizes the region.

New theoretical knowledge, general theories such as Mendelism, and concrete knowledge of species and individuals radically changed the planning and execution of the breeder's work at the beginning of the 20th century. The introduction of Mendelism was a practical asset insofar it changed the idea and purpose of plant breeders and hybridizers.[6] The acceptance and use of Mendelian laws of inheritance were connected to agriculture not only in Mexico but also in other countries such as the United States and England. However, because of its geographic proximity and the type of academic and technical exchange between Mexico and the United States at the beginning of the 20th century, the development of genetics in Mexico can be seen as parallel to that of the United States though there are significant differences.

I will try to analyze the scientific conditions and social relations that allowed the introduction and establishment of genetics in Mexico in the early 20th century, which was consolidated and institutionalized during the second half of the century. I will examine the effect that small communities had during the introduction of genetics in Mexico, making an emphasis on the main role played by two groups, that of engineer Edmundo Taboada and that of the Rockefeller Foundation, during the period between the 1930's up until the late 1950's.

In the first section I will try to briefly explain the first mention of Mendel's laws by Alfonso L. Herrera, despite the fact that it had no effect in the creation of institutions dedicated to the problems of inheritance. Regardless of the development of ideas and postures towards inheritance by the medical Mexican community in the 19th century, genetic principles did not contribute until the 1930's through agricultural programs that intended to carry out plant breeding and that responded, in great measure, to economic necessities derived from political postures of Mexican governments after the Mexican Revolution that took place between 1910-1921. This subject will be treated in the second section.

In the final part of the present work, the subject to be treated will be genetics applied to plant breeding which began during the government of General Lázaro Cárdenas del Río (1934-1940) under the guidance of agronomic engineer Edmundo Taboada Ramírez (1906-1983). Nonetheless, genetics applied to plant breeding was developed in two trends: the one introduced by Taboada in the Office of Experiment Stations (OCE, *Oficina de Campos Experimentales*, later called Agricultural Research Institute, IIA, *Instituto de Investigaciones Agrícolas*) and the one introduced by the Rockefeller Foundation. These two trends focused in solving problems of different strata of Mexican agricultural population.

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5 During the twentieth century other technics such as the creation of mutations were introduced, and more recently genetic technologies, like the ones used in genetically modified organisms.

6 Methodologically, there are two ways to approach the problems of inheritance. One is the study of pedigrees, as was the case in the 18th century when some human characteristics such as polydactyly, hemophilia and color blindness, were studied and recorded. The other method is by breeding that was employed by two schools in the 19th century, the species hybridizers and the animal and plant breeders, which had very different interests and objetives. See, Mayr, 1982.

1. The first mention of Mendel in Mexico

The years between 1810 and 1869 stand out in Mexican history as a period in which the country was immersed in a series of terrible internal conflicts and continued foreign interventions generated by capitalistic interests of European powers and the United States. During these years Mexico faced an attempt of reinvasion (Spain, 1829), several violent mutilations of its territory in the north caused by the United States and two wars with France (1838 and 1864). There were economic, administrative, political, social and cultural internal problems.

In the field of science the immediate repercussion was translated into a certain impoverishment in comparison with the advances that were achieved during the time of the Borbonic reforms (last decade of the 18th century). The armed struggles originated by the Movement of Independence (1810-1821) caused the departure of the majority of Spanish and German scientists that had come from Europe following the Borbonic Reforms, scientists that had carried out a great labor within Novo Hispanic science. Nonetheless, as documented by Guevara Fefers scientific activity did not completely disappear and despite adverse condition some areas where developed.[7]

During the second half of the 19th century in Mexico, in good part due to French influence, the medical community had developed the notion of "inheritance" in the sense of understanding certain diseases that appeared recurrently in family lines or those that presented themselves in certain age-ranges, and that until that moment were incurable. The ideas of inheritance during the 19th century in Mexico suffered an important transformation; there was a transition from vitalism to reductionism, a change that was inplemented in the 1870's with the introduction of positivist thought in Mexican intellectual circles. There was an impulse of experimentation for hypothesis verification and explanations were connected with material entities. Towards the end of the 19th century Mexican scientists like other scientists around the world were searching for the general principles underlying the "laws of heredity."

At the beginning of the 20th century the Mexican medical community kept these ideas and it was not until 1904 that the first explicit reference to "Mendel's law of dominance" appeared in the writings of Alfonso L. Herrera (1868-1942), but more in an evolutionary context than in a practical or applied one.[8] Whether the medical community was not convinced of the truth and implications of Mendel's theory or whether its most urgent interests were far from the theoretical problems involved in the transmission of hereditary diseases, in conjunction with the limitations that the economy applied to research budgets during revolutionary times, the fact is that programs about genetic investigation were not initiated in medicine nor in the incipient biology.[9]

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7 Guevara Fefer, 2002.

8 Herrera was son of the notable Mexican naturalist Alfonso Herrera (1838-1901), who enjoyed many privileges from the government of President Porfirio Díaz (1877-1911). Alfonso L. Herrera obtained a degree in pharmacy in 1889, and was immediately appointed to the zoology and botany chair at the Teachers College (*Escuela Normal para Maestros*) and as an assistant naturalist at the National Museum (*Museo Nacional*) both in México City. In 1890 he was also appointed assistant in the Natural History Section of the National Medical Institute (*Instituto Médico Nacional*) in México City. In 1902, Herrera established the first general biology course in Mexico at the *Escuela Normal* and, in 1904, published the textbook *Concepts of Biology (Nociones de Biología)* to be used in the course. Herrera's book and his teaching represent the first serious introduction of modern biology and Darwinism in Mexico.

9 Barahona and Gaona, 2001.

Without any doubt, Herrera is the most important Mexican biologist of the late 19th and the early 20th centuries.[10] He was a great connoisseur of Lamarck, Darwin and Haeckel, Trevinarius and Humboldt, Cuvier and Lyell as well as Hugo de Vries and Mendel. His two most important works *Biología y Plasmogenia*[11] and *Recueil des Lois de Biologie Generale*[12] are recognized as his most important scientific contributions to biology.[13] In these two works Herrera speaks of variation in the context of his evolutionary conception (plamogeny) as produced by use and disuse and the direct influences of the environment. For Herrera there is an innate tendency to variation, but he blurs the line between variation and selection, in accordance to his Lamarckian vision of inheritance.

For Herrera morphological and functional variations are caused by mutations. The mutagenic action is carried out by means of determinant influences of cellular physico-chemical factors. It may be seen that Herrera's thought is linked more to the polemic between soft versus hard inheritance of the late 19th century in other countries.[14]

The work of Herrera constitutes an important bastion for Mexican biology.[15] However, in the field of genetics, Herrera's work had no impact due to the lack of development of research lines on genetics and/or the lack of institutions dedicated to genetics research. Nevertheless, by 1900 Herrera participated actively in the Commission of Agricultural Parasitology (*Comisión de Parasitología Agrícola*), where agricultural research in Mexico was pioneered at the beginning of the 20th century. Established in 1900 by the Ministry of Development, its work was centered on fighting plant pests, specially the extermination of the orange fruit fly. According to Olea Franco it was created in the right moment because in 1899, the Horticultural Council of California had forbidden the import of Mexican oranges, as the fly that infested them was considered dangerous to the orange industry in California. In this way in 1900 Herrera was the head of a team created to research the orange plantation in the state of Morelos. Their first work was to start a campaign for the extermination of the pest. Herrera and collaborators doubted that the fly could get established in California because the climate was very different from Morelos, and because there were no pests in other states in the country. Despite these investigations the final disclosure was that the Mexican orange was forbidden in California, and in the following years research in the fruit fly larvae were

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10 Beltran, 1951.
11 Herrera, 1924.
12 Herrera, 1897.
13 Beltrán, 1968, and Beltrán, 1982.
14 Mayr, 1982.
15 Herrera was criticized because his approach was at odds with the urgent social needs of the time, which called for improved economic development and basic health, instead of advancing theories about the origin and evolution of life. His opponents insisted that practical studies should have priority over theoretical concerns. Moreover, Herrera's evolutionary ideas were in conflict with religious and social prejudices held by political and religious sectors that had considerable social influence. The institutionalization of biology in Mexico was a complex process, closely related to the establishment of a biological community and the beginning of this discipline in Mexico, and thus leading to the formation of a specific discourse. This process was also influenced by the political environment of the time in which the revolutionary conflict (1910-1917) and then, the institutionalization of the Revolution (1929), motivated academic groups to look for better places to develop their activities. Control of biology returned to a community which had been previously consolidated. It was impossible to think of an autonomous biology that shifted away from medical control. See, Ledesma and Barahona. 1999; Barahona and Ledesma. 2002, and, Ledesma and Barahona. 2003.

going to be one of the most important research projects of the Commission. It was dissolved in late 1907 and Herrera went back to his evolutionary studies.[16]

2. Political backgound and agriculture in Mexico

Mendelian genetics was introduced in the United States and other countries through agriculture in the late 19th century and the early 20th century.[17] In the United States animal and plant breeders that searched practical results, incorporated Mendelism more quickly than other academic groups.

Genetics applied to plant breeding began to be used almost immediately after the "rediscovery" of Mendel's laws by E. M. East and C. H. Shull in the Agricultural Experimental Station of Connecticut and in Cold Spring Harbor respectively in the year 1905. These first studies of inbreeding and crossbreeding were carried out in maize. Since then, this type of research spread to other universities of agriculture in the United States, such as the universities of Minnesota, California, Washington, Ohio, and Illinois among others.

One of the most important achievements of the studies carried out in the United States was the production of double hybrid maize by Gorge H. Shull, Edward M. East and Donal F. Jones, in the late 1910's when they were looking for the inheritance patterns of quantitative characters.[18]

This development was marked by the economic interest that its introduction to agriculture meant for the large enterprises, therefore programs were developed that included among their purposes the introduction of hybrid maize in other countries like Mexico and Colombia, where the native varieties of maize with open pollination basically competed against the idea that hybrids were responsible for the increase in crops in the United States. This was an example of agricultural techniques and genetic knowledge exported from their point of origin, the United States, to peripheral countries like Mexico; however it took its own direction in Mexico in order to adapt to local conditions, necessities, and political circumstances.

Scientific agricultural investigation, coordinated by government institutions has its origin in the *Porfiriato* (1877-1911). Porfirio Díaz's government showed a great interest in encouraging agricultural exportation since this generated foreign currency and it helped to get the equilibrium in the balance of payments.[19] The support for the generation of agricultural products of exportation included not only the legal facilities for producers, national as well as foreign,[20] but also the introduction of machinery and modern agricultural implements, as well as the application of medical and biological sciences in the care of crops and animals (mostly cattle).

Díaz' dictatorship favored higher education and scientific research in accordance with the French model, together with the positivist tradition, introduced to Mexico by Gabino Barreda during the regime of President Benito Juárez (1858-1861; 1865-1867; 1871-1872). Francisco I.

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16 Olea Franco, A. 2002. The Comission was disolved by the Minister of Development Olegrio Molina, who founded the Estación Agrícola Central one year later and annexed it to ENA at San Jacinto.

17 See Paul and Kimmelman, 1988, and Palladino, 1993.

18 See East, 1936, and Shull, 1946.

19 Webster, 1992.

20 For example, for the acquisition of "uncultivated" properties (that in many cases belonged to indigenous communities) and the use of federal waters.

Madero's call for universal suffrage and the prohibition of reelection gave rise to an armed uprising (November 20, 1910) that marks the start of the Mexican Revolution. After Díaz' resignation, Madero assumed the presidency on November 6, 1911, but he was assassinated in February 1913 by Mexican Army General Victoriano Huerta, who remained in power until 1914, as the war against the usurping government continued. After taking the capital city in 1915, Venustiano Carranza, one of the revolutionary leaders, headed a new government. Carranza promulgated a new political constitution in 1917, but was assassinated in 1920. Political instability prevailed through the 1920s, because the right wing forces continued the struggle and formed governments alternating with those of the Revolution until the late 1920s.

During the administration of Porfirio Díaz, legal frameworks and agricultural tools were developed; agricultural research was stimulated by the creation of the first experimental stations, professional level agricultural education, and the modernization in 1907 of the National Agricultural College (*Escuela Nacional de Agricultura*),[21] giving a more technical orientation to its careers. The modernization of the ENA was very important since it allowed the development and consolidation of agricultural instruction in Mexico, and became the cradle of technicians capable of connecting with agricultural communities, offering the benefits of scientific knowledge, taking advantage of the local farmers' knowledge and providing orientation to agricultural politics.[22]

After the revolution, new curricula and titles were created, such as "agronomic engineer," "veterinarian," and "technician in agricultural mechanics and agronomy."[23] By the 1920s there were already programs for improvement of cotton cultivars, the study, introduction, and improvement of new and cultivated agricultural varieties, and the cataloging of hybrids and their possible uses.

Since 1929, during the administration of Emilio Portes Gil (1928-1932), the Department of Agriculture and Promotion (*Secretaría de Agricultura y Fomento*) developed a plan to improve land redistribution and reorganize the production of the raw materials that the country needed.[24] Both activities were ideals that emanated from the Mexican Revolution. The "ejido"—a form of communal land-holding and social organization—was revived (its historical roots date from prehispanic and colonial times) under the slogan: "the land belongs to him who cultivates it;" it

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21 The creation of the ENA goes back to the 19th century. In 1832 the *Ospicio de Santo Tomás* in the Federal District was transformed into the first School of Agriculture by government decree, imparting courses in botany, practical agriculture and applied chemistry, but it was closed because of political problems. Later in 1843 there was a second attempt for its creation but this one also did not work. It was not until 1850 that the school was created again in the *Colegio de San Gregorio* in the Federal District, and in 1853 it was fused with the Veterinary School, creating the National School of Agriculture and Veterinary. In 1854 it was moved to the Convent of San Jacinto, in the Federal District, as the ENA. In 1861 by decree of president Benito Juárez, the first "Organic Law of Public Instruction" was established, which made it dependant of the Ministry of Public Instruction, but in 907 it became dependent on the Ministry of Agriculture and Promotion. Between 1914 and 1917, the ENA was closed due to the armed conflicts and moved to the *ex-hacienda de Chapingo* in the State of Mexico in 1923, where it is found today as the Autonomous University of Chapingo. It is in that moment where it adopted the motto: "Teaching the exploitation of the land, not of man."

22 According to Olea Franco, enrollment at ENA was smaller in the middle 1920s than in the years 1908-1910. This means that enrollment grew more in the years prior to the revolution than under the revolutionary government of President Plutarco Elías Calles. After the 1920s the ENA population estimated was between 1 and 2.5 thousand students. Olea Franco, 2002.

23 Reyes, 1981, p. 127.

24 Portes Gil, 1929.

could not be taxed or mortgaged because it was a family good transmitted only in a hereditary manner.

In 1932, during president Abelardo L. Rodríguez government (1932-1934), the National Agronomic Commission (*Comisión Nacional Agraria*) was created within the Department of Agriculture and Promotion, with the following objectives: guaranteeing that the national plant and animal products would satisfy, totally and foremost, the needs of the whole population, and establishing the regulatory norms needed by public agencies, within the principles of an economy directed towards a social organization of agriculture based on the *ejido*. There was a great effort towards improving the teaching of technical agriculture, through the creation of the "agricultural engineer" major at the ENA, which had a totally practical approach.

During the 1930s and 1940s, two political tendencies can be distinguished in Mexico's power circles—with roots dating back to the *Porfiriato* which influenced research in plant genetics. On one side were those who, as heirs of the Mexican Revolution, believed that farmer agriculture, based on a tradition of communal land-holding, had priority over the creation of a successful agriculture; on the other side were those who thought that Mexican agriculture could only improve by becoming a large-scale private enterprise, far from socialist agrarianism.[25]

During the administration of the General Lázaro Cárdenas del Río (1934-1940), research was started seeking to increase large scale food production, whereas during the *Porfiriato* a primary objective had been the exportation of grains. A main objective of General Cárdenas—a convinced agrarian—was to transform the organization of agriculture and to grant credit and technical support to farmers. The first agronomists trained in the new agricultural techniques shared the "Cardenist" philosophy and focused on solving problems affecting the average farmer.

On March 18, 1938 General Cárdenas nationalized oil, provoking a dispute that lasted until the early 1940s. The foreign corporatations operating in Mexico rejected the right of the Mexican government to nationalize oil and not receiving any economic compensation. The American and British-Dutch oil companies and their governments, imposed economic sanctions on Mexico, and many Mexican imports such as silver, were at stake, because suspending them would have been an important economic blow to Mexico. The economic pressure imposed on Mexico by the US government and the oil companies took place in the midst of an economic crisis that made Mexico's position unstable.[26] The WWII context allowed the relative settlement of this dispute, with repayment of foreign loans being a never-ending task. The presence of the Vice-President-elect Henry A. Wallace at the inauguration of President Manuel Avila Camacho on December first, 1940, was a good sing of the changing times in bilateral relations. A crucial number of agreements for the wartime alliance were accelerated, and the US committed itself to loan money, give technical assistance, export technology, and help introducing in Mexico modern agricultural technologies.[27]

The scenario of a farmer policy based on the *ejido* changed drastically with the government of General Manuel Ávila Camacho (1940-1946); the capitalist tendency reappeared, supported by the private sector, favoring levels of production that would surpass the family needs of the *ejido*-

[25] Hewitt de Alcántara, 1985.
[26] Meyer, 1977.
[27] Mexico provided laborers, petroleum, strategic mineral, henequen and other imprtant plants fibers. See Olea Franco, 2002.

based farmer, so as to meet the food needs of the greatly expanding cities and, above all, the needs of the developing industries.[28]

3. The Office of Experimental Stations and the Rockefeller Foundation, two trends in Mexican agriculture.

3.1. The work of Edmundo Taboada and the Office of Experimental Stations (OCE)

Concern for the improvement of agricultural technology was an intermittent part of Mexico's official politics since the beginning of the 20th century,[29] however researches intended for the augmentation of food production did not begin until the 30's, mainly during Cárdenas' administration, and even with more strength during the 40's, with the active participation of agronomic engineer Edmundo Taboada Ramírez.

Edmundo Taboada Ramírez was born in Ciudad Guzmán, Jalisco, on December 12, 1906. He studied elementary school in Ciudad Guzmán and entered the ENA in 1922, where he graduated as an agronomic engineer with a master in irrigation in 1929. From 1928 to 1929, still as a student, Taboada worked as a topographer in the National Commission of Irrigation (*Comisión Nacional de Riego*) and later worked in the *Sistema de Riego del Mezquital* in Tula, Hidalgo, as a planning and calculation assistant. In 1930 he entered the Ministry of Agriculture in the Department of Chemistry and Soils and in 1931 became the head of the Special Analysis Section of the Central Chemistry and Soils Laboratory of the Agricultural Direction.

None of Taboada's teachers knew about genetics, so he read his first genetics book as a request of Waldo Soberón, the head of ENA and director of the Section of Experimental Stations when Taboada joined it, in order to explain certain principles to him. He had great mathematical skills, so he found quantitative genetics very appealing. He was self-taught and became an expert on genetics. From this came the idea of sending Taboada to study abroad and learn genetics formally.

In 1932 Taboada traveled to Washington, D.C. for two months in order to study the analysis of soils carried out by the Bureau of Soils of the United States' Agricultural Department. He was appointed agronomical attaché in the Mexican embassy in Washington, D.C., so that he could enter in the United States to study. In 1932 he studied genetics, applied plant genetics, cytology, mycology, physiology, and wheat, bean and maize improvement at Cornell University in New York under the direction of R. A. Emerson and H. K. Hayes, but he was not formally admitted into the graduate program or given official recognition for the courses he took. He would later receive an invitation by geneticist H. K. Hayes at the University of Minnesota, USA, to study plant parasitology, especially in wheat rust with Dr. E. C. Stakman.

With the purpose of studying grinding methods and experimental planning with relation to the improvement of wheat varieties, Taboada traveled in 1933 to the Experimental Central Farm

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[28] Hewitt de Alcántara, 1985.

[29] As I have said, there were two opposed visions of rural development, one that emphasized the importance of adapting modern technologies in agriculture while slowing down agrarian reforms, and the other that urged for a deep reform in Mexican agriculture.

in Ottawa, to study the organization of agricultural research programs that were used by the net of Canada's Agronomic Experimental Stations.

Upon his return to Mexico in 1934, Taboada was appointed Head of the Agronomic Experimental Station at *El Yaqui*, Sonora, a position from which he soon resigned due to medical reasons. At this station Taboada initiated his first genetic investigations, which consisted in selecting between different varieties of sesame those which were better adapted to Sonora's environmental conditions. Since 1936 Taboada was a professor at ENA, where he imparted courses in general genetics, plants genetics and agronomic experimentation and investigation. He wrote the first book in genetics text in Mexico, *Apuntes de Genética* in 1938, with the intention of imparting his courses.[30] This book encompasses the history of genetics, Mendelism, the chromosome theory of inheritance, cytogenetics, mutation, gene interaction, and population genetics. There are many references to Charles Darwin and natural selection, explaining how selection works on natural populations and the evolutionary process. Taboada describes with admiration the work of Thomas Hunt Morgan, the leader of the *Drosophila* research group at Columbia University and CalTech, and the work of Emerson, who was the leader of the Maize Genetics Group at Cornell University. For Taboada, the works of Darwin, Morgan, and Emerson were the cornerstone of biology. His textbook treated the various topics in a simple manner, with emphasis on the basic genetic principles. Taboada's *Apuntes de Genética* became very important for teaching genetics and also for the popularization of genetics in Mexico.[31]

With the creation of the Section of Experiment Stations in 1928 under the Ministry of Agriculture and Development, national programs of scientific research were promoted, especially for the genetic improvement of wheat and maize or phytotechnic, paving the way for the creation of an experimental station netwok. Taboada was appointed Head of the OCE in 1940, Director of the IIA from 1947 to 1960, Secretary of the National Council of Research and Superior Agronomic Instruction at the Ministry of Agriculture and Livestock from 1960 to 1964, and Consultant for the Ministry of Agriculture and Livestock from 1965 to 1970.

As I have pointed out, the philosophy of economic development during Cárdenas administration was an agronomist one; Cárdenas believed that high productivity in the Mexican countryside was intimately linked to social structure changes that would transform the great capitalistic agronomic properties in cooperatives of peasants and farmer workers. In this manner, the first Mexican agronomists instructed in the application of new agronomic technologies shared Cárdenas philosophy and were more concerned with finding solutions to the practical and social problems faced by peasants than with importing foreign technology.[32]

The Cardenist group headed by Taboada[33] was formed and carried out its researches within the experimental stations where, for the first time, the more usual hybridization techniques that Taboada had imported from the United States and Canada were implemented. [34]

The OCE was created in 1940 and Taboada was its first director.[35] At the beginning, this office coordinated ten experimental stations segregated in the entire country. During its first six years of life, in these stations different varieties of maize adapted to the ecological and economical

[30] Taboada first taught mathematics and immediately afterwards genetics. When another geneticist, the spanish emigré José Luis de la Loma y de Oteyza, arrived at ENA in 1938, he passed down to him the genetic teaching reponsabilities. See, INIA, 1985.

[31] Taboada, 1938, and Barahona et al, 2003.

conditions of producers from different states were selected. For example, the first variety of improved maize was obtained in 1940 and was called Celaya. It was an open pollinated variety obtained through selection, superior to the local varieties then cultivated and tested by farmers in the state of Guanajuato. Regarding wheat production, a collection of varieties from farmer's fields were initiated, performance tests of the best agronomic qualities were carried out, and the first crossbreeding between high producing Mexican varieties, susceptible to the stem's *chahuixtle*, and American varieties with low adaptation qualities but resistant to this disease, was accomplished. Researches with rice, sesame, sugar cane, rubber, beans, potato, cotton, olive, figs, hemp fiber and guayule were also carried out.

For Taboada, the implementation of an experimental method was necessary since it could give an impulse to Mexican "scientifc" agriculture.[36] The best way to carry out experimental work consisted in experimenting inside laboratories provided with special equipment (besides greenhouses, instruments for maize emasculation and controlled crossbreeding, among others) to obtain control of all possible varieties, installed in the experimental agronomic stations.

Genetic improvement, always linked to Taboada's experimental method, can be expressed in this way: it has been observed in certain species of plants like maize, which have a process of natural open pollination, that in the course of long successive self-fertilization, productivity is reduced to half of the previous generation. In this way, if the process is long enough, successive generations diminish to a very low state of productivity, due to the fact that populations become completely homozygotic. "As more successive self-fertilizations are carried out, progeny is each time more uniform. The increase of uniformity is fast in the first generations, but it becomes slower as the number of self-fertilizations escalates, if this number is large enough (about five or ten successive generations) populations become completely uniform."[37]

In this way, a self-fertilized line of maize by itself cannot be used as an agronomic seed. "When studying the decrease of productivity and the decrease of heterozygotic genotype, it is observed that the parallelism between both processes is considerably narrow. It is confirmed that the productivity of successive populations is strongly linked to the amount of heterozygotes present in those populations."[38]

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[32] During Cárdenas' administration 18 million hectares were distributed among communities and common lands (*ejidos*). In this manner, the amount of hectares in the social sector increased to 25 million (land outside private property). The object of the agronomic distribution during Cárdenas' administration sought not only the satisfaction of a popular demand stated in the Constitution of 1917, but also the formation of small productive units, with self-feeding capacity. The basic unity of the Reform model was the conformation of common lands (*ejidos*). This refers to an endowment of lands that were given to a population nucleus so they could make use of it in the way they saw the fittest. Besides the endowment of lands and financing, the Agronomic Reform of the Cardenato included the establishment of an education system that allowed the formation of technical professionals to help in the development of common lands. Therefore, in association with common land nucleus, schools were created where children and young people should acquire knowledge of agriculture, cattle and other specific activities that the ecologic medium allowed.

[33] Between 1938-1940 from 20 to 30 people were working on sesame, sorghum, maize and beans. Among Taboada's most oustanding collaborators were Eduardo Limón in El Bajío and Clemente Juárez in Torreón, Coahuila. Limón's knowledge and training in experimental genetics was superior to Taboada's. Limón worked in obtaining inbred lines of maize in order to cross them and obtain hybrid seed. See, Olea Franco, 2002.

[34] See Barahona and Gaona, 2001, and Gaona and Barahona, 2001.

Taboada dedicated himself to produce what he called *stabilized maize varieties* starting from the open pollination varieties created during earlier years. "There are several types of high yield corn seeds. The highest yields are obtained with the so called "hybrid" corn, but their exceptional productivity only lasts the first cycle. In subsequent cycles, the productivity decreases so rapidly that sometimes its yield is inferior to that obtained with ordinary seeds, forcing the farmer to acquire new seeds each year […] Improved stabilized varieties with open pollination are another type of high yield maize […] Thanks to their characteristics, the open pollination varieties are better for our poorest farmers and are nearly as productive as the hybrid types."[39]

The seeds were collected from the peasants in different regions of the country, and tested in experimental stations, private fields, and even church gardens. Taboada and collaborators knew nothing about the characteristics of the seeds, thus they began planting them, describing the traits of plants and their growth, establishing times for sowing and harvesting, registering their reaction under different growth conditions and so on.[40] In this way, research was seen as a learning process to improve agricultural practices.

To obtain the stabilized corn varieties, Taboada first obtained lines with the fewest agronomic deficiencies and exhibiting good crossing results. Taboada would first cross any two given lines and select those particular combinations that exhibited high yield, obtaining eventually several combinations of lines that would be genetically stable, i.e., with productivity that remained high from one planting season to the next. These were distributed in the 1950s among Mexican farmers, especially in areas of small traditional farms (some of these varieties are still sown nowadays).[41] In this way Taboada was able to develop the "stabilized" maize that has been widely used by farmers since, in spite of not having the highest yield, as it could be used in successive generations with no additional cost. Taboada claimed that farmers needed to get it only once and then could go on cultivating it and selecting seed from their own harvest.

Taboada and his group accepted some varieties of hybrid maize then sown in the United States, from American colleagues in the 1940s. They did cultivation tests, but they concluded that the hybrid maize seed could not simply be planted elsewhere and, of course, the objetive of the IIA was to produce improve stabilized varietes of maize, not hybrid ones, that could be planted in all

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35 Another institution created during Cárdenas' administration was the Biotechnic Institute (*Instituto Biotécnico*, IB, 1934) within the Ministry of Agriculture and Development. The IB had a section on plant genetics and a botanical laboratory. It only lived 6 years, during which researches explored the evolutionary history of corn and used this information to purify indigenous maize crops. This is not surpising since its leader, Enrique Beltrán, was the most distinguished student of Alfonso L. Herrera (whose points of view towards biology and genetics has been discussed earlier in this paper). Researches at the IB motivated the notion that science ought to be used to purify farmer's varieties by inbreeding and hybridization, to solve scientific, economic, social as well as cultural problems. When President Avila Camacho came to power in 1940, the IB was reorganized and closed doors, and the researchers were dispersed. See, Matchett, 2006.

36 For Taboada, scientific research was necessary to improve the Mexican field, and the establishment of an agronomic experimental method, based on the laws of inheritance, was necessary as it could improve the scientific character of this discipline. The use of genetics was mainly about: 1) obtaining pure lines of native varieties; 2) the formation of new varieties through hybridization; and 3) the improvement, through hybridization, of created varieties, other already existing native varieties or imported ones.

37 Taboada, E. 1981.

38 Ibid.

39 Secretaría de Agricultura y Ganadería, 1952.

regions in the country inasmuch as they facilitated the acceptance by peasants and farmers, who did not require buying seed for every new crop. In1960 the IIA was merged with the Office of Special Studies, created in 1944 as part of a program of cooperation between the Mexican government and the Rockefeller Foundation.

3.2 The Office of Special Studies and the Rockefeller Foundation

The first activity of the Rockefeller Foundation (RF) in México was the 1923 campaign against yellow fever. After a major reorganization in 1928, the RF continued its emphasis on public health and medicine, but began to pay more attention to scientific education. Between 1940 and 1949 the RF launched a major agricultural program in Mexico, with two main goals, to improve food-crop production (corn and wheat) and to train Mexicans in agricultural techniques.[42]

In the beginning of the 1940's with the change of administration from Cárdenas to Manuel Ávila Camacho (1940-1946), the project of a capitalist orientation to agriculture reappeared in the government; the tendency was to increase production in the proper private sector of Mexican agriculture so that it could provide a surplus to feed the ever growing cities and could supply the new industries. This was due to rearrangements in the Mexican political class and the problems of supplying the great metropolitan areas. So, another group of Mexican researchers was formed, integrated in the Mexican Agricultural Program (*Programa Agrícola Mexicano*, PAM), specifically within the Office of Special Studies (*Oficina de Estudios Especiales*, OEE), a product of the involved cooperation between the Mexican government and the Rockefeller Foundation (FR) of the United States, in the introduction of the "technological package" characteristic of the "green revolution" that began in Mexico as a pilot project and was later transferred into other Third World countries.

Since 1936, there was talk in the RF about beginning conversations with the Mexican government with the intention of cooperating in agronomic politics. However, the oil expropriation in 1938, that had an effect on North American and British enterprises, complicated the bilateral relations and set back the possibility of establishing a joint program. When General Manuel Ávila Camacho stepped into the presidency he began negotiation with the Rockefeller Foundation in 1941 and established a program of agronomic cooperation with the intent of working on the increase of agronomic productivity in Mexico. The committee sent by the Rockefeller foundation was formed by E.C. Stakman, head of the Phytopathology Division of the University of Minnesota, Paul Mangelsdorf, director of the Botanic Museum of Harvard University and Richard Bradfield, head of Cornell University's Agronomic Department. The implementation of the PAM began in 1943 with Jacob G. Harrar as its first director. This program

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40 Although it was easy to multiply the seed in the experimental stations without further expense, the peasants had no funds for doing that, because after harvesting the crop they would need money for packaging, treatment, and transportation. Then, "Taboada proposed to the State Government to get a loan and buy all Celaya improved seed, then store it and distribute it with the collaboration of the heads of the main maize-growing municipalities. The later should be asked to promote the seed for the following growing season and to set the price of seed by the ton…. Agricultural researchers would keep an amount of the income to continue seed multiplication." Olea Franco, 2002.

41 Taboada, 1960.

42 See Cueto, 1994. For the role played by the RF in the rise of biology, see Kay, 1993.

had as main objective the basic research of useful methods and materials to increase basic crops and enhancement of the formation and training of professionals.

After the program officially began, Dr. Stakman returned to Mexico with the director of the program for the purpose of consulting Mexican scientists and to establish the basis and specific actions that should follow. Both proceeded according to the consulting committee's preliminary report that recommended an initial focus on the following branches of agronomic science: 1) soils; 2) genetics; 3) disease and pest control; and 4) cattle. American specialists and Mexican researchers agreed, after an exhaustive study, on a two-objective plan: the central activity would be the fundamental research of useful methods and materials for the increase of basic alimentary sustenance crops; but since this program had to be, in time, totally Mexican, there was an agreement to enhance, as a second task, a training program for training Mexican researchers.[43]

In that manner the OEE was born mainly dedicated to the breeding of maize and wheat,[44] and the introduction of a technological package of incomes and practices, improved seeds, chemical fertilizers, insecticides and herbicides, and irrigation, necessary elements for the exploitation of new, genetically improved, varieties.

The OEE's program reflected a scientific, technological and methodological content that was traditional of the agricultural colleges of the United States, whose work was intrumental in the commercialization of agriculture. The PAM headed in Mexico by the RF depended also on the connections with the financial and industrial institutions associated with the introduction of new agricultural technologies. Mexican government sponsored, through the OEE, international loans to Mexico for petrochemical inputs, agricultural machinery and equipment, genetically improved varieties of cattle, and pharmaceutical drugs.

According to Olea Franco, these research activities were a case of tutelage of Mexican agricultural researchers by American scientists who were chosen by the RF to constitute the different research teams who worked in Mexico for about seventeen years. The social orientation carried out by the OEE was only one of the many expressions of the abandonment by the Mexican state of the agrarian reform program launched by Cardenas few years ago. [45]

The "green revolution" had no success in Mexico regarding maize,[46] since it brought the polarization of different sectors of agriculture, due mostly to the fact that they were orientated to major producers that could buy machinery and incomes, and not to all farmers, and because wheat being a self-fertilizing plant that is very sensitive to latitude and altitude changes, it was assumed that farmers already knew their plants and had their techonologies and seed.[47] This revolution was later exported to India, Philippines and Pakistan, and from there to Afghanistan, Ceylon, Indonesia, Iran, Kenya, Morocco, Thailand, Tunes, and Turkey.[48]

However, in terms of scientific research and technological application, the activities of the OEE were unprecedent in Mexico. By the end of 1945, seven American scientists employed and

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43 Harrar, 1950, p. 14.
44 In that time, 72% of the national surface was dedicated to the farming of these two grains.
45 Olea Franco, 2002.
46 The program of wheat breeding, carried out by Norman Borlaug was successful in Mexico. Borlaug was awarded the Nobel Peace Price for his work with wheat in 1970.
47 The IIA tried to improve what the farmer knew about wheat, but did not substitute it for somenting else.
48 Barahona and Gaona, 2001, and Gaona and Barahona, 2001. For the Green Revolution discussion in Mexico, see Fitzgerald, 1994; Frankel, 1963; Griffin, 1971, and Reyes, 1981. See also, Jennings, 1988.

paid by the RF, with Ph.D. degrees, were heading the research programs. The number of American scientists with the same degree doubled. By the end of 1950, twenty-five Mexican graudates were part of the OEE, and their number increased in the following years.

The RF had a scholarship program for graduate studies in the United States to young Mexican agrononomists who where part of the OEE. Mexican agronomists with graduate studies abroad became the directors of agricutural schools, experimental stations, research laboratories, and government head offices.

It must be said, that during the presidency of Avila Camacho, the cooperation with the United States was crucial. In 1942, the Second Inter-American Conference on Agriculture took place. Seventy-six official delegates accompanied by 43 other members of official delegations, and 77 collaborating delegates took part of it. The first conference was held at Washington in 1930, but the second was a great success, bringing a large number of agricultural and plant scientists from all the Americas attending. A summary of the subjects discused at this conference included: soil conservation, soil surveys, and the standardization of techniques and terminology; control of agricultural pests and diseases; agricultural education, especially the provision of more scholarships for Latin Americans; and livestock improvement and the provisions of unified systems of registration for thoroughbred stock.[49]

Although the OEE was referred as part of the Ministry of Agriculture, the RF headed, staffed, and directed all its activities. It grew to 21 American scientists and 100 Mexican associates. By the 1950s more than two thousand maize varieties had been collected mostly in Mexico but also in North and South America, These varieties were kept in seed banks and treated as private property.

The OEE contributed importantly to other research programs, such as the Institute of Research on Rice in the Philippines, the International Institute of Tropical Agriculture in Nigeria, The International Center of Tropical Agriculture in Colombia, and the International Center for the Improvement of Maize and Wheat (*Centro Internacional del Mejoramiento del Maíz y Trigo*) in Mexico.

Towards the end of the decade of the 1980s, it became apparent that there was no reason to keep two institutions dedicated to plant improvement. The OEE was being increasingly directed by Mexican specialists who had been trained with the aid of the RF, while the latter's interests were focused on the exportation of the Green Revolution's new technology to other South American countries, especially Colombia, so that it increasingly left the running of the Office in Mexican hands. In 1961, the IIA merged with the OEE, forming the National Institute of Agricultural Research (*Instituto Nacional de Investigaciones Agrícolas*). This institution took control of all the experimental fields, equipment, and personnel.

Conclusions

The introduction of genetics in Mexico had a parallel with the development in the United States and Europe only in some of its currents. Before 1900, where there was not a discourse on genetics,

[49] Olea Franco, 2002. Although one of the main subjects of the Conference was the creation of a unified system of registration, intellectual property in México only began in the 1990s. In previous times, the only way to guarantee the intellectual property was to hide all the procedures to obtain the varieties.

but rather of a broader term of inheritance, it was handled and conceptualized in Mexico within medicine. After 1900, when genetics surface as a science, its more practical or technological side, phytotechnics or plant breeding was developed in Mexico.

Interest in plant breeding was developed by agronomists with the support of the Mexican governments as long as this represented higher yields and therefore an increase in the economical value of their crops. Nevertheless, research in classic genetics with the intent to discover general principles, the construction of genetic maps, or the explanation of evolutionary patterns, was not practiced in Mexico until the 1960s, in the way that it was practiced in other countries like the United States. However, Mexican researchers that were instructed in phytotechnics, possessed the full body of basic genetic knowledge necessary to understand the hereditary mechanisms that took place during experimentation (as proven by *Apuntes de Genética* written in 1938 by E. Taboada). They also had a considerable understanding of population genetics, which was being developed independently from maize genetics.

The programs developed by the IIA and the PAM were specific and comprised almost exclusively the improvement of varieties with commercial and economic value. Independently from the political tendencies and the social and economic level of agronomic producers towards whom the positive results of genetic improvement carried out by Edmundo Taboada and the PAM were intended, methodologically, both lines followed a common research pattern. It always began by collecting genetic material conformed by the seeds of the plants subject to experimentation (maize, wheat, beans etc.) coming from different parts of the Republic or imported, its planting in experimental fields and the observation of characteristics of phytotechnic interest that each possessed, followed by the selection of those varieties that presented the most adequate characteristics for the intended purpose (greater yield, greater resistance to disease, early maturation, etc.). Once these varieties were obtained, experimentation could proceed by means of crossbreeding with the intention of producing hybrid varieties with even better characteristics than the parental varieties. However, the conception and use of breeding techniques lead to the instrumentation of different agronomic practices according to political positions.

One of the main objectives of IIA was the implementation of experimental stations in different parts of the country in order to increase the production of wheat, corn, cocoa, rice, sesame seed, and beans. For Taboada, the goal of Mexican geneticists was to genetically improve varieties and successfully adapt them for planting in the different agricultural regions of the country. One of the biggest successes of the Institute was to get a variety of corn with high productivity similar to that of hybrid corn, but which would retain its high productivity from one harvest to the next, without the need of producing new hybrid seed for each planting season.

Taboada's stabilized corn varieties were the most important achievement of Mexican agriculture. This work was focused on solving farmers' problems and improving maize genetics research in Mexico. The stabilized corn varieties benefited farmers but didn't contribute significantly to economic change in large-scale agriculture. Economically, the introduction of hybrid seed was more important. It led to the capitalization of the farms and the creation of a flourishing business, namely, the production and sale of seed.

Taboada argued there were some substantial differences between research and extension programs at IIA and OEE. Taboada claimed that an agricultural researcher must know the

characteristics not only of land farmers crops, but also their needs and problems, and local practices for sowing and harvesting, otherwise he would be isolated without knowing the reality, nor frame of reference or idea, even if he knows what books say.[50]

In regard to maize improvement, the approach of the OEE and the RF was contrary to Taboada's. The OEE dedicated most resources to the production of high yield hybrid seed that could only be purchased by farmers who had substantial financial resources. This seed performed best with fertilizers and its efficiency depended upon being planted in irrigated areas. The OEE's approach had prevailed during the 1950s in the Department of Agriculture. In 1948, 80% of corn cultivars had been planted with open pollination varieties, but by 1956 the production program of the Department dedicated 96% of its capacity to hybrid seed production, which benefited the commercial production of corn and irrigated agriculture.[51]

These two tendencies shared the same objectives, to achieve an increase in basic food production in Mexico, and also the same methodologies of Mendelian hybridization; however, they focused agronomic research in different manners. Besides, there was an important difference in the economic and administrative support provided by the federal government during the 40's and 50's. The political discrepancies generated a rather distant relationship between both institutions during those decades.

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[50] Taboada, 1985.
[51] For discussion about the influence of the PAM on Mexican Agriculture, see Fitzgerald, 1994, and Cotter, 1994.

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Herbert Spencer Jennings, Heredity, and Protozoa as Model Organisms, 1908-1918

Judy Johns Schloegel

In early 1908, Herbert Spencer Jennings published his first research exploring hereditary phenomena in protozoa. The article, which explored the fate of "new or acquired" structural characteristics in protozoa, was the first in a series of articles continuing through 1917 that appeared under the heading of "Heredity, Variation and Evolution in Protozoa." Jennings conceived of the research in this series as a logical progression from his earlier research on the behavior of lower organisms, which he carried out in the ten years following earning his Ph.D. at Harvard in 1896. As he explained at the outset of this article, although this new research appeared to be a "complete departure" from his earlier experimental program, it was "in reality a logical continuation" of that earlier work, which foregrounded the question of how behavior "happens to become so largely *adaptive*." [1] Jennings explained that many behaviors, identified as processes such as learning or habit formation, were found to arise in the lifetime of the individual organism. Some adaptive behavioral features, however—referred to with such terms as reflex, tropism, or instinct—did not arise in the lifetime of the individual, but were said to be inherited from one generation to the next. Uncovering the processes by which adaptive characters were inherited, Jennings explained, was the problem that he subsequently aimed to tackle.[2]

The two research programs were unified by a further feature, however—namely, the use of protozoa as experimental research organisms. Jennings' decision to use the unicellular protozoa in his earlier behavioral studies was informed by two critical lines of thought: (1) the nascent conceptualization of protozoa as models of biological phenomena and of other living entities—in this case, of cells in multicellular organisms; and (2) adherence to an evolutionary framework that emphasized the biological importance of the protozoa due to their apparent simplicity and primordial nature. Both concepts emerge in Jennings' thought in 1896, when he began to plan and carry out a semester of post-doctoral research funded by Harvard University in the laboratory of the physiologist, Max Verworn, in Jena.

Following the completion of his doctoral dissertation, which was largely critical of numerous accounts of cell cleavage grounded in developmental mechanics (*Entwicklungsmechanik*), Jennings aimed in his postdoctoral research to produce what he believed would be a more satisfactory account of early development. In Verworn's laboratory, he embarked on experimental study of the behavior of unicellular organisms with the objective of producing models of the actions of groups of embryological cells. Jennings largely abandoned this original project, however, as he became interested in the behavioral responses of unicellular organisms as scientific objects in their own right. He nonetheless continued to develop a conception of protozoa as models of general biological phenomena in the years that followed.

Jennings' conceptualization of protozoa as models was circumscribed by his adherence to progressive evolution, which he adopted during his residence in Jena, well-known as the

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1 Jennings (1908a), p. 578.
2 Ibid., pp. 578-9.

intellectual center of German evolutionary thinking. His adoption of a progressive evolutionary framework was informed particularly by the teachings and writings of Verworn, who was himself a devoted student at Jena of Ernst Haeckel and the evolutionist and physiologist, Wilhelm Preyer. Verworn championed the utility of protozoa for physiologists due to their standing "nearest to the first and simplest forms of life."[3] Jennings, like Verworn, believed that such organisms in turn exhibited the simplest and most evolutionarily fundamental living phenomena that generally were obscured in higher organisms by the evolution and overlayering of increasingly complex phenomena in higher organisms.[4]

In this paper I consider the rationale for Jennings' use of protozoa as model organisms of hereditary phenomena and the central role these organisms played in his articulation and defense of a broad conception of heredity in the early decades of the twentieth century. Further, I wish to consider Jennings' relationship to a genetics/heredity enterprise, or epistemic space, as it was being defined between 1907, when Jennings embarked on hereditary research, until the end of the Great War.[5] From the outset, Jennings was motivated in his hereditary studies—as was the case with other leading American geneticists such as William Castle and T. H. Morgan—to demonstrate evolution experimentally.[6] Unlike many early geneticists, however, Jennings adhered to the principle of progressive evolution, leading him to prioritize the study of hereditary phenomena in the simplest organisms possible. In each of the major hereditary problems that he and others debated during the period—including the efficacy of the inheritance of acquired characteristics and of selection, and the significance of pure lines and Mendelian inheritance, Jennings turned to the asexually-reproducing protozoa for experimental insights. While the effort to uphold a generalized conception of heredity on the basis of research with specific organisms may appear counter-intuitive, for Jennings, the unique evolutionary status of the protozoa as the simplest of the cellular organisms made them perfect for illuminating hereditary mechanisms at their most fundamental level.

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By the time of the publication of his first article on heredity on the eve of his fortieth birthday, in 1908, Jennings had established himself as one of the United States' foremost zoologists. His 1906 monograph, *The Behavior of Lower Organisms*, while widely criticized and debated for its progressive evolutionary assumptions, was hailed as methodologically incontrovertible; in the same year Jennings earned the coveted position as successor to William Keith Brooks at the Johns Hopkins University, and served as director of the Zoological Laboratory until he retired in 1938; he served as president of both the American Society of Zoologists in 1909 and the American Society of Naturalists in 1910; and, during the same period, he became recognized as a rare and formidable philosophical thinker in the American biological institutional landscape. It was with a

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3 Verworn (1899), p. 51.
4 See Schloegel (2006), especially pp. 49-69.
5 On the epistemic space of heredity at the turn of the century, see Müller-Wille and Rheinberger (2005). See also Rheinberger (1997).
6 See for example, Allen (1978) on Morgan and Rader (1998) on Castle.

certain level of confidence that Jennings set out to tackle fundamental problems of heredity at a moment of great ferment in hereditary thought.[7]

In his first article on heredity, published in 1908, Jennings maintained that the primary interest that guided his study was that of the evolution of unicellular organisms.[8] Later that year, in the second article in the series, he refined the "central problem" that concerned him as one of heredity.[9] Such an evolution in thinking was certainly not unusual among zoologists, many of whom came to the problems of heredity through their preoccupation with the unresolved problems of evolution. More specifically, however, Jennings, like his contemporary, T. H. Morgan, was guided by a primary concern about the mechanisms underlying the evolution of adaptive features.[10] Jennings is notable throughout his early publications on heredity for his agnosticism about the possible mechanisms of heredity and evolution. In his first article on heredity in 1908, for example, he indicated his agnosticism as he defined his use of the term: "I use the word 'heredity' merely as a brief and convenient term for the 'the resemblance between parents and progeny,' without implying any underlying entity, and without prejudice about the grounds of this resemblance." While rejecting the likelihood that natural selection among individual organisms could be the sole mechanism of evolution, Jennings aimed to turn attention to the mechanisms underlying the "internal adaptations" within organisms.[11]

In his plan for elucidating "how organisms have arisen," Jennings aimed first to clarify what he considered to be the "normal" processes of heredity and variation, i.e., to uncover the similarities and differences that are normally found to arise in the passing from one generation to the next. With such baseline information in hand, he envisioned, it would then be possible to intervene experimentally in these normal—or "racial"—processes to investigate the primary question of how inherited modifications arise.[12]

Critical to this undertaking was the use of the "simplest organisms." The protozoa were valuable, Jennings explained, because of their rapid rate of reproduction (at least one generation a day) and most especially because reproduction occurred in the "simplest forms."[13] In particular, the protozoa were of interest due to the widespread assumption among zoologists that, since they don't separate into somatic and germ cells, they possess fundamentally different hereditary processes than those of the metazoa. Since reproduction in the protozoa occurs by simple division, i.e., they reproduce asexually, many had concluded that the protozoan progeny are the same as the parents—as Jennings himself wrote in 1906, that "the offspring *are* the parents, merely subdivided."[14] This assumption was generally accompanied by the reasoning that, since there is no distinction between the soma and the germ in protozoa, characteristics attained by the parents would be perpetuated in the offspring. Consequently, as Jennings explained, "if the difference really exists, the Protozoa are much more plastic in evolution than are the Metazoa."[15] The first

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7 On Jennings, see Schloegel (2006); Kingsland (1987); Sonneborn (1975); Ritter (1912).
8 Jennings (1908a), pp. 577-583.
9 Jennings (1908b), pp. 393-4.
10 Morgan (1903).
11 Jennings, 1908a, pp. 584 (footnote), 582.
12 Ibid., p. 583.
13 Ibid.
14 Ibid., pp. 584-5; Jennings (1976 [1906]), p. 320.
15 Jennings (1908a), p. 584.

experimental task that Jennings set for himself in his hereditary studies then was to determine whether characteristics acquired by the individual during its lifetime are in fact perpetuated in their progeny.

Specifically, Jennings turned his attention to the inheritance of localized, structural characters in the ciliate *Paramecium*, as compared to the unlocalized characters brought about by such processes as acclimatization, which affect the organism as a whole. The inheritance of localized characters was viewed by some, particularly August Weismann, to achieve a higher standard of proof of inheritance. Through isolation and culturing, Jennings pursued a series of experiments that followed the transmission of structural abnormalities that appeared naturally in the population.

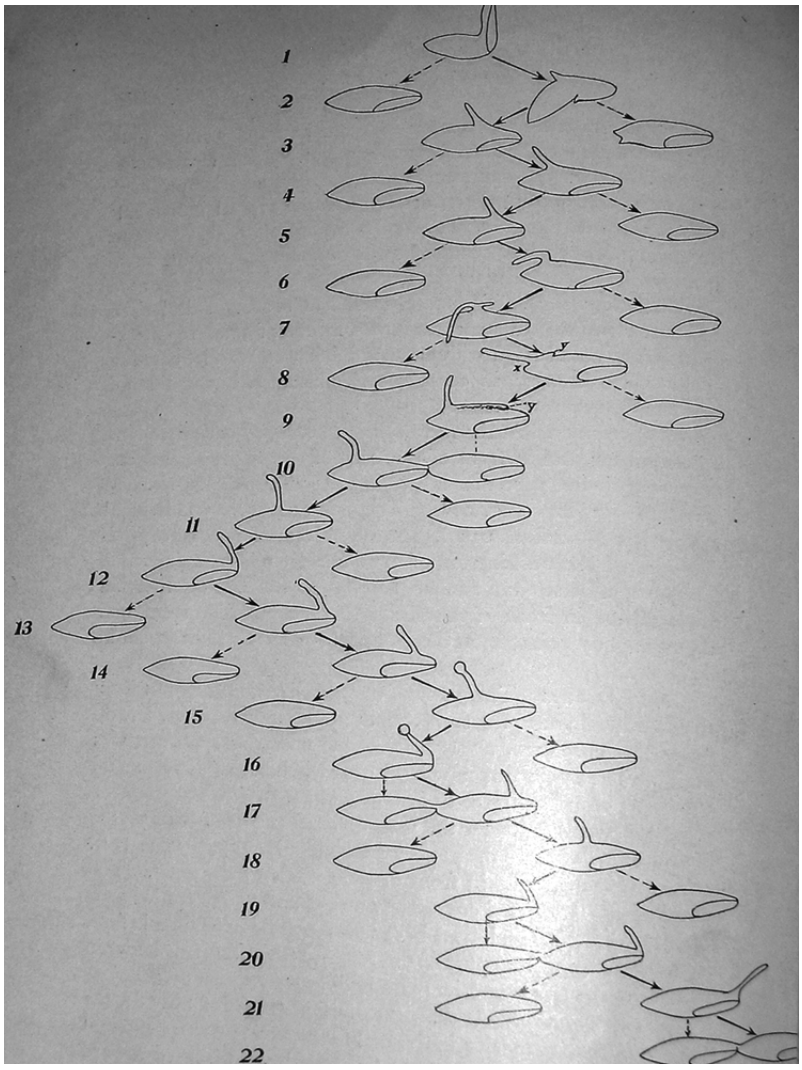

Figure 1. Transmission of structural abnormalities in *Paramecium*. From H. S. Jennings, "Heredity, Variation, and Evolution in Protozoa. I. The Fate of New Structural Characters in Paramecium, in Connection with the Problem of the Inheritance of Acquired Characters in Unicellular Organisms," *The Journal of Experimental Zoology* 5 (1908): 577-632, 594.

In several series cultured from an unusually bent individual paramecium over many generations, the abnormality was transmitted to only one of the two individual progeny, thus failing to produce a new race. In one case, however, Jennings was able to observe the formation of what he considered a new race, when he followed a line in which the individuals resulting from fission remained united in chains. Chains of individuals were inherited in all subsequent generations of both the anterior and posterior fission products, demonstrating the basic insight that, if a new character is to be inherited, the modification to the parent cell causes it to somehow behave differently at reproduction, thus causing it to produce the characteristic anew in each progeny .[16]

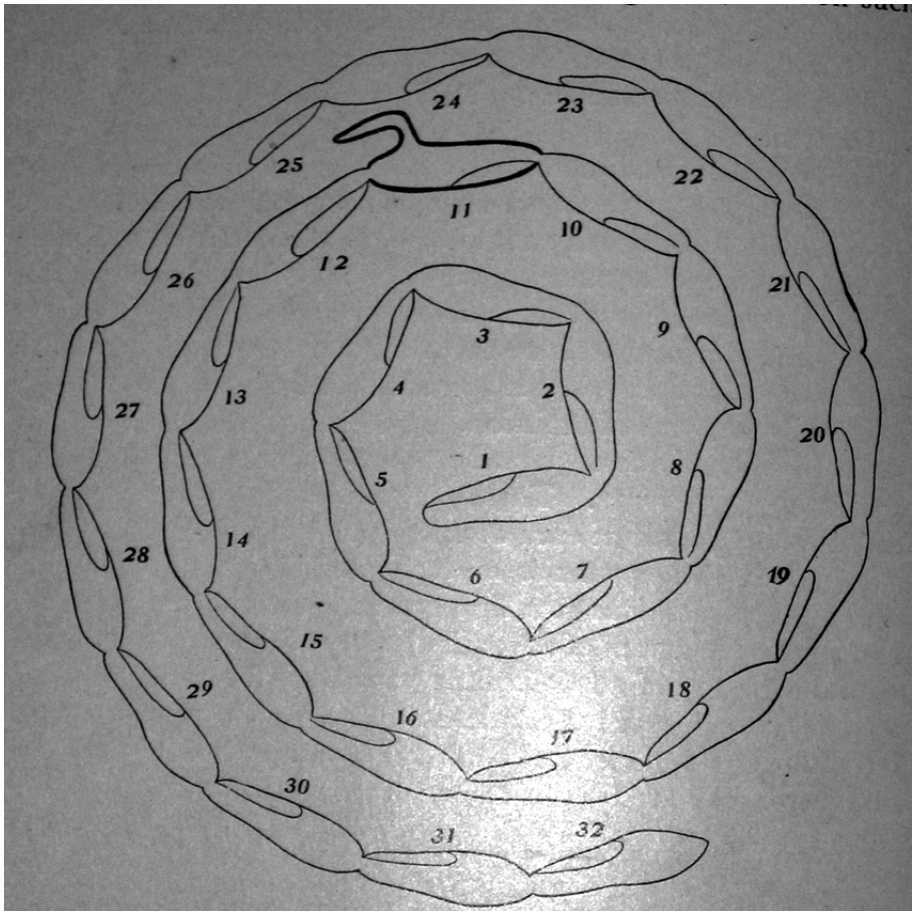

Figure 2. Inheritance of Chains in Paramecium. Ibid., p. 600.

Jennings, of course, realized that this demonstration of the inheritance of chain formation did not involve some kind of germinal material—and this was exactly his point. The case of chain formation enabled him to demonstrate the fundamental similarity between protozoa and metazoa—a similarity that he had come to recognize only recently—and, at the same time, to demonstrate the value of protozoa as model organisms for the study of heredity. As Jennings noted,

16 Ibid., pp. 618-25.

> It is of course possible that the origin of new permanently inherited characters is not normally through mere modifications of the external parts of the cell, such as we see in our illustrative cases [of chain formation.] Possibly there must be originally some modification of more recondite parts—nucleus, chromosomes, or the like—and that these then secondarily act upon and change the outer parts. This would add farther complication, but would not change the essential point, which is that in order that a characteristic may be inherited, it must be due to some modification that causes a change in the processes of reproduction.[17]

In the first case, Jennings maintained that his observations demonstrated that the protozoa were not, in fact, more plastic than the metazoa. Furthermore, his investigations demonstrated that the barrier to the inheritance of acquired characters was not the separation of the germ and soma, but rather the process of cell division, which meant that "the problem of how new inherited characters arise is the same in Protozoa as in Metazoa."[18] This consequently supported his second point that protozoa were ideal organisms for the study of how new inherited characters arise, since: (1) the basic hereditary process was fundamentally the same in both protozoa and metazoa; (2) at a practical level, the protozoa multiply rapidly, for expedient results; and (3) finally, the single cellularity of protozoa made their exposure to environmental influences more feasible and, at the same time, hereditary effects in them more readily observable.[19]

Over the course of the next few years, Jennings became increasingly committed to the value of protozoa as model organisms in the study of heredity despite the largely negative results that he continued to receive. In his second heredity paper published in 1908, Jennings turned his attention from the inheritance of acquired characteristics to selection, as another possible means for demonstrating evolution experimentally. In these investigations, focused on the size of *Paramecium*, he found that the large amount of variability in the progeny descended from a single individual was largely attributable to growth of the individuals in the course of the life cycle and to different environmental conditions. When growth and environment were controlled to the extent possible, the remaining variability exhibited by the line of descendents could not be affected by selection and thus was not heritable: despite persistent efforts to select for the largest and smallest offspring, the individuals in the resulting line did not deviate from the mean size of the line.[20] These results gave way to Jennings' adoption of Johannsen's notion of a "pure line" as a label that more tellingly communicated the imperviousness of races, or the series of individuals descended from a single individual, to selective pressures. [21]

Jennings' thinking about pure lines appears to have cemented his commitment to the utility of protozoa as model organisms. In three different articles appearing in *The American Naturalist* between 1909 and 1911, Jennings again championed the various virtues of protozoa for use in the study of heredity and variation. In particular, he emphasized the value of protozoa for shedding light on debates about the effectiveness of selection and in making concrete the controversial notions of "pure line" and "genotype," which were held by many to be hypothetical or theoretical

17 Ibid, p. 625 (footnote).
18 Ibid., p. 627.
19 Ibid.
20 Jennings maintained that if growth and environmental conditions could be completely controlled, "all the evidence indicates that the standard deviation and coefficient of variation would be zero." Jennings (1909), p. 333.
21 Jennings (1908b), pp. 521-4.

terms. In the well-known symposium on pure lines and genotypes at the American Society of Naturalists meeting in December 1910—the year that he served as president of the society—Jennings declared of pure lines and genotypes that

> These things, whatever we call them, are concrete realities—realities as solid as the diverse existence of dogs, cats and horses. I find in many biologists not working in genetics an incorrigible bent for seeking under such a term as genotype something deeply hypothetical or metaphysical, and for characterizing it therefore boldly as purely imaginative. This is merely because such workers have not the things themselves before them.[22]

The material nature of these entities, Jennings explained in another article appearing during the same period, was readily apparent when protozoa were employed for hereditary study, since "unicellular organisms are essentially free germ cells,"[23] which when perpetuated in isolation series, are in fact a pure line, or the material embodiment of a genotype. These entities, however, "become a little elusive, a little abstract," in higher organisms that interbreed and therefore are not "pure."[24] In cases where selection had been shown to take place, he maintained it was because the investigator had not first isolated their material into pure races.

In addition to the value that he attributed then to the protozoa as model organisms for the study of heredity and variation, Jennings increasingly championed the value of the pure line itself as a tool for hereditary analysis. The "absolutely permanent" nature of the pure line made it a "dissecting knife" that cut away obscurity and confusion, transcended the acrimonious debate, and focused the investigator of heredity on the still unanswered question: what are the sources of the minute hereditary differences upon which evolution operates?[25]

The rhetorical positioning in this statement and in the paper as a whole is, I argue, critically important. This moment in 1910 is one of the few times prior to 1918 that Jennings presents himself as a "geneticist" engaged in an enterprise called "genetics." Far more typically, as has been seen here, he referred to his research during this period as concerned with problems of "heredity." In general, Jennings aimed to uncover the most fundamental mechanisms of heredity and advance a generalized conception of heredity—both of which he believed would surpass Mendelian inheritance or even the theory of the gene, in significance. In this particular context, however, before a large group of biologists and naturalists many of whom indeed were skeptical of the new genetics/heredity enterprise as a whole, Jennings presented himself as a "geneticist." He did this not because of an investment in any particular theory or account of inheritance or any particular mechanism—because he largely did not adhere to one. Rather it was because of his considerable and growing investment in protozoa as model organisms for the study of heredity and the legitimacy that the scientism and precision of the pure line or genotype concept conferred on the protozoa. Jennings aimed as much, perhaps even more, for pure lines to serve protozoa as he did for protozoa to serve pure lines.

Outside of rare moments like these, however, Jennings couched his experimental research program with protozoa during this period in terms of studies of *heredity*. He moved from his

[22] Jennings (1911), p. 80.
[23] Jennings (1909), p. 322.
[24] Jennings (1910), p. 139.
[25] Ibid., pp. 137, 141.

studies in animal behavior to heredity in 1907 not because of any specific interest in or commitment to Mendelism, but because of the many unanswered questions about heredity that were highlighted by the rediscovery of Mendel's laws. Generally speaking, then, Jennings aimed to position his studies of protozoa within the epistemic space of heredity so as to emphasize the fundamentality and generality that he pursued and to distance himself from the more limited conceptions that were connoted by the term "genetics."

Postscript

Jennings reclaimed the mantle of "genetics" and engaged in much of the same type of rhetorical positioning of himself as a geneticist like that seen in the 1910 discussion of pure lines and genotypes when he engaged in his public critiques of eugenics throughout the 1920s. He clearly found it advantageous for the success of his critique to maximize his identity as an "insider" to the genetics enterprise.[26]

By the second half of the 1920s, Jennings was teaching a course entitled "Non-Mendelian Genetics," which he viewed to be a term synonymous with "uniparental genetics," and was the basis of a monograph that he published by the name of "the genetics of protozoa" in 1929. As I have suggested here, these terms would have seemed rather nonsensical to Jennings fifteen years earlier. At the outset of his course in 1927, he defined *genetics* as "the analysis of the production of the differential characteristics of organisms" and *non-Mendelian genetics* as the "lesser known portion" of genetics "which is not subject to the laws grouped under the name of Mendelism."[27] Non-Mendelian genetics was essentially a replacement for Jennings' earlier use of the term "heredity," and he continued to maintain that the insights generated by the program would possess a generality not offered by Mendelian genetics. That Jennings adopted the term "genetics" in the late 1920s suggests, at least in the American context, the large extent to which Mendelism, the theory of the gene, and also eugenics had largely defined the terms of hereditary discourse.[28]

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[26] See Schloegel (2006), especially pp. 72-111.
[27] Sonneborn (1927-28), pp. 1-3.
[28] Schloegel (2006), especially pp. 127-39.

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Clones, Pure Lines, and Heredity: The Work of Victor Jollos

Christina Brandt

Introduction

On December 29th, 1910, scientists of the American Society of Naturalists met at a symposium with the title: "The Study of Pure Lines or Genotypes." Just a year before, the Danish botanist Wilhelm Johannsen had published his book *Elemente der exakten Erblichkeitslehre*, where he had introduced the neologism "gene" and the differentiation between the concepts of a "genotype" and a "phenotype."[1] At this symposium in December 1910, Herbert Spencer Jennings, a zoologist at John Hopkins University, was determined to convince the audience that Johannsen's genotypes were not merely hypothetical things or something "purely imaginative,"[2] as some critics had argued. Instead, Jennings wanted to persuade his colleagues of the reverse: that genotypes had a real existence and were "facts that strike you in the face."[3] He claimed that they were "concrete realities—realities as solid as the diverse existence of dogs, cats and horses."[4] Jennings realism was highly influenced by the research object he had been working with for a couple of years: the unicellular organism *Paramecium*. At the same symposium, Jennings tried to illustrate what "pure lines"—or real genotypes—looked like in the case of this research object. In translating the world of *Paramecium* into the world of higher organisms, Jennings drew the following metaphorical picture:

> To get a clear grasp of the matter I believe that those not working with lower organisms will find it worth while to try to realize the condition which the investigator in this field (that is research on *Paramecium,* C.B.) has before him. A comparison may help. In lower organisms the genotype is actually isolated, each in a multitude of examples, which live along without admixture, visibly different from all others, for many generations, before again plunging into the melting pot of crossbreeding. In higher organisms we should have the same thing if every rabbit, every dog, every human being, multiplied by repeated division into two like itself, till there were whole counties inhabited by persons that were replicas of our absent president; cities made up of copies of our secretary, and states composed of duplications of the janitor I saw outside. Every human being, as it now stands, represent a different genotype (save perhaps in the case of identical twins), and these genotypes become inextricably interwoven at every generation. It is therefore easy to see how the genotype idea might appeal to workers among higher organisms as a mere hypothesis.[5]

What might have sounded slightly fanciful to Jennings audience is a common image in today's debates on cloning. Representations of mass duplication of human beings are frequently used in

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1 Johannsen 1913 [1909].
2 Jennings 1911. p. 80.
3 Ibid, p. 80/81.
4 Ibid, p. 81.
5 Ibid, p. 81.

the realm of popular media and science fiction to illustrate the horror of future cloning possibilities. In such images, cloning is understood as a kind of a serial mass production, as the production of an endless series of identical human beings out of one prototype. One could easily be tempted to think that these images of clones as the results of serial reproduction are very recent phenomena. However, what I want to argue today is that the concept of the clone as referring to serial (re)production or serial replication is something that was developed very early in the 20th century life sciences. Later, I will return to Jenning's quotation, with which I have introduced my discussion because it comes from precisely the historical period in which the terminology of the clone originated.

In my paper, I will be dealing with one chapter of the very early history of the "clone" (as a scientific concept) and cloning (as a scientific practice). I will address the transition of the clone concept from its origins in horticultural and plant breeding into a laboratory research tool in the first two decades of the 20th century. With this transition, a specific aspect in the history of the concept emerges, namely the use of cell clones as technical objects, that is: as specific research tools for experimentation.

My argument in this paper is the following: although the term "clone" was introduced within the context of horticultural breeding (where it designates a group of plants that were asexually propagated from a single ancestor plant) it soon became a concept used in the space of the laboratory. During the 1910s and 1920s, the term "clone" was introduced to refer to research objects which had standardized qualities because they were serially reproduced from one original or ancestral cellular unit. I will focus on early genetical work on protozoa, because it was in this field of protozoology that "pure lines"—then redefined as "clones"—of unicellular organisms began to be used as standardized research tools. Scientists such as Herbert S. Jennings or the German zoologist Victor Jollos started to apply the method of "pure line breeding" (developed by the botanist Wilhelm Johannsen in his well known work on beans) to the research on unicellular organism, especially on *Paramecium*. Their research on clones of *Paramecium* aimed at the general investigation of genetic constitution and heredity as well as questions about the inheritance of acquired characteristics.

Thus, in the beginning of the 20th century, the scientific career of the "clone" concept started with the rise of the genetics of unicellular organisms, its demand for uniformity, and the quest for standardized research objects—clones that could be used as a kind of model organism.

But before I go into detail, let me start with a few sentences on my general perspective: This paper is part of a broader project on the history of cloning, in which I regard the concept of the clone as a kind of "boundary concept" that went through very different scientific and non-scientific fields over the course of the 20th century. The main questions of the project are: what kinds of semantic shifts, what kinds of exchange and feedback between different spheres are related to these processes of circulation? The project addresses the relationship between material practices and concept formation within bioscientific research. Furthermore, I am interested in the impact of popular representations and cultural images that arose around the figure of "the clone."

During the 20th century, the concept of the clone circulated among very different research fields (such as plant breeding, botany, cytology, tissue culture, genetic engineering and

developmental biology as well as reproductive medicine.) As this occured, the epistemic status of the clone changed over time: Thus, in my perspective, there are three interrelated fields that are important for understanding the history of cloning: 1) the emergence of the clone as an epistemic and as a technical object within different experimental systems during the 20th century 2) the clone as an interdisciplinary and inter-discursive element, and 3) the clone as a cultural phenomenon. In this paper, I will focus on questions concerning the first aspect: My main question today is, how the notion of the clone, which was first used to refer to some plant products, such as some special fruits, was introduced into the laboratory. Thus, the question is: How did the "clone" become an experimental object and concept?

The paper has two parts: First, I will briefly follow the history of the clone concept and its introduction to the study of unicellular organisms. I will outline the discussion about the scope and limits of the concepts of "clones" and "pure lines" that began around 1910. The passages I am about to quote will show that the definition of what a "clone" was oscillated between two opposite poles: a presumed genetic identity, on the one hand, and on the other: the idea of genealogical origins.

In the second part I will discuss one specific experimental approach, working with clones in more detail, namely that of the German protozoologist Victor Jollos. His research, which was very much stimulated by Jennings, led to the concept of "Dauermodifikationen" (persisting modifications). The existence of *Dauermodifikationen* was highly debated among German geneticists in the 1920s. Here, I will turn to questions of today's workshop: the changing practices of early genetics and their impacts on the notion of heredity. In the last part I will discuss how Jollos concept of *Dauermodifikationen* stimulated the discussions of cytoplasmic inheritance in Germany during the 1920s.

"Clones" and "pure lines": struggle for exact meanings

Like the gene concept, the notion of the clone was first introduced to biology at the beginning of the 20th century. Whereas the "gene" referred to an abstract or even ideal unit (according to Wilhelm Johannsen's use of the term), the notion of the clone referred from the very beginning to a concrete material object. It was Herbert J. Webber, a botanist from the Plant Breeding Laboratory of the US Department of Agriculture, who coined the term "clone" in 1903—having searched for more than two years for a "suitable term to apply to those plants that are propagated vegetatively by buds, grafts, cuttings, suckers, runners, slips, bulbs, tubers, etc."[6] Webber argued that "the plants grown from such vegetative parts are not individuals in the ordinary sense, but are simply transplanted parts of the same individual, and in heredity and in all biological and physiological sense, such plants are the same individual."[7] Webber then defined "clons" (sic) as "groups of plants that are propagated by the use of any form of vegetative parts (....) and which are simply parts of the same individual seedling."[8]

6 Webber 1903, p. 502.
7 Ibid, p. 502.
8 Ibid. p. 502.

This was the original definition of a "clone" in plant breeding at the beginning of the 20th century. If you trace the history of the concept, you will soon find the following short articles, published in the journal *Science* in the years 1911 and 1912 (that is only one year after the above mentioned symposium of the American Society of Naturalists) with the titles: "Genotypes, Biotypes, Pure Lines and Clones" respectively: "Genotype and Pure Line."[9] The authors are Herbert Jennings and the botanist and plant breeder Geo H. Shull. Responding to each other, both scientists tried to clarify the semantics of the newly arising concepts in the emerging discoursive framework of genetics.

Many historians have already emphasized the importance of "pure lines" for the emerging field of genetics. In his well known work, Johannsen had designated a group of beans, which were all descendants of the same orginal self-fertilizing plant, a "pure line." He had observed that the variations in weights of all beans descending from beans that belonged to the same "pure line," could always be described with the same variation curve. Besides playing an important role in the field of plant breeding (and its economics), "pure lines" or "pure cultures" were also central for the field of applied microbiology and the brewery industry from the last decades of the 19th century onward.[10]

Pointing to the diverse uses of the term "pure line," Jennings argued that an expansion of that definition, originally introduced by Johannsen, was inevitable. Moreover, he argued that a new term was needed, a term that included—in addition to the feature of a "genealogical series"—the issue of "genetic identity." According to Jennings, "pure lines" designate a "genealogical series in which there arises no diversity in hereditary characteristics"[11] and he gave a list of such cases of pure lines:

> Pure lines in this sense might be expected, from what we thus far have learned,
>
> (1) in cases of vegetative reproduction,
>
> (2) in at least some cases of parthenogenesis (where no reduction division occurs),
>
> (3) in case of self-fertilization of homozygotic organisms,
>
> (4) in case of inbreeding of a group of genotypically identical homozygotic organisms.[12]

Only the third group referred to Johannsen's definition of a "pure line." Therefore, Jennings concluded that "it appears that we badly need a term that will include 'genotypically identical' series of forms"[13] arising in other cases than in Johannsen's definition of the term.

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9 Jennings 1911b; Shull 1912; Shull 1912b.
10 For the analysis of Johannsen's work see Roll-Hansen 1978; Roll-Hansen 2005; for the central importance of "pure lines," and the notion of "purity" in early genetics and breeding research, see Bonneuil (this volume), and Müller-Wille (2007).
11 Jennings 1911b, p. 841.
12 Ibid. p. 841.
13 Ibid. p. 842.

Jennings' redefinition and his search for a new term that included the aspect of "genotypically identical series of forms" did not remain unanswered: Only three weeks later, in January of 1912, the US botanist George H. Shull responded to Jennings with a short article on "Genotypes, Biotypes, Pure lines, and Clones."[14] Discussing the cases Jennings had mentioned, Shull recommended the use of Webber's notion of "clone" or "clonal varieties" to refer to the "vegetatively reproduced potato and paramecium (...), in contradistinction to the self-fertilizing 'pure lines' of beans." [15] Furthermore, he suggested "the general adoption of the word 'clone' for all groups of individuals having identical genotypic character, and arising by asexual reproduction of any sort, including apogamy (i.e. so-called 'parthenogenesis' unaccompanied by a reduction division)." [16]

Whereas the individuals of the "pure line" were necessarily homozygous, the individuals of a clone were not. This difference was one reason to argue for a new terminology. But the main goal was, similar to Jennings', to find a term that would denote the "identical genotypic character" of a series of descendants arising by asexual reproduction (instead of self-fertilization). In his first note from January 1912, Shull was very enthusiastic about the important fact that clones could be regarded as having "identical genotypic characters." Nevertheless, something—or somebody—must have unsettled the author's view. Only three weeks later, Shull published a revision of his proposed definition. On February 2nd, 1912, we find another notice in *Science*, in which Shull explained: "Further consideration convinces me that this restriction (that is: the restriction of the term clone to 'groups of genotypically identical individuals,' C.B.) is highly undesirable because it is impracticable."[17] The botanist now argued that, "it would be quite impossible to know for a certainty that two twigs used as cuttings or cions from the same tree had the same genotypic constitution."[18] Thus, he revoked his previous emphasis on genotypic identity and redefined the clone as "a group of individuals traceable through asexual reproductions (including parthenogenesis (...)) to a single ancestral zygote, or else perpetually asexual."[19] "This definition," he concluded, "puts the word 'clone' on exactly the same footing as the expression 'pure line', making it a purely genealogical term and involving no implication whatever as to the genotypic equality of the individuals included in the single clone."[20]

From these quotations we can see two things: With the application of the method of "pure line breeding" to protozoa research, there arose a need for a new terminology. This led to the introduction of the concept of the "clone" into this field. But secondly, at the same time, there was a discussion about whether clones could be regarded as genetically stable objects. At this time, the "clone" was mainly a genealogical term. Statements about the genetic stability of clones could not be made with certainty; on the contrary the stability of the genotypic identity of the material was itself the subject of the research. Or as Jennings had emphasized in 1910, the questions were: Can

14 Shull 1912.
15 Ibid. p. 27.
16 Ibid. p. 28.
17 Shull 1912b, p. 183.
18 Ibid. p. 183.
19 Ibid. p. 183.
20 Ibid. p. 183.

selection change genotypes? "Can environmental action permanently modify them?"[21] These questions resulted from the controversial debates about the evolutionary role of selection and variation. Once Johannsen had shown that selection had no effect on pure lines, he—like many other geneticists—concluded that mutations (or discontinous variations) were more important than selection in bringing about evolutionary changes. Darwinists, on the other hand, emphasized the primary power of selection and regarded evolution as a process based on continous hereditary variations.

With this I now come to my second issue: the work of Victor Jollos, whose research on "variability and heredity in microorganisms"[22] also started within this realm of evolutionary questions.

Victor Jollos' work on Paramecium*: the clone as a technical object*

Let me start with some biographical notes:[23] Victor Jollos was one of the early coworkers of Max Hartmann, whose department at the Kaiser Wilhelm Institute for Biology emerged as one of the leading centers for genetic work on unicellular organisms in Germany in the 1920s. Born in Odessa (Ukraine) in 1887, Jollos spent his entire youth in Germany. After completing his *Abitur* he studied with Richard Hertwig in Munich and received his PhD in zoology in 1910. In 1912, Jollos became research assistant at the Institute for Infectious Diseases in Berlin (the "Robert Koch Institut"), where he worked in Max Hartmann's Department for Protozoological Research. When Hartmann was appointed to the newly founded Kaiser Wilhelm Institute (KWI) for Biology in 1915, Jollos followed him there. From 1925 to 1929, he spent a few years as professor of zoology at the University in Cairo/Egypt. After that, he continued working in Hartmann's group at the KWI in Berlin. With the rise of the Nazi Regime, Jollos was forced to leave Germany. In 1934, he emigrated with his family to the USA. Despite the support offered by colleagues such as Jennings and Tracy Sonneborn, Jollos never got an adequate position in the USA, possibly because of the differences in research styles between the German and the US scientific landscapes.[24] In 1941, Jollos died in Madison/Wisconsin.

Jollos started his research on *Paramecium* in 1910 shortly after his PhD, when he was still in Munich, and he continued this research when he went to Berlin. Except for the years during World War I, when Jollos was engaged in medical work (he got an additional degree in medicine in 1918),[25] the research on *Paramecium* kept him occupied until the early 1920s.

Stimulated by Jennings' approach, Jollos regarded research on *Paramecium* from the very beginning as a promising tool for experimentation around general questions concerning heredity. Even in his first papers on this subject Jollos emphasized that there was in principle no border

[21] Jennings 1911, p. 81.
[22] See title Jollos 1914.
[23] For Jollos' biography see Brink 1941.
[24] For this aspect see the discussion in: Dietrich 1996.
[25] See Brink 1941.

between protozoa (or unicellular organisms) and higher organisms. Protozoa research, he argued, could offer valuable insights into general questions of heredity.[26]

The original material for Jollos' work—the *Paramecium* populations—came from different lakes around Munich and Berlin (see Fig. 1). He isolated 9 different strains of *Paramecium caudatum* and 3 different strains of *Paramecium aurelia* from these populations. These strains showed differences in three categories: 1) their length, 2) their resistance to extreme temperatures, and 3) their resistance to arsenic acid. This material (as it is listed on the table) provided the basis for a complex system to produce "pure cultures" or "clones" of *Paramecium*. Until the early 1920s, Jollos developed a complex system consisting of a huge number of clonal lines derived from his original 12 strains of *Paramecium*.

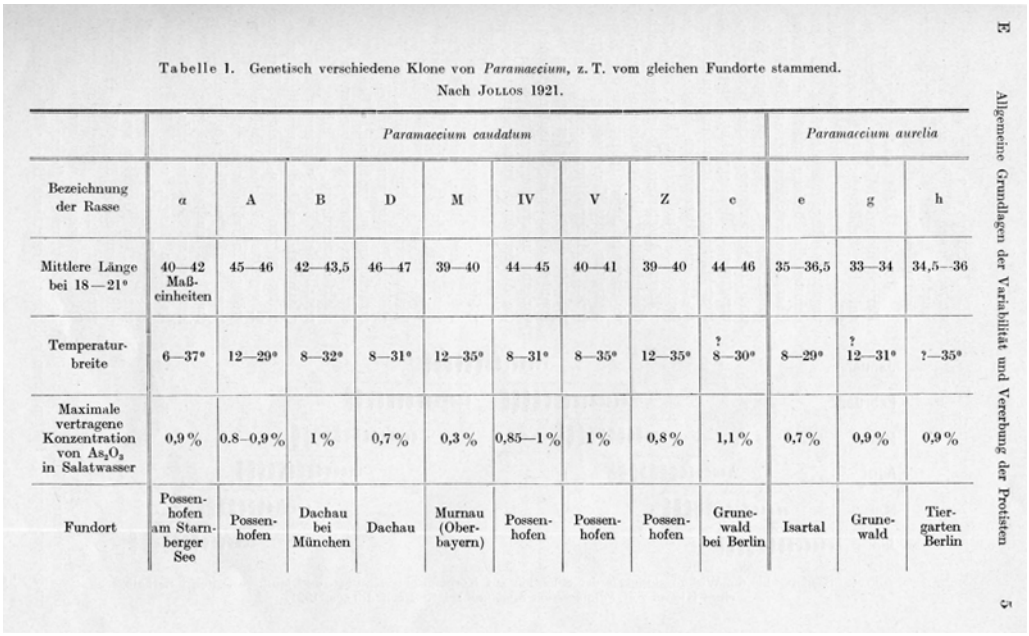

Tabelle I. Genetisch verschiedene Klone von *Paramaecium*, z. T. vom gleichen Fundorte stammend. Nach Jollos 1921.

	Paramaecium caudatum									*Paramaecium aurelia*		
Bezeichnung der Rasse	α	A	B	D	M	IV	V	Z	c	e	g	h
Mittlere Länge bei 18—21°	40—42 Maß-einheiten	45—46	42—43,5	46—47	39—40	44—45	40—41	39—40	44—46	35—36,5	33—34	34,5—36
Temperatur-breite	6—37°	12—29°	8—32°	8—31°	12—35°	8—31°	8—35°	12—35°	? 8—30°	8—29°	? 12—31°	?—35°
Maximale vertragene Konzentration von As_2O_3 in Salatwasser	0,9 %	0.8–0,9 %	1 %	0,7 %	0,3 %	0,85—1 %	1 %	0,8 %	1,1 %	0,7 %	0,9 %	0,9 %
Fundort	Possen-hofen am Starn-berger See	Possen-hofen	Dachau bei München	Dachau	Murnau (Ober-bayern)	Possen-hofen	Possen-hofen	Possen-hofen	Grune-wald bei Berlin	Isartal	Grune-wald	Tier-garten Berlin

E Allgemeine Grundlagen der Variabilität und Vererbung der Protisten 5

Figure 1. Jollos research material: Different clones of *Paramecium* and their origins. Source: Hämmerling 1929, p. 5.

When Jollos started this work, he was still speaking of "individual lines" ("Individuallinien"),[27] explicitly in reference to Johannsen's concept of a "pure line." Yet, we also find the debate about the diverse semantics of a "pure line" mentioned in Jollos' writings. The need for a term to better fit the conditions of asexual propagating objects also influenced Jollos' work. Soon he began to speak of "clones" to designate his experimental material. In principle, each *Paramecium* that started to propagate by cell division could be the origin of a new clone, that is: of standardized objects for research. The crucial point of this system was the calibration of the environmental conditions. Jollos had to make sure that no conjugation or parthenogenesis occurred, and that the Paramecium propagated only by cell divisions.

[26] See for example Jollos 1914, p. 33-34.
[27] Jollos 1913, p. 225, p. 227, p. 229

The questions with which Jollos began his research were about the influence of environmental conditions on the genotype. He varied parameters such as temperature (or treatment with poison). He tried to change the clones in such a way that their reaction norm ("Reaktionsnorm") was altered and that this changes became stable and inherited. To induce inherited changes, Jollos did the following: He exposed these different clones of *Paramecium* over a specific time period to ever increasing levels of arsenic acid; clones from those cultures of *Paramecium* that survived within the first level of arsenic were transferred into another, slightly higher level of arsenic medium and so on. Each step involved the production of new clonal lines for further experimentations. By this procedure, Jollos was able to generate clones that showed an increased resistance to arsenic. When clones of these lines were placed into an arsenic-free medium (and the procedure was started again) this acquired resistance persisted over periods of hundreds or more cell divisions, sometimes periods of longer than half a year. However, there was always a point in the end when all clones declined to the original level of arsenic sensibility. Especially after a conjugation (and an exchange of nuclear material) had occurred, there was a return to the original characteristics.

The most important outcome of this research, was the concept of *Dauermodifikationen* (persisting modifications)—a notion which was introduced by Jollos to explain these surprising findings. As early as 1914, Jollos spoke of *Dauermodifikationen* as a third kind of variation that could neither be regarded as a mutation nor as mere modification.[28] In the following years, he devoted his whole energy to a clarification of this phenomenon.

Jollos's research on *Dauermodifikationen* was widely discussed. As Jan Sapp has shown, a lot of neo-Lamarckian scientists "viewed it as providing evidence for the inheritance of acquired characteristics."[29] However, Jollos himself did not share this opinion; he was convinced that the observed persisting modifications did not challenge the stability of the genotype. Nevertheless, Jollos' research led to another important distinction that was part of another discussion in the 1920s, namely the issue of cytoplasmic inheritance: In 1921, as a result of his Paramecium work, Jollos distinguished two different kinds of transmission phenomena ("Übertragungserscheinungen") and variations, which he related to two different cellular substances:

> 1) The transmission of hereditary factors (genes) and their variations, which are related to the structures of cell nuclei (chromosoms), and 2) the transmission of changes ("Übertragung von Veränderungen") that are based on modifications ("Umstimmungen") of the cytoplasm or other structures. Only variations belonging to the first group can be regarded as genotypic variations, or mutations, and only this kind of variation is a hereditary variation in the stricter sense. All variations of the second group are variations that belong to the category of modifications and *Dauermodifikationen*.[30]

During the 1920s, Jollos research was regarded as a major experimental contribution to the view that the cytoplasm played a significant role in the hereditary processes. In particular, Joachim Hämmerling, another coworker of Max Hartmann, interpreted Jollos' results in the context of the

[28] Jollos 1914, p. 20.
[29] Sapp 1987, p. 61.

so-called "Kernplasmaproblem"—the discussion of nuclear-cytoplasmic relation in genetics. Hämmerling, who also popularized Jollos' concept of *Dauermodifikationen* in a small book (with the same title) in 1929, argued along the lines of scientists like Carl Correns and Fritz von Wettstein. [31] For him, the existence of *Dauermodifikationen* showed that the cytoplasm had a strong impact on the gene action ("Genentfaltung"). Whereas Jollos himself spoke more cautiously of an active role of the cytoplasm in hereditary processes, Hämmerling speculated whether the cytoplasm could be regarded as an autonomous genetical constitutive element just as important—or maybe even more important—as the nucleus. I mention this last because we find here another interesting link to the history of cloning. Around that time, Hämmerling started his nuclear transplantation experiments with *Acetabularia*—which can be seen as some of the first successful nuclear transfer experiments.

Let me conclude: One could certainly discuss the debate about *Dauermodifikationen* and cytoplasmic inheritance in more detail. However, my interest here has been to outline the transition of the notion of a "clone" (that was developed in the field of horticultural breeding) into a concept that was introduced to the space of laboratory practices. My argument has been that the scientific career of the clone concept (as referring to a standardized research material/research tool with all of its semantics of identiy and purity) started with the rise of the genetics of unicellular organisms. How far we can understand these developments in the broader context of the rise of model organisms at the beginning of the 20th century is an issue of further discussions.

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[30] "An Stelle der alten Begriffsbestimmung der Vererbung als Übertragung von Anlagen auf die Nachkommen, einer Begriffsbestimmung, die die Mannigfaltigkeit der Übertragungserscheinungen nicht berücksichtigt, setzen wir also die Einteilung: 1. Übertragung von Erbanlagen (Genen) und deren Veränderung, die mit Kernstrukturen (Chromosomen) in Zusammenhang stehen und 2. Übertragung von Veränderungen, die auf Umstimmung des Plasmas oder bestimmter gesonderter Strukturen beruhen. Nur Abänderungen, die zur ersten Gruppe gehören, sind als genotypische, als Mutationen oder nach der in dieser Arbeit verwandten Ausdrucksweise als "im strengen Sinne" erbliche Abänderungen zu bezeichnen. Alle Umstimmungen der zweiten Art gehören zur Kategorie der Modifikation und Dauermodifikation." Jollos 1921, p. 207.

[31] Hämmerling 1929, p. 59-65.

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Pedigree vs. Mendelism. Concepts of Heredity in Psychiatry before and after 1900

Bernd Gausemeier

Psychiatry is one of the most important contexts for the emergence of a science of heredity. In the late 19th and early 20th century, the inheritance of mental diseases was not only a major concern to the medical community, but also a highly disputed matter of public discourses. Nevertheless, our knowledge about psychiatric (and, in general, medical) concepts of "hereditary diseases" in this era is still quite fragmentary. This may be due to the fact that the pre-Mendelian use of the term "heredity" might appear vague and incoherent from a modern perspective. But if we want to understand the meaning of "heredity" in 19th century psychiatry, we have to apply other criteria than theoretical congruity: since we are dealing with a *medical* discourse, we have to consider the aetiological and nosological concepts in which the notion of "hereditary diseases" was embedded. Moreover, we have to look at the practices that were used to record and to analyze "hereditary" phenomena. In this paper, I will primarily focus on the latter aspect: the impact of statistical and genealogical techniques on the perception of hereditary diseases. On this basis, I will discuss the precarious state of Mendelism in early 20th century medicine. Mendelian theory, as historians of medicine are beginning to realize, was by no means enthusiastically accepted by physicians and psychiatrists.[1] I want to argue that this resistance was not due to a lack of scientific understanding among medical researchers, but to the specific place of the concept "heredity" in medical thinking and practice.

Statistics

Most 19th century psychiatrists were convinced that hereditary disposition was the major cause of mental diseases. Accordingly, it was a part of their professional routine to inquire about indications of madness or other abnormalities in a patient's family. Ever since the emergence of modern psychiatric institutions in the early 19th century, mental asylums—especially in France—collected such information and converted them into statistical records stating the number of "hereditary burdened" cases among their inmates.[2] These figures—the earliest form of quantitative data concerning human heredity—provided the major basis for 19th century discussions about the pathogenetic role of heredity. Their value, however, appeared questionable since the numbers published by different asylums diverged strikingly. The influential German alienist Maximilian Jacobi criticized in 1844 that most mental hospitals contented themselves with a cursory inquiry of the patient's relatives.[3] While Jacobi held that a more conscientious style of investigation would provide more reliable data, Wilhelm Griesinger, the founding father of German academic psychiatry, raised more basic objections concerning the uses of asylum statistics. Besides the ratio of cases allegedly based on a "hereditary disposition," alienists

1 Rushton 1994, p. 144.
2 Cartron 2007.
3 Jacobi 1844, p. 598 ff.

meticulously listed the number of patients who had suffered from alcoholism, physical diseases or professional setbacks, and often used these data to assess the aetiological importance of the respective phenomena. For Griesinger, this approach was both inadequate and deceptive, because it created an artificial separation between aetiological factors whose true meaning could only be understood in the context of a particular life history. It was the foremost task of the scientific psychiatrist to examine the whole genesis (*Bildungsgeschichte*) of the mainfest disease, by grasping "all those subtle threads at their beginnings which are at their ends interwoven into a web of delusion (*Wahngespinst*)."[4] Griesinger had no doubt that heredity was usually the most important aspect in this complex of pathogenic factors. Family history, thus, was a crucial part of psychiatric anamnesis, but it had to be treated in conjunction with the patient's individual biography, as its pre-history.

This view was not unusual among 19th century psychiatrists. Even if the hereditary disposition was commonly regarded as the prime aetiological factor, it was not seen as a force that necessarily "produced" a certain disease, but rather as a potential that could be evoked and altered by certain environmental influences. Griesinger's objections reflect the fundamental conflict between the clinical and the statistical meaning of "heredity": while for the practitioner, it was one aspect in a complex psychopathological process, it became an isolated category in asylum records. The administrative practices of large clinical institutions, thus, created a space in which "heredity" became a visible entity.[5]

From an aetiological perspective, the presence or absence of "hereditary influences" was primarily a hint regarding the curability of the case. Though older convictions that "hereditary" diseases were necessarily incurable[6] were quite out of fashion by the mid-19th century, many psychiatrists held that "hereditary" cases tended to develop into specific, severe forms of mental diseases. Bénédict Morel, the renowned degeneration theorist, regarded the "hereditary" diseases as one nosological class. Morel's approach was developed further into the concept of hereditary diathesis, which was widely accepted in late 19th-century psychopathology, especially in France.[7] According to this idea, all mental and nervous diseases emanated from the same kind of hereditary disposition. Its manifestation was believed to aggravate in the course of generations—severe forms were regarded as the result of continued neuropathic degeneration in a family, while all kinds of excentric or aberrant behaviour could be interpreted as its primary forms.

This perception accorded with the most simple forms of asylum statistics, in which any information about insane, criminal or just "suspicious" relatives similarly generated an entry into the column for "hereditary" cases. In the second half of the 19th century, however, some statistical surveys issued by psychiatric institutions went beyond giving the mere percentage of "predisposed" patients. Since asylums collected personal data like age, religion or profession from their new entries, it was possible to establish the most diverse correlations between these items and "hereditary" disposition, or to calculate if "hereditary burdened" patients were more likely to recover or to relapse.[8] More sophisticated reports differentiated the notion of heredity according

4 Griesinger 1867, p. 132 f.
5 This development may partly explain why—as López-Beltrán (1992, 36 f) states—the noun "heredity" began to be used as a general concept in the French medical community during the 1830s.
6 Waller 2007.
7 Dowbiggin 1991, p. 119 ff.

to degree of kinship—"direct" heredity (i.e. observed diseases in the parental generation), "indirect" respectively "atavistic" heredity (grandparents) or "collateral" heredity (siblings).[9] This specific style of categorization is characteristic for 19th century medical concepts of heredity: the term "heredity" primarily referred to a pathogenic force appearing in different "grades," not to the constant transmission of a certain trait.

Psychiatrists, thus, had no lack of statistical data referring to the factor "heredity." Those inclined to laborious statistical work rather ended up producing hundreds of tables which yielded no results of scientific value. Asylum directors who realized this unsatisfactory situation nevertheless blamed it on the insufficient state of psychiatric record-keeping. A standardization of statistical methods in all major psychiatric institutions, they hoped, would generate a basis for truly scientific studies.[10] In the 1860s and 70s, the reform of asylum statistics became a vividly discussed topic among German alienists. Following the 1867 International Congress for Psychiatry in Paris, there had been international efforts to develop standard schemes for asylum statistics.[11] After these plans had been thwarted by the 1870/71 war, the Association of German Alienists authorized a commission to conceive census forms and statistical tables for the common use in all German asylums. Similar discussions took place in Switzerland, where a national standard scheme was adopted in 1872.[12]

Psychiatrists engaged in these discussions were aware that a kind of statistics generating more precise data about aetiological factors like heredity required more specific categories, more detailed information and, consequently, more work. Characteristically, the German Alienist's commission declared that it was preferable to restrict the new schemes to data whose "scientific value was recognized from all sides" and to simplify statistical procedures by "leaving out the administrative and aetiological considerations (with the exception of heredity)."[13] Apparently, it went without saying that "heredity" was a most crucial aetiological aspect that could easily be determined, while the "scientific value" of almost any other kind of information turned out to be controversial—especially the question of nosological categories. In the 1870s, there was at best a rudimentary system for the classification of mental diseases. Different psychiatric schools followed different nosological concepts. As the asylum director Friedrich Wilhelm Hagen put it, psychiatrists were no "typesetting machines" who were able to sort aetiological facts into pre-defined categories, but human beings dealing with individual life histories.[14] He feared that statistical standardization would only result in time-consuming work that produced nothing but an ever-increasing accumulation of numbers and tables.[15] Once again, Hagen's position exemplifies the tension between the administrative practice of record-production and the customs of anamnesis: while statistical surveys demanded well-defined and fixed categories, the individual cases often ruled out such clear-cut evaluations.

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8 Tigges 1867.
9 Hagen 1876, p. 208 f.
10 Tigges 1867, p. 119.
11 Anon. 1873a, p. 459-460.
12 Anon., 1873a; Anon., 1873b.
13 Nasse 1873/74, p. 241.
14 Hagen 1871, p. 278.
15 Ibid., p. 269.

Yet nosological specifications were necessary if alienists wanted to understand the distribution of certain forms of mental diseases and the respective role of heredity in their aetiology. In 1874, the Association of Alienist's commission issued standard forms which distinguished seven forms of mental disease.[16] Further, they asked if cases of mental disease, nervous disease, alcoholism, suicide, "remarkable character" and criminal acts were noted in parents, siblings, grandparents, uncles and aunts. In contrast to prior forms of asylum records, the Association of Alienist's scheme allowed to determine the percentage of "hereditary" cases for each nosological category and to specify the nature of "familial disposition." Yet its application only aggravated the inherent problems of asylum statistics: due to the large array of categories, the absolute figures often became too low to be of statistical significance. The first survey using the scheme abstained from specifying the ancestors' diseases because this practice would have fragmented the material even more.[17] Characteristically, the same survey noticed only one regularity of heredity—the "law" that psychopathological phenomena were most likely to be transmitted from mother to son and from father to daughter. The structure of asylum records favored speculations about specific maternal and paternal "influences" on the offspring, since they always listed male and female patients separately. Apart from such traditional beliefs, even the more sophisticated statistical practices produced nothing that could be regarded as new, commonly accepted knowledge about heredity. Despite the fact that it increasingly moved to the center of psychiatric studies, heredity was not yet a scientific object in its own right. It was not because the prevailing methods of asylum statistics were essentially about establishing correlations. They allowed to relate "heredity" to other phenomena (e.g. sex, age, nosological categories) but not to analyze the ways of hereditary transmission—a problem that only began to bother psychiatrists by the time when a science of heredity emerged.

Genealogy

By the 1890s, more and more voices in the German psyciatric community rejected the statistical approach altogether and called for a turn to genealogical methods. The Jena psychiatrist Otto Binswanger, for example, categorically stated that "the questions raised by the recent works about heredity will, in clinical research, only be solved through the accurate study of individual family trees but not through mass statistics."[18] The phrase "recent works about heredity" referred, of course, to August Weismann's theory of the continuity of germ plasm and the debates it had sparked off. This new biological discourse about heredity did not only exert a strong influence on the medical community because medical scientists had to take sides in the struggle over the possibility or impossibility of an inheritance of acquired characters. It evoked a new awareness that the notion of heredity, as it was traditionally used in medicine, was rather a means of clinical classification than a biological concept. As the psychiatrist Robert Sommer clarified, one had to distinguish between the mere observation of certain pathological traits within a family history

16 Anon. 1874. The scheme distinguished melancholia, mania, secondary psychic disorder ("*Sekundäre Seelenstörung*"), paralytic psychic disorder, imbecility, "delirium potatorum".
17 Hagen 1876, p. 207 f.
18 O. Binswanger, preface to Rohde 1895, p. IX.

("*Heredität*"), and the positive proof that such a case was in fact based on biological inheritance ("*Vererbung*").[19] Psychiatrists became aware that their old use of the term "heredity" referred to an analogy between phenomena in different generations, while the *scientific* problem was to establish a causal relation between these phenomena. In other words, it was only at the end of the 19th century that heredity became a scientific object in medicine, i.e. that medical scientists began to ask *how* a certain disease was transmitted and *what* about it was transmitted. The means to investigate this was the pedigree.

Doubtlessly, psychiatrists had studied family histories long before the 1890s. Ideas about the "hereditary transformation" of diseases or the progressive degeneration of families clearly rested upon observations on several succesive generations. Richard Krafft-Ebing's statement that his knowledge about the heritability of nervous diseases was based "on the exhaustive study of the pedigrees of many hundreds of sick persons."[20] indicates that genealogy provided a form of tacit knowledge about heredity. The common form to represent and to analyze heredity in 19th century psychiatric journals and books, however, were statistical tables.

Large-scale genealogical studies on the inheritance of mental diseases were first initiated by the the influential Swiss alienist August Forel. In 1895, his assistant Jenny Koller published a study that was not only based on family histories of patients from Forel's Burghölzli asylum, but also on genealogical material collected among other social groups. [21] The comparison of the occurence of mental diseases in the pedigrees of "healthy" and "mentally ill" people showed that also the former were often "hereditary burdened," though to a lesser extent than asylum patients. This approach was, effectively, an extended version of old-style asylum statistics. It responded to critics who objected that inquiries only based on patient records necessarily exaggerated the role of the "hereditary burden," because they comprised no comparative material.[22] The inclusion of "normal" genealogies indicated that traces of "hereditary" madness were not confined to certain degenerated families, but omnipresent.

This aspect, however, was not the main reason why genealogical methods became an increasingly popular matter of discussion in German medicine after 1900. Many physicians and psychiatrists were influenced by Ottokar Lorenz's 1898 handbook of genealogy.[23] Lorenz, an historian, did not only define genealogy as a borderline method linking the historical and the biological sciences, he also forcefully argued that scientists would only be able to understand the problem of heredity by applying proper genealogical methods. As stated before, psychiatrists were open to this kind of advice, because it appeared as a counterdraft to the practices of asylum statistics. While asylums and clinics collected masses of family data based on oral information that was, in addition, mostly restricted to two generations, individual family studies opened up a "vertical," more specific perspective. Wilhelm Strohmayer, Lorenz' most ardent follower in psychiatry, stressed that medical genealogy was about going "more into the deep than into the breadth" since "a few, but thorough investigations about heredity are more useful than countless

19 Sommer 1901, p. 67.
20 Krafft-Ebing 1869, p. 443 f.
21 Koller 1895.
22 Grassmann 1896, p. 1018.
23 Lorenz 1898.

inaccurate ones."[24] Extensive pedigrees including reliable psychopathological data would allow to understand the laws of transmission.

Most adherents of medical genealogy, however, believed the scientific study of human heredity could only be advanced through larger samples of adequate genealogical material. Robert Sommer, the most influential advocate of medical genealogy, and other psychiatrists called for the establishment of regional or national centers compiling pedigrees assembled in psychiatric asylums and clinics.[25] The idea of such large-scale projects raised the question of methodical standardization. Medical genealogists devotedly argued about the best way to compile data, the number of generations to be included, and the most concise form to depict family relations. A crucial question was in how far family histories provided data satisfying the needs of a medical investigation. The idea of following a certain trait over a longer succession of generations was adapted to the history of aristocratic dynasties—most notably the much-discussed example of the facial features running in the Habsburg family.[26] Beyond that, it was only applicable to cases of rare and specific diseases in families with an unusually good genealogical tradition. The most remarkable study of this kind was published in 1913, after more than a decade of fieldwork, by the Swedish neurologist and eugenicist Herman Lundborg, who traced a particular epileptic illness over 6-7 generations.[27] His claim that the disease could be attributed to a Mendelian recessive gene rested on a comparatively reasonable line of argument. However, Lundborg also listed other features of the ramified kinship he had studied: alcoholism, madness, violence, aberrant behaviour, crime—in a word, the expressions of proceeding degeneration. Lundborgs work represents two basic tendencies of medical genealogy: on the one hand, he claimed to provide an "exact" analysis of a hereditary disease, on the other, he compiled diverse biographical particulars which were unreservedly taken to be related by means of heredity. Further, its paper-wasting reproduction of 50 large pedigrees strikingly documented the practical intricacies of the genealogical approach.

Most practitioners conducting medico-genealogical studies were not faced with this problem, but rather with families hardly providing reliable biographical information beyond the grandparental generation. They were aware that the genealogical structure of most families could at best be reconstructed up to the great-grandparental generation.[28] A controversial topic among medical genealogists was the question if studies in human heredity had to consider only the direct ancestry of a proband or also the collateral lineages, i.e. aunts/uncles and grandaunts/granduncles. Following the latter option, the ophthalmologist Arthur Crzellitzer conceived a "kinship chart" that arranged the ancestors around the living proband in the center.[29] Printed on a squarish sheet of paper, Crzellitzer's form provided a solution for an urgent practical problem of medical genealogy: it allowed to collect a large number of family studies concerning a certain trait in a reasonably concise way—e.g. in a folder or a flip box.

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[24] Strohmayer 1908, p. 483.
[25] Sommer 1913, p. 394 f.
[26] E.g. Lorenz 1898, p. 402-408; Strohmayer 1911; Haecker 1911.
[27] Lundborg 1913.
[28] Crzellitzer 1908, p. 575; Jolly 1913, p. 382.
[29] Crzellitzer 1908.

Crzellitzer's charts achieved some attention, but not a wide distribution. In the years between 1900 and World War I, large parts of the German medical community were concerned with practical questions of genealogical research, but there never emerged a large, concerted project like the Eugenics Record Office in the USA. The idea of such a central institution was propagated by a group centered around the *Zentralstelle für deutsche Personen- und Familiengeschichte* in Leipzig, an association of genealogists closely in touch with psychiatrists and eugenicists.[30] It was based on the belief that a treasury of well-reconstructed pedigrees, compiled with the help of hobby genealogists and physicians, would generate valuable material both for historical and for medical purposes. This comprehensive outlook explains much of the popularity of genealogy in the medical community, but it also contributed to its eventual failure. Historical and medical family research, after all, did not only have different objectives, but also required different techniques of data-arrangement.

Mendelian Statistics

The flaws of the medico-genealogical discourse were obstinately pinpointed by the practising physician and medical statistician Wilhelm Weinberg. The difficulties to obtain reliable medical data about past generation, as he first stated in 1903, did not only make family studies problematic, but utterly useless for the study of disease inheritance.[31] While most medical genealogists supposed that good genealogical material would inevitably generate insights into the inheritance of certain traits, Weinberg held that studies in human heredity were only possible if there was a sharply defined phenomenon to be investigated and a sufficient supply of reliable data about it. Weinberg was by no means a dispraiser of genealogy as such: he was experienced in the use of family records for studying diseases like cancer and tuberculosis. But he argued that if medical scientists wanted to understand the regularities of heredity, they had to disengage from singular case studies and to process genealogical material according to rigid statistical methods. This was also necessary, according to Weinberg, „to eliminate the influence of social factors." Since families usually formed a constant „environment," genealogical case studies tended to blur heredity and tradition.[32]

After he became acquainted with the Mendelian theory by the mid-1900s, Weinberg began to develop a method that stood out both against pedigree studies and older forms of medical statistics. Many adherents of medical genealogy accepted Mendelism, most notably the group of American eugenicists associated with the Eugenics Record Office (ERO). The ERO approach was based on the collection of pedigrees (usually comprising three generations) containing a certain trait. From its average distribution in the respective generations, it was deduced whether the trait was transmitted according to the recessive or dominant Mendelian mode.[33] Weinberg's approach was clearly different: he understood that doing Mendelian genetics was not about investigating *pedigrees*, but about *constructing generations*. Between 1908 and 1914, Weinberg published a large

30 Breymann 1912.
31 Weinberg 1903.
32 Weinberg 1908, p. 378.
33 Cannon/Rosanoff 1911; Rosanoff/Orr 1911.

number of contributions to a statistical theory of Mendelian human genetics which place him, in retrospect, among the founders of population genetics.[34] His ideas were by no means ignored, but their practical implications were barely realized by medical scientists. A significant exception was the psychiatrist and eugenicist Ernst Rüdin, who adopted Weinberg's views on medical genealogy and statistics in the early 1910s.[35] In the following years, he developed a project aiming at the proof that the main forms of nervous diseases were transmitted as Mendelian traits, drawing constantly on Weinberg's statistical concepts and his personal advice.[36]

In 1916, Rüdin published his study on the inheritance of *Dementia praecox* (Schizophrenia). For this purpose, he had compiled a large number of schizophrenia patients in clinics and asylums. The next step was to detect all the siblings (who potentially comprised additional *Dementia praecox*-cases) and the parents of the patients. All these relatives were, as far as possible, examined by a medical expert. In this way, Rüdin was able to construct a Mendelian 'F1'- and a 'P'-generation, with secure medical data on each individual. The Rüdin/Weinberg method was based on the hypothesis that the disease in question emanated from a recessive factor. If this was assumed, all the parents had to be regarded as heterozygote bearers of the factor, except for those families where one parent also displayed the disease. These cases were separately treated as heterozygote/homozygote crossings. If the "recessive" hypothesis was correct, the ratio of ill people among the sibling series born from two 'normal' parents had to be 25%, respectively 50% in the group born from one sick parent. The statistical proof was, of course, a little more complex. In 1912, Weinberg had pointed out that it was impossible to achieve correct Mendelian ratios with a sample only comprising manifest bearers of an assumedly recessive trait. Since the records necessarily missed all the double-heterozygote couples that produced no manifestly ill offspring at all, both the parental and the filial generation were incomplete and the ratios were distorted. Weinberg developed mathematical tools to eliminate this source of error.[37] It is especially this methodical contribution that shows what distinguished Weinberg from the practices of medical genealogy—not only his statistical skills, but primarily his awareness that Mendelism was about calculating with the *unseen*.

In theory, the Weinberg-Rüdin method was doubtlessly the first genuinely Mendelian approach to human heredity. But apart from accurate statistics, a Mendelian approach requires a clearly defined trait. If such traits exist at all in humans—striking and rare features like polydactily or haemophilia had been the first viable objects of Mendelian studies—this was surely not the case in the realm of psychiatry. Rüdin's object of study, *Dementia praecox*, was not only a complex disease, but a highly contested nosological concept. As stated above, the classification of mental diseases had been a major problem in all attempts to standardize psychiatric statistics in the late 19th century. In the 1890s, a large part of psychiatrists began to accept Emil Kraepelin's sophisticated nosological system as the new gold standard for clinical classification. Dementia praecox was a central category in Kraepelin's system, a nosological "unit" that was characterized by a specific aetiology and psychopathology. Nevertheless, influential colleagues disagreed over this point: other concepts of schizophrenia included a much wider scope of symptoms and morbid

[34] On Weinberg's biography cf. Früh 1996.
[35] Rüdin 1911.
[36] Weber 1993, 109 f.
[37] Weinberg 1912, 166 ff.

phenomena than Kraepelin's definition.[38] The question at stake here was if nervous and mental diseases could be divided into clearly distinct pathological "units" or if they formed a "family" of interrelated clinical phenomena.

When Rüdin intended to prove that *Dementia praecox* could be attributed to a Mendelian factor, thus, he also ventured to demonstrate that Kraepelin's definition and his entire systematic approach were correct. Yet Rüdin's description of his work shows how difficult it was to treat *Dementia praecox* as a constant "trait." According to Kraepelin, the disease became manifest up to the age of 40, so siblings who died before that age could not clearly be counted as "ill" or "normal" cases. Further, the manifestation was considerably affected by environmental influences. Finally, the whole psychophysical personality of the patient affected the manifestation of the trait.[39] It largely depended on triggering factors—traumata, alcoholism or extreme physiological situations like childbirth—if and when it appeared. In short, Rüdin had to include the whole genesis of the disease into his calculations. But he mainly considered the other exogenous and endogenous factors because they "obscured" or distorted the clear picture of Mendelian inheritance. Heredity was not the only pathogenic cause, but the only one that counted.

Nevertheless, his reductionist efforts were not crowned with success. After all calculations and corrections, his sibling series only showed less than 5% instead of the expected 25% of Dementia patients. He resorted to the alternative explanation that the disease was caused by two recessive factors, but measured by his own methodical claims he had failed to establish a clear Mendelian scheme. The same was the case for his subsequent studies on the transmission of other Kraepelinean "disease units." When he was about to become Nazi Germany's most influential eugenicist in 1933, he frankly admitted that for none of the major mental and nervous diseases a Mendelian mode of inheritance had been unquestionably established.[40] The most sophisticated approach of Mendelian human genetics in the first half of the 20th century clearly demonstrated that it was *not* possible to "mendelize" complex mental diseases.

This failure notwithstanding, Rüdin's reductionism offered a new perspective for the psychiatric concept of heredity. The focus on a nosological "unit" like *Dementia praecox* was a turn against traditional concepts of "hereditary transformation" or "neuropathic disposition," that is against the practice of counting diverse pathological features as appearances of the same hereditary tendency. Rüdin did not categorically rule out that there might be hereditary dispositions manifesting themselves in various clinical phenomena rather than specific Mendelian factors causing certain pathological "traits." But he argued that his approach was the only way to test both options.[41] There is no doubt, however, that he was convinced of the fundamental correctness of his Mendelian hypothesis. Being an ardent eugenicist, he held that a psychopathology based on Mendelian principles—in place of the old cloudy notion of "hereditary disposition"—would allow to identify a risk of hereditary ill progeny with scientific certainty.[42]

Further, Rüdin's approach profoundly changed the scope of genealogical methods. Rüdin's co-workers directly interrogated patients and their relatives, but they also collected material from

38 Roelcke 1996.
39 Rüdin 1911, p. 547.
40 Rüdin 1934, p. 134.
41 Rüdin 1916, p. 139 ff.
42 Rüdin 1911, p. 495.

registry offices, church registers, hospital files, records of police, military and legal authorities, and finally family histories. The fruit of this genealogical field work was processed in the form of index cards.[43] This method was geared to compute data relevant for a certain problem (like the inheritance of *Dementia*), but it also allowed to recombine the material for different projects. Pedigrees were only internally used to visualize family relations. Incited by the structuralist idea of Mendelism, Rüdin had transformed medical genealogy into a database technique.

Non-Mendelian genealogy

Rüdin's Mendelian research program was exceptional in the medical realm. Many other medical researchers in Germany accepted Mendelism as an interesting theory which provided, for example, a nice way to explain why hereditary diseases „skipped" generations.[44] But they were generally unable to integrate Mendelism into their aetiological and nosological thinking, most notably the concept of the unit-character.

Psychiatrist and occasional genealogist Robert Sommer offers a characteristic example for this tendency. Though he did not explicitly reject Mendelism, it was incompatible with his medico-genealogical approach. When he argued for area-wide family research projects, it was because he hoped for insights into the "familial relations of the mental diseases and their distribution in the whole country."[45] In this view, the question was not how certain diseases were transmitted but how they were related. Pathological characters were not at all transmitted in a constant form, they were transformed. In the same spirit, the asylum director Hans Roemer stated that the crucial question about pathological heredity was "according to which rules the slight and the severe alterations of psychic health are interlinked."[46] Understanding heredity was a way to understand the nosological relations between diseases, not their respective modes of transmission. In this perspective, the enthusiasm for pedigrees so vigorously attacked by Weinberg made perfect sense: "familial relations" between diseases and anomalies were best studied by using extensive genealogies of "interesting" families. Sommer's perspective was even broader: for him, the essential question was how mental diseases and "normal" mental qualities were related. The „normal personality" already alluded to its psychopathological potential—not only in individuals, but also in whole families. While Rüdins approach was based on the clear definition of a disease as a distinct feature, Sommer's idea of family research was about "finding the family type in its various manifestations."[47] Rüdin collected and arranged specific data about populations, Sommer envisaged psycho-pathological family histories.

Mendelism, thus, was incompatible with a widespread medical concept of heredity, but the problematic relation between Mendelism and medicine was scarcely discussed in an explicit way. A remarkable exception in this respect was the Rostock pathologist Friedrich Martius. Like Sommer, Martius accepted Mendelism in principle, but he disputed its applicability to the human

43 Rüdin 1916, p. 25 ff.
44 E.g. Kraepelin 1909, p. 177.
45 Sommer 1913, p. 394.
46 Römer 1912, p. 293.
47 Sommer 1907, p. 108.

domain. His attack on the poor quality of pedigree studies claiming the "Mendelian" transmission of ill-defined characters like "musicality" would have met approval from Weinberg, but his critique went beyond methodical flaws:

> The now fashionable attempts to adjust pedigree material—which is so abundantly at hand in the medical literature—to the Mendelian numerical proportions suggest a congruence which does not exist so far and is little likely to exist. For the human material is by its nature contrary to the application of the experimental method working with pure lines.[48]

Weinberg or Rüdin would have objected that even if "pure lines" in the sense of Wilhelm Johannsen did not exist in human populations, it was possible to construct statistical purity with respect to a certain trait. But for Martius, *diseases were not traits* at all,[49] and statistical purity was not an indisputable value in clinical medicine. Argueing from the viewpoint of the practitioner, he consequently asked for the benefits of Mendelism for clinical practice.

Martius pinpointed the implicit motivation for many adherents of Mendelism in medicine, namely the claim that if it was once established how a disease was transmitted, it would be possible to predict it with mathematical precision and—if the state once adopted eugenic principles—to eliminate it. Even if it was proven that certain diseases behaved like dominant or recessive factors, Martius asked, what was won? It was still impossible to predict the offspring's state of health with complete certainty, and accordingly the exact knowledge of the Mendelian scientist did not lead any further than the experience of the pre-Mendelian physician.[50] For the practicing physician, he claimed, it was sufficient and much more valuable to know the principles of "scientific genealogy." While the Mendelian view only created an illusion of certainty, accurate family research exhibited the facts of heredity "as they really exist in human beings."[51] This was not a naive statement of an unimaginative traditionalist. Martius realized that Mendelism introduced the reckoning with virtual realities into medicine. He sensed that with the interest for the invisible logic of the genotype, the focus shifted away from the actual object of the medical study, the patient and the disease. In so far, Martius formulated a sharp-sighted criticism of eugenic aspirations, though he was himself an old-school hereditarianist and eugenicist. While Martius' vision of eugenics was a "reasonable" form of premarital "counselling" based on accurate family studies, Rüdin's approach implied the control of populations.

Conclusion

The two concepts of genealogical methods discussed here—represented by Sommer and Martius on the one hand and by Weinberg and Rüdin on the other—do not only correspond to diverging ideas about heredity, but also to essentially different concepts of disease. While the "traditional" medical concept of heredity attributed plasticity and variability to hereditary diseases, the Mendelian view implied their stability and specificity. And exactly this view was hardly compatible

[48] Martius 1913, p. 222.
[49] Ibid., p. 190.
[50] Ibid., p. 186.
[51] Ibid., p. 188.

with the experiences of the clinical practitioner. A physician or psychiatrist investigating a patient and his/her family history was not confronted with "traits," but with dynamic and variable phenomena. Further, he had little need to know how exactly a certain disease was transmitted.

Nevertheless, Mendelism entered medicine mainly due to the efforts of eugenicists. But it was much more successful as an *idea* than as a formative *method*. The Weinberg/Rüdin approach was clearly exceptional in this regard. While it strikingly demonstrated that it was inadequate to conceive complex diseases as simple Mendelian traits, it still marked a break with the medical fascination for genealogy. Wilhelm Weinberg's attack against medical genealogy did not only rest on the insight that pedigrees were an inappropriate tool for a Mendelian approach, but also on the awareness that genealogical methods imprinted their own logic on the concept of heredity. In a way, his arguments preceded Wilhelm Johannsen's much more explicit 1911 diatribe against the idea of "ancestral influence."[52] Johannsen's insistent statement that the „modern view of heredity" was not at all about the transmission of ancestor's "qualities," but about something strictly non-personal and non-physical—the Mendelian factors—was most likely inspired by his knowledge of contemporary medical genealogy. Both for Weinberg and Johannsen, the concept of heredity had to be cleared from all remnants of genealogical thinking before it could become scientific. This claim, however, made little impact on the medicine of their time. But even after a "century of the gene" and the rise of molecular techniques, genealogical practices are still a significant part of contemporary human genetics and genomics. Does this mean that we still adhere to genealogical rather than to a "modern" view of heredity? At least it shows that the science of human genetics, after all, deals with humans and human relations, not only with genes. If we talk about heredity, we still touch questions about descent, ancestry, and personal identity.

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[52] Johannsen 1911, p. 130.

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Pedigree Charts as Tools to Visualize Inherited Disease in Progressive Era America

Philip Wilson

Within the burgeoning field of eugenics history, pedigree charts have received minimal attention. This remains somewhat puzzling if one accepts the claim that "almost all studies of human heredity" in the early 1900s "tended to involve the collection of pedigrees." It was, after all, these studies in particular that provided the "facts of human inheritance necessary for the construction of eugenic breeding programs."[1] This lack of attention may, in part, be due to the longstanding marginalization of the study of images in favor of text, at least within the history of science and medicine.[2] The relatively minor study of the interpretation of images overall suggests, as art historian Barbara Maria Stafford argued, that images have long been "shunted to the edge of what really matters."[3]

Pedigree charts were hardly a new concept of representing information during the Progressive Era, at least for the genealogically minded. Indeed, they had been used for centuries in attempt to trace human lineages back to the Biblical Adam. The term "Pedigree," or etymologically, *pied de grue* (a crane's foot), derives from the symbol used in medieval genealogical tables or trees that, looking like the multi-pronged avian's foot, denoted a succession of generations.[4] Charting pedigrees was primarily performed "from historical or legal motives." Biology, per se, had "no place" in the early study of these charts.[5]

The medical use of pedigree charts in the U.S. was pioneered in 1845 by Philadelphia physician Pliny Earle as he visually documented five generations of one family's history of color blindness.[6] Yet, this representation of heredity from a medical viewpoint was little copied throughout the nineteenth century. Rather, these charts were predominantly used by animal breeders to record and to predict favorable matings. But as Progressive Era America clamored over the U.S. Government devoting considerably more resources to the proliferation of its agriculture and farm animals than it did its own human population, the pedigree chart reemerged in the study of humans during the "classical era" of genetics.[7] (See Figure 1) Slowly throughout this period, the pedigree chart became a standardized scientific tool to medical audiences, using simple, readily recognizable symbols to denote particular meaning regarding heredity and disease. In due course, this tool eased communication about the developing understanding of hereditary patterns of human disease, bridging classical genetics from the theoretical, to the experiential, to the clinical.

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1 Ludmerer (1972), p. 55.
2 Sander Gilman (1988) and Barbara Maria Stafford (1991) have long noted this point. For an excellent overview of the importance of carefully chosen images, see Tufte (2001). One notable exception is Mark Jackson (1995) who has focused upon the visual representation of feeblemindeness in early 20th century eugenic literature.
3 Stafford (1991), p. 6.
4 For an interesting etymological ramble through pedigrees and the nomenclature of nature, see Potter and Sargent (1974).
5 Popenoe and Johnson (1922), p. 39.
6 Rushton (1994), pp. 12-14.

Figure 1. American Eugenics Society Pedigree Cartoon. Quips on Eugenics - Archive Problems. Source: Folder, Box C - 2 - 6 : 15, Harry H. Laughlin Papers, Pickler Memorial Library, Truman State University, Kirksville, Missouri, USA.

In the U.S., the greatest popularization of the pedigree chart as a tool to visualize inherited human characteristics or traits emanated from the work of the Eugenics Record Office (ERO), in Cold Spring Harbor, Long Island, New York. ERO-trained fieldworkers organized data gathered from throughout the U.S. on charts—what they termed "Mendelian Blanks," a phrase that attested the bias of their outlook—to represent the incidence and prevalence of particular traits or characteristics that were thought to be hereditarily passed along familial lines.[8] These traits included physically visible conditions such as eye and hair color, multiple births and birthsdefects including hare-lip and cleft palate as well as diseases including tuberculosis, syphilis, and alcoholism. The leading U.S. publication of popular science, *Scientific American*, claimed that these pedigree charts represented a true "inventory of the blood" of the nation.[9]

This paper explores ways in which Harry H. Laughlin, superintendent of the ERO from 1910 to 1939, used this tool to maneuver the flow of information gathered within this repository of human inheritance data to scientific and medical communities as well as to the public. It focuses in particular upon the relationship between inheritance and disease as represented in the pedigree charts that the ERO prepared and distributed during Laughlin's superintendency. Laughlin's published writings and correspondence relating to inherited human disease that appeared during

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7 As an example of the apparent lack of attention on humans, Downing (1918), p. 149, argued that the "expert dairyman carefully inquires into the purity of strain and ancestral performance of the animal he mates with his choice cows. The farmer insists on a hog with certified ancestors. We have sense enough to apply such knowledge of heredity as we possess to our farm stock. It seems little enough to ask that we should exercise as much good sense in producing children as we do in the production of hogs and corn." Such claims were still pouring forth a decade later. M.R. Ferris (1929), secretary to the Council of the Institute of American Genealogy, The National Clearinghouse for Genealogical Information, wrote to Laughlin with the sentiment, "Certainly you will agree that the systematic preservation of the lineages of human beings in the interest of better citizenship is infinitely more important than the registration of livestock pedigrees in the interest of better beef." Kimmelman (1983) analyzed the agricultural context within which human eugenics arose.

8 The Mendelian leaning of the ERO has been widely noted. See, for example, Rushton (1994) and Turney & Balmer (2000).

9 Collins (1913).

this period will also be examined in order to better contextualize his use of ERO pedigree charts. The popularity of these particular ERO tools of visualization throughout the United States and Europe is also briefly explored. Their explicit and implicit intended uses in various venues will be examined, including their appearance at the International Eugenic Congresses of 1912, 1921, and 1932, at the Chicago World's Fair of 1933-34, in many country and state fairs across the U.S., in routine ERO mailings across the country and to Europe, in the correspondence between physicians who sought to update classifications of inherited human disease, and in popular biology textbooks and marriage manuals. In conclusion, special attention is focused upon how the pedigree chart as a spatial arrangement of hereditary patterns of disease prompted discussions about the need for a new healing space—the hereditary clinic.

Human Heredity, Disease and the ERO in Progressive Era Americ

The concept of a Progressive Era in U.S. history (approximately 1890–1920) invokes myriad views. One such view represents the time when the U.S. strengthened its position in relation to other leading nations worldwide. Doing so required a double-faced, Janus-type look into both its past and its future. As a nation just over a century old, the U.S. had expended considerable effort, first in fighting to maintain its independence, and more recently, to hold itself intact as a nation. Over that century, the U.S. had also accumulated an expanding genealogical record.

Within some circles, it was thought that the nation's strength and endurance was closely correlated with the physical constitution of its people. The New England physician, Edwin M. Fuller argued that the relatively young U.S. still had a chance to fend off becoming laden with hereditary disease.

> The older a nation grows, the larger the percentage of hereditary diseases are manifest, and ... after a century's growth, our nation appeals in silent language to our profession for remedies and intelligent barriers which may be stationed at the portals of society, that the ignorant and easily captivated masses may be warned of the approaching dangers to society and individuals.[10]

Later during the Progressive Era, and particularly following the Great War (World War I), the U.S. had become globally recognized as a supreme world power. A concomitant need arose in the minds of many to maintain the healthy stock of the American peoples. Should the U.S. population become less pure and "infected" with socially undesirable traits, they argued that the country's political and economic stronghold would begin to crumble. Looking toward the future, many progressive-minded thinkers argued that in order to prosper even further—and more rapidly—a need existed to better understand the genealogy, breeding potential, and healthiness of the nation's human reproductive stock.

A major shift in thoughts about heredity and disease followed the rediscovery of Gregor Mendel's work during this era. While working at the newly opened University of Chicago, Harvard-trained zoologist, Charles B. Davenport summarized Mendel's findings for an English

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[10] Fuller (1887), p. 206.

reading audience.[11] Within a few years, Mendel's principles of genetics were being applied not only to plants and animals, but to humans as well. The recessive nature of the trait for albinism in humans was first reported in 1903, followed by similar findings about hereditary deafness in 1905. Two years later, Davenport reported that eye color and hair form (i.e., straight versus curly) pedigree charts of family lineages were interpretable in terms of Mendelian inheritance. No longer did heredity pursue "vague" questions, argued geneticist E.B. Wilson. Rather, it had become approached in terms of a quest to answer very "clear, concise mathematical problems."[12] Another contemporary explained that heredity was "not the outcome of constitutional transmitted qualities and the condition but is the transmitted quality itself. . . . Of course, heredity, being an abstract noun, cannot be measured except as it is made manifest in concrete things such as stature and other measurable qualities."[13] The rediscovery of Mendel's principles ushered in a new phase of investigating heredity; a phase shifting from descriptive, morphological explanations of hereditary tendencies to an experimental and statistical based science of genetics.

By 1910, a number of diseases had become labeled as hereditary.[14] Geneticists and physicians claimed that certain disorders, including Huntington's chorea, presenile cataract, and chronic familial jaundice were derived from specific hereditary "determiners" in the "germ plasm." The presence of the determiner in these disorders was manifest in the visible signs of the disease. If individuals with this type of determiner reproduced, Davenport claimed that "at least half" of the offspring would be "similarly affected."[15]

Another major group of disorders was viewed as having originated from a "normal" (i.e., disease-free or at least symptom-free) individual carrying a specific defect in his or her germ cells that did not induce any physically apparent signs but which, when transmitted and "unite[d] with a similarly defective germ cell from the other parent," inflicted the offspring with disease.[16] His view was consistent with that of the "Constitutionalists" who envisioned human bodies as "carriers of the pathological histories of their race or type" and who argued that it was by passing along "defects" of these "histories" from one generation to the next tended towards "racial degeneration."[17] Preventing the hereditary transmission of such disorders as epilepsy, manic depressive insanity, alcoholism, and cleft palate presented the additional challenge of identifying apparently healthy carriers of particular disease traits.

Davenport became Director of the Carnegie-funded Station for Experimental Evolution in Cold Spring Harbor, Long Island, New York, in 1904. Six years later, he established a division of this station, the Eugenic Record Office (ERO), that focused solely upon eugenics. For the next thirty years, America's most significant advances in promoting eugenics stemmed from this

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11 Davenport (1901). For a biographical overview of Davenport and his contributions to hereditary thinking, see MacDowell (1946) and Kevles (1985).

12 Wilson (1908), pp. 200-222.

13 Laughlin, "What is Heredity?", p. 2. Henceforth, all references to the Harry H. Laughlin Collection at Truman State University's Pickler Memorial Library are described as "Harry Laughlin Papers." A useful finding aid entitled "Guide to the Harry H. Laughlin Papers" is available both in print at Pickler Library and online at <http://library.Truman.edu/manuscripts/laughlinindex.htm>.

14 For historical explorations into the hereditary thinking underlying venereal disease and tuberculosis—two major chronic diseases of the period—see Wilson (2003, 2006)

15 Davenport (1912).

16 Davenport (1912), p. 7.

17 Cantor (2000), p. 356.

office.[18] The ERO promoted a widespread understanding of the hereditary propensity of disease together with solutions for preventing such diseases in future generations.

In 1910, Davenport hired Harry Laughlin to supervise work at the ERO. Laughlin began his career teaching agriculture, natural science and a course in early civilizations at his *alma mater*, Kirksville State Normal School in Missouri (now Truman State University).[19] While teaching science, he became interested in the new field of genetics. He attracted considerable attention from cattle breeders for his research into the heredity of coat color in shorthorn cattle. In his agricultural lab, Laughlin exposed his students to Mendelian concepts of heredity through breeding experiments involving some uncommon varieties of poultry. Desiring information to classify his newly bred products, he had initially contacted Davenport, who later invited him to the Brooklyn Institute of Arts and Sciences to take his genetics course during the summer of 1907. The two remained in contact, and, in January 1909, Davenport visited Laughlin while traveling to the annual Animal Breeder's Association (ABA) meeting in Columbia, Missouri. At the ABA meeting, Davenport convinced Laughlin to turn his interests toward the hereditary study of another animal: humans.

The study of human heredity required different approaches than that of other animals. For humans were "slowly reproducing" animals who were "not subject to laboratory experimentation for genetic research like *drosophila* or the white mouse," thus, Laughlin argued, "it is necessary" in man to consider "as experiments" the history already made in migration, mating, and size of family, and to secure firsthand description of individual persons, their "personal case histories," and "records of their blood-kinship."[20] The analysis of such pursuits, however, required more patience than in laboratory animals. For to secure the "final correction of the measure of hereditary traits" in humans, one had to wait for a time when specific "generations shall have passed." Only then would "all of the descendants and collateral kin . . . have developed and exhibited their inborn traits of character." Only then will these "facts . . . be available for throwing light upon the innate qualities of the propositus." It is this passage of time, he continued, that "secures unbiased judgments" and "treats defects and talents with equal impartiality" when "arriving at personal and family estimates." Time again was critical for transforming the hereditary "gossip of one generation . . . [into] cold historical data in the next."[21]

Laughlin was already experienced with human genetic studies having previously engaged his college students in gathering family data about traits that were presumed to be hereditarily influenced. As an advocate of the pedagogical power of visual displays, he had guided them in preparing their own families pedigree charts in an attempt to discern hereditary patterns in the repetition and variance of eye color in successive generations.[22] It was regrettable, Laughlin argued, that "the study of humanity is not an exact science like chemistry." For by establishing

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18 For extensive historical accounts of the ERO, see Allen (1986) and Watson (1991).

19 Substantial biographical material on Laughlin appears in Hassencahl (1970), Reilly (1991), King (2000), and Bruinius (2006). Barkan (1991) provides a significant treatment of the immigration concerns of eugenisists during Laughlin's period. See also Laughlin (1922).

20 Harry Laughlin Papers (1939), p. 13.

21 Laughlin (1921a), p. 23.

22 Laughlin (1910, 1914). Laughlin published his eye color heredity work with ten "advanced students" in 1919. As a college student, Laughlin (1899) had advocated his belief in the importance of using expositions as a venue for publicly displaying knowledge.

such a science, he envisioned its practitioners taking young individuals, analyzing their character, and "improving" them by "supplying" qualities that were lacking and "modifying" those perceived as "abnormalities."[23]

Laughlin and the ERO Fieldworkers

Laughlin and Davenport organized the ERO around several missions of operation. Accordingly, the ERO was designed to:

1. Serve eugenical interests in the capacity of repository and clearing house.
2. Build up an analytical index of the traits of American families.
3. Train field workers to gather data of eugenical import.
4. Maintain a field force actually engaged in gathering such data.
5. Cooperate with other institutions and with persons concerned with eugenical study.
6. Investigate the manner of the inheritance of specific human traits.
7. Advise concerning the eugenical fitness of proposed marriages, and
8. Publish results of researches.

Several of these goals specifically involved the production, storage, and analysis of pedigree charts. Above all else, Laughlin repeatedly distinguished the need for ERO pedigree charts to delve beyond those typically used by genealogists (see figure 2). The genealogist, he argued, "strives to work out the family net-work, giving the names, dates, and connections." What was missing, however, was "a description of the natural, physical, mental, and temperamental qualities of each member listed . . . ." Once this information was provided, Laughlin concluded, we would have a "record of practical pedigree-value, one which can be used in tracing the descent and re-combination of natural qualities within the family-tree."[24] Laughlin summarized, the "usual outline of the genealogist . . . is merely the skeleton" upon which ERO efforts must "clothe it with the sinews and organs of Natural Traits" if pedigree charts are to "have any scientific value."[25] Even then, he noted, the mere charting of biological information was only the beginning. "Individual Analysis Cards," listing all of each pedigree members' constitutional traits, tendencies, and disorders were also required to complete the "critical biological biography" for each family. For when displayed in this manner, the "bare facts concerning the natural capacities and shortcomings of various members of a family . . . constitute an instructive guide for the family."[26]

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[23] Harry Laughlin Papers, "Ideal Young Man."

[24] "Eugenics and Other Sciences." (1920), p. 77.

[25] Harry Laughlin Papers, "A Few Points to Observe in Writing up Notes." Elsewhere (Harry Laughlin Papers, 1939a, p. 15), Laughlin acknowledges that the genealogists" biographical accounts were of some help to eugenics research as "records of human functioning which check[ed] constitutional traits diagnosed or collected from other sources." See also "Eugenics and other Sciences." (1920).

[26] Harry Laughlin Papers, (1915) Sections II and III. Banker (1923), p. 306, suggested the word "ecography" to account for the complete biological and historical component of family histories. The ERO was not alone in providing instructions of the construction of human pedigree charts. J.F. Munson (1910), a physician working at the Craig Colony for Epileptics in Sonyea, New York, published easy-to-follow guidelines in the *New York Medical Journal.*

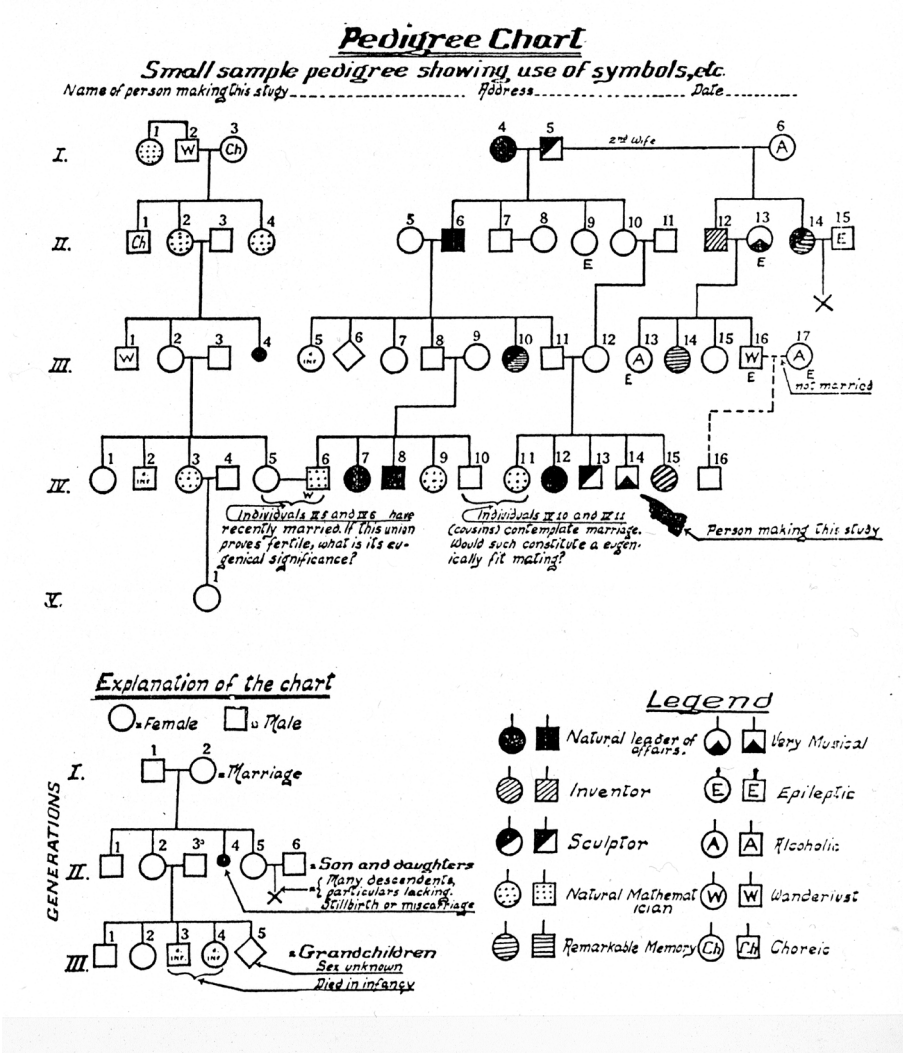

Figure 2. Sample Pedigree Chart, Davenport and Laughlin (1915) How to Make a Eugenical Family Study.

Laughlin's ERO efforts were aligned with those that eugenicists Paul Popenoe and Roswell Hill Johnson articulated in *Applied Eugenics* (1922). There they claimed that genealogy has its application to science by "furnish[ing] means for getting knowledge of the laws of heredity." Such an application made it possible for individuals to "better understand" their "place in the world" and "to marry better."[27] With this collaborative approach in mind, it was argued that the "Golden Age of genealogy is yet to come." For in such an Age, genealogy would "become the study of heredity, rather than the study of lineage." Or rather, insofar as humans were concerned, "heredity" would become functionally defined as "the interpretation of genealogy."[28]

When constructed with critical care, pedigree charts and the accompanying analysis cards—collectively referred to by the ERO as "scientific genealogies"—would be able to serve multiple

[27] Popenoe and Johnson (1922), p. 330.
[28] Ibid., pp. 335–337.

purposes. On one hand, they provided essential information for every individual to "inquire into the natural endowment of its . . . members and by pedigree study to find out how the traits of each would be transmitted in given matings—to be calculating and forehanded in mate selection, so that the offspring will present fortunate combinations of desirable family traits." To this end, Laughlin argued, "every family should establish a permanent Family Pedigree Archive, for only through the information conveyed by such may the facts of fortune be worked out,—or, to put it in the old way, may one see where the finger of destiny points." Indeed, it would serve a greater value still if "several branches of one's own family" could have their investigations "coordinated by a Family Association" whereby a "most excellent and useful scientific pedigree record" of the whole family would be produced, a task requiring "but little effort on the part of each branch." [29] Such a study, he noted, becomes "almost priceless" to a given family, particularly after the "oldest person consulted in preparing it has passed away." For, "as a rule, an individual is personally acquainted with but three generations of his or her kin and connections, and without personal knowledge and care [,] character analysis is very difficult."[30] Indeed, it "should be considered a filial duty as well as a duty to society to secure at the earliest opportunity from the oldest living members of one's family detailed facts concerning those who still live in the memory of their contemporaries."[31] It will be "a happy day for our national welfare," indeed, "when the keeping of . . . [a family pedigree] archive becomes a national family habit." Each family merely "needs but an organizer" to accomplish this goal. [32]

Ever the organizer himself, Laughlin envisioned his own pedigree archiving task on a much grander scale. Similar to what he urged each family to acquire, Laughlin sought for the ERO to become the national pedigree archive. By acquiring "all authentic family history studies," the ERO "seeks ultimately to have an index of the network of the family kin, and of the natural heritable traits of all of our better American families." As this "ideal[ized goal] becomes realized, it will become less difficult," he concluded, for "representative families by using the [ERO's] files . . . to work out their pedigrees in practical pedigree—i.e., trait prediction—fashion."[33]

To achieve this national aim, Laughlin coordinated the collecting and recording of family data through an extensive outreach program. From 1910 through 1924, he and Davenport trained teams of "field workers" in the principles of human genetics and provided them with skills necessary to gather extensive family histories.[34] The field workers were mostly young college-educated women. As political historian Diane B. Paul has argued, women were "especially well suited" for eugenic fieldwork. They had the ability to form the sympathetic relationships with families in order to persuade them to divulge familial information. Additionally, the women's "intuition and sharp eye for detail" allowed them to "swiftly and accurately" assess an individual's physical, mental, and tempermental traits. And, alas, reproductive matters by convention fell into

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29 Harry Laughlin Papers, "The Permanent Family Pedigree Archive".
30 Harry Laughlin Papers, (1915).
31 Davenport and Laughlin (1915), p. 3.
32 Harry Laughlin Papers, "The Permanent Family Pedigree Archive".
33 Harry Laughlin Papers, "Eugenics", p. 6.
34 For a telling account, see Bix (1997). Laughlin (1929) claimed to have overseen the training of 258 field workers between 1910 and 1924.

a woman's provenance.[35] Not surprisingly, one of the desired qualities of a field worker was that she professed to "like pedigree study."[36]

Relying upon his pedagogical prowess, Laughlin exposed field workers to a series of lectures and lab activities on eugenics. The range of topics he addressed included chromosomal structure, anthropological measurement, elementary statistics and discussions of the medical conditions deemed to be, at least in part, hereditary such as skin pigmentation, insanity, cataracts, and epilepsy. Readings centered around Brown University biologist Herbert E. Walter's *Genetics* and were also drawn from intelligence measurement authors Alfred Binet, Lewis M. Terman, and Robert M. Yerkes. Additionally, Laughlin led these students through an experimental study of cross fertilized and pure bred corn in order to allow them to personally uncover the Mendelian laws regarding the segregation and recombination of hereditary traits. In subsequent discussions, students used visible evidence obtained from their corn experiments as analogies for the transfer of "defective" traits and "unfit" matings in the human population. Students were also provided with ERO-established guidelines instructing them how to make a eugenic study of a family. Laughlin posed questions including the following to acquaint his students with charting pedigrees.

1) Peter's wife's mother was feebleminded. Peter was normal and so was his wife, but their son was affected. Where else must the taint have existed?
2) I married a widow that had a grown-up daughter. My father visited us and married my step-daughter. I had a son born and my father had a son. Tabulate the relationships.
3) Mr. Harold Leek married Ida Smith, daughter of Egbert Smith. The bride was the daughter by first marriage. His (Egbert's) marriage was with the daughter of Joseph Leek, Harold's father. Chart and indicate in words the curious relationship existing.[37]

Field worker students also gained experience in analyzing pedigrees of "social defectives." In one comparative pedigree exercise, students first examined Family A, which showed a "great susceptibility to manic depressive insanity." It was known that among some of the members of this family, a "very light exciting cause was sufficient to call for an attack." Family B's pedigree showed only one of the near kin to have become insane, and that only "through the most formidable array of exciting causes." However, other members of Family B "had traits shown on the pedigree chart which were sufficient indicators of insanity, which might attack a given member." Students then compared the analysis of these families with "that of so-called normal families" in which no exciting cause "would have been sufficient to break down an individual to the point of insanity."[38] To gain experience in charting family pedigrees of actual "social defectives," students were sent on supervised educational visits to study the patient populations in nearby clinics at King's Ridge, Amityville, Letchworth Village, and Central Islip. They also visited immigration control facilities on Ellis Island.[39]

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35 Paul (1995), pp. 54-7.
36 Harry Laughlin Papers, "Qualities Desired in a Eugenical Field Worker".
37 Harry Laughlin Papers, "Pedigree to be Charted by Class", pp. 1-2.
38 Harry Laughlin Papers, "Outline of Notes for Condensed Statement and Examples of the Principals of Eugenics," pp. 1-2.

In contrast to Laughlin's encouragement of America's best families to submit their own family pedigree studies to the ERO, he focused ERO field workers' efforts towards documenting the pedigrees of those he deemed as "socially defective" or "socially inadequate." Fear was already looming over the increasing numbers of "degenerates" in the U.S. before the Great War. State legislators deemed such individuals as the "greatest problem that confronts our nation," and they claimed the "degenerates" were present in "a greater multitude" than anyone could count.[40] Supportive of their concern, Laughlin and his field workers provided the essential ingredient that legislators had been missing: specific quantification of the "social deviants" who, it was argued, by their "inferior blood" were viewed as a great and costly "menace to society."

Sociologists had long engaged in elaborate discourse over the "3Ds" of society (the defective, the dependent, and the delinquent classes). By the mid 1910s, many found this classification scheme to be too inclusive to guide specific actions toward improving societal discord. More precise definitions were needed to identify those special classes of society who "need special care, restraint or direction, who as a group do not contribute in net to the general welfare . . . but who on the contrary . . . entail a drag upon those members of the community who have sufficient insight, initiative, competency, physical strength, and social instincts to enable them to live effective lives without particular social custody."[41]

Typical of his immodest proposals, Laughlin sought to rectify this nosological nuisance, and he campaigned for the official adoption of the term "socially inadequate" as a more precise designation of the "3Ds" within society. According to many ERO publications, Laughlin subdivided the "socially inadequate" to include 1) the feeble-minded, 2) the insane, 3) the criminalistic, 4) the epileptic, 5) the inebriate, 6) the diseased—including those with tuberculosis, leprosy, and venereal disease, 7) the blind, 8) the deaf, 9) the deformed, and 10) the dependent—including orphans, old folks, soldiers and sailors in homes, chronic charity aid recipients, paupers and ne'er-do-wells.[42]

Every state institution soon became eager to host or hire an ERO-trained field worker who collected information about the ancestry of the insane, the feeble-minded, the criminals, the diseased, and the paupers housed therein. Field workers became veritable "human research machines."[43] Data was organized on what were called "Mendelian Blanks"—family pedigree charts that contained particular information about the incidence of specific traits or characteristics thought to be hereditarily linked. These traits included physically visible traits such as eye and hair color, multiple births and birth defects including hare-lip and cleft palate together with diseases including tuberculosis, syphilis, and alcoholism. Although special talents in music, math, sports, or invention were also recorded, particular focus was given to the subjective

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39 Harry Laughlin Papers, "A Corn Breeding Experiment." Henry H. Goddard (1910), noted eugenicist and superintendent of the care of the institutionalized feeble-minded in Vineland, New Jersey, also supplied specific instructions for fieldworkers in the preparation of pedigree charts.

40 *Report of the Commission on the Segregation, Care and Treatment of Feeble-Minded and Epileptic Persons in the Commonwealth of Pennsylvania*, (1911).

41 Laughlin (1921), p. 68.

42 For further discussion of these categories, see Wilson (2002).

43 Bix (1997), p. 640. Zenderland (1998), p. 159, commented upon the similar training of field workers and social workers, yet noted that the former worked under the rubric of nature whereas the later worked under the rubric of nurture.

assessments of mental ability and physical defects. It was hoped that analyzing traits in the form of pedigree charts would enhance the understanding of inheritance patterns of particular diseases. As an example, the ERO's "Schedule for Recording First-hand Pedigree-data in Hereditary Eye Defect and Blindness" stated that it was the immediate aim to "secure for study [the] authentic pedigrees of families with hereditary eye defect to the end that the rules of inheritance of definite eye defects may be more clearly determined."[44] Field workers carried their own copies of the ERO's special bulletins including No. 2 *Study of Human Heredity*, No. 6 *The Trait Book*, No. 7 *The Family-history Book*, and No. 13 *How to Make a Eugenical Family Study*. These publications, which attempted to standardize pedigree reporting methods, were also readily available for purchase by the public.

In order to better appreciate the ERO fieldworkers' use of pedigree charts in the field, let's turn briefly to the instruction that they received from Laughlin.

Pedigree Charts and the ERO

Although the ERO acknowledged that information about family histories had "for many years" been obtained through the application material, medical examinations, and letters from relatives regarding "defectives" in "the better organized Hospitals and Institutions," such information was "far from satisfactory." The ERO claimed that "experience had shown that there is only one way to get a satisfactory family history of a stranger and that is to go, or to secure a trained assistant to go, to the various members of the family and with tact and patience and time secure the necessary facts."[45] Using field workers to "go to the homes" and to "interview persons that can and will give the desired information" would, it was claimed, enhance the precision and accuracy of the data obtained. Such workers were to first learn all they could about a patient from the office files at the institution, even obtaining addresses of patient's relatives and friends. Although they were encouraged to focus upon the specific trait being studied (i.e., the primary trait), field workers were also urged to embrace further opportunities to "learn of other traits that may be significantly or incidentally associated with the primary trait."[46] "Just before starting out to visit the relatives and friends," the field worker is to visit the patent "in his ward or cottage." Then, "armed with recent personal knowledge of the patient, which assures her cordial welcome" the fieldworker proceeds to visit the patient's home and "interviews the relatives, friends, and family physician." The field worker must endeavor to "see as many relatives as possible," as "facts omitted or overlooked by one [relative] are often recalled and told in full detail by another." And, "by this means information already obtained is confirmed." Once this data is collected and recorded, a pedigree chart is to be constructed.[47] Field workers were sent out with the assurance that "the parents or other relatives of the patient" would be "pleased to think that the hospital or school takes such an interest in the patient as to send a visitor to the home."[48]

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44 Harry Laughlin Papers, "Schedule for Recording First-hand Pedigree-data on Hereditary Eye Defect and Blindness", p. 1.
45 Davenport (1915), p. 18.
46 Davenport, Laughlin, Weeks, Johnstone, and Goddard (1911), p. 7.
47 Davenport, Laughlin, Weeks, Johnstone, and Goddard (1911), pp. 1-2.

As many members of the "restricted" and "extended" families as possible were to be recorded on the pedigree chart.[49] Fieldworkers were urged to "lay great stress upon the reliability of the sources" of the information that they obtained, checking the "testimony of one informant against another." The traits and personalities of those individuals in the collateral lines (i.e., any line other than your direct ancestors) of the pedigree were to be strongly considered since a better understanding of their genotype would "throw light upon the germ-plasm of the propositus." Field workers were warned "Don't diagnose!"—and to use terms including 'insane,' 'feebleminded,' 'criminal,' 'neurotic,' and 'normal' with great caution. Rather, they were instructed to provide sufficient details to "enable an expert to draw some conclusions from the data."[50] Standard symbols were to be used to represent afflicted and unafflicted individuals, specific lines of generational lineage, and specific traits and afflictions (see figure 3). The ERO produced a *Trait Book* to ensure that standard symbolic representations were known.[51] Some disease or "defective" conditions were so frequently studied that they acquired specific color representations on pedigree charts. For example, red was used to encode for epilepsy, green for insanity, violet for criminalistic tendencies, and black for feeble-mindedness.[52] Finally, fieldworkers were alerted to provide the names and addresses of "defectives who need Institutional care." As such, the data that they collected became particularly "useful information . . . when application is made for admission" to respective institutions.[53]

The ERO relied upon the pedigree chart as their most common tool of assimilating and promulgating information about the nation's reproductive stock, both the lineages of favorable stock as well as those of the "socially inadequate." Such charts served practical measures for the ERO by "determin[ing] . . . the eugenical fitness" of a contemplated marriage, "gauging the specific educability or the hereditary potentialities of a given individual," and "evaluating the intrinsic value of . . . [a] family, whenever such knowledge may aid . . . [that] family in directing along profitable lines the education of its youth and in encouraging biologically fortunate matings of its marriageable members."[54] Originally a tool for genealogists and biographers, this chart was modified by fieldworkers and others at the ERO so that it could just as easily be used to express biological aspects of all the individuals within a given family. By incorporating all of the known

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48 Davenport (1915), p. 18.

49 The "restricted" family consisted of the propositus, his siblings, and the consorts and children of these siblings; the father of the propositus and the father's siblings and consorts and their children; the father's father and the father's mother as well as the corresponding relations on the mother's side of the family. The "extended" family included, in addition to the restricted family, a history of the uncles and aunts by marriage, the consorts and children of the cousins, the siblings of the grandparents and their consorts and children, as well as their children's children, and of the eight great-grand-parents. Davenport and Laughlin (1915), p. 6.

50 Harry Laughlin Papers, "A Few Points to Observe in Writing Up Notes".

51 Among the disease traits or characteristics listed were: alcoholic, blindness, Bright's disease, cancer, chorea, cripple, criminalistic, deafness, dementia, dropsy, eccentricity, encephalitis, epileptic, goiter, general paralysis of the insane, gonorrheal, hysteria, ill defined organic disease, insane, kidney disease, locomotor ataxia, manic depressive insanity, migrainous, neuropathic condition, obesity, paralytic, paranoia, pneumonia, senile, sexually immoral, shiftlessness, softening of the brain, syphilitic, traumatic insanity, tubercular, vagrant, varicose veins, and vertigo.

52 Davenport, Laughlin, Weeks, Johnstone, and Goddard (1911), p. 4.

53 Davenport, Laughlin, Weeks, Johnstone, and Goddard (1911), p. 2.

54 Harry Laughlin Papers, (1915).

and gathered data about a particular family on one sheet of paper, these charts maintained a visual simplicity.

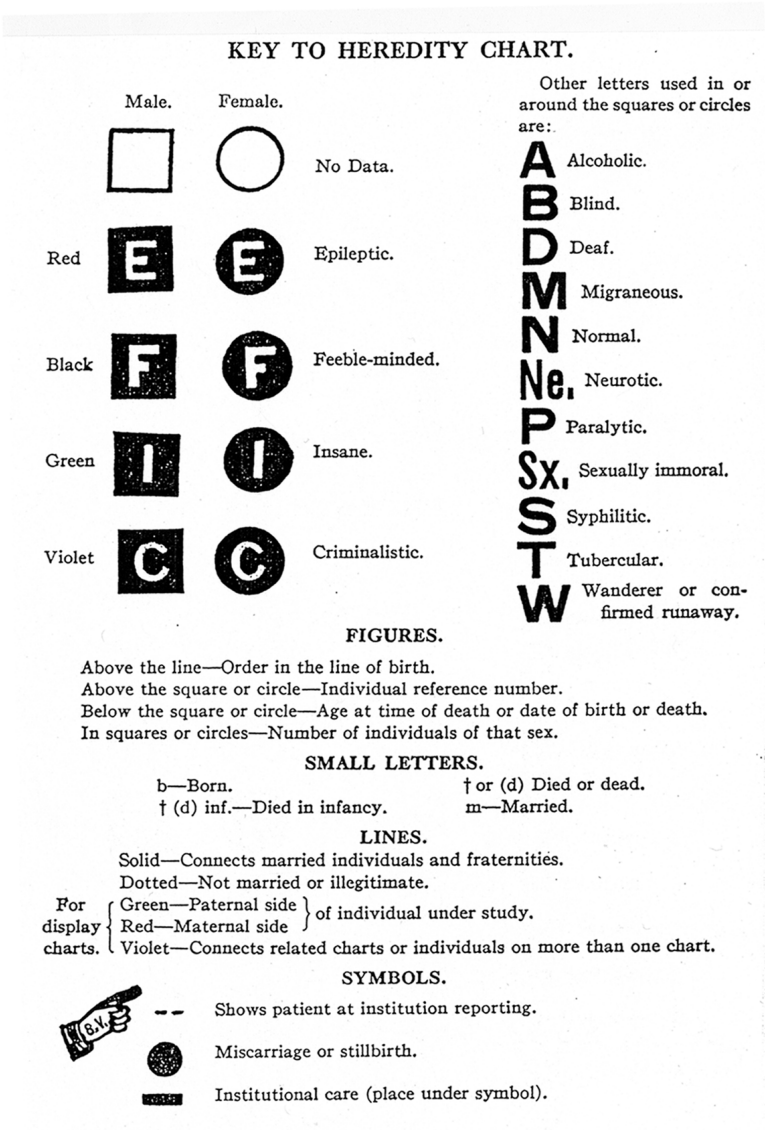

Figure 3. Key to Symbols used in ERO Pedigree Charts, ERO Bulletin No. 2 (1911) *The Study of Human Heredity* (1911).

Overall, pedigree charts objectified, quantified and visualized many previously invisible aspects of disease. They penetrated into the germ layer giving new insight into the genotypic level regardless of whether any aspect of the disease was phenotypically expressed.[55] In that way, they allowed for better discrimination of hereditary difference between individuals. But as ERO efforts demonstrated, they also provided a new way of imaging or re-presenting disease.[56] As such, they

[55] For a contemporary discussion of genotype, see Johannsen (1911). Sapp (1983) further contextualizes the genotype-phenotype distinction as iterated during this period. The word "idiotype" was used somewhat synonymously with "genotype" in literature of the period, particularly in that of the Constitutionalists' writings on the body.

became a conceptual tool for more fully appreciating patterns of inheritance for particular diseases. They also revealed a new structural knowledge that gave a better glimpse of the movement of disease via the germ plasm throughout a given family.

In and of themselves, these tools exhibited connections and offered some cautions as to what to look for in existing and future generations. On their own, however, they did not offer infallible explanations of particular patterns of inheritance. Many different humans had gathered information for pedigree charts, and thus, this process left considerable sources of error. Perhaps an even greater source of error arose from the potential of missing information in one or more generations. Quite often, field workers and others relied solely upon the subjective views of one family member to account for various states of disease in all of that individual's known relatives. Even if that individual divulged all that he or she knew, much of this view may have stemmed from hearsay. Others, it was noted, may have been cajoled by fieldworkers into giving information that they thought the fieldworkers wanted to hear. Finally, no system was in place to verify either the information that was collected or its recording. Although pedigree charts did exemplify one attempt of the scientification of society that marked much activity in the U.S. during the Progressive Era, the reality of data collection, at times, failed to uphold objectives of valid and verifiable information gathering according to the expectations of the scientific method. Or, in other words, as critics claimed, they were "insufficiently critical to establish what actually is true."[57]

Within the world of medicine, pedigree charts became shorthand representations of the presence and potential patterns of disease. As with any shorthand system of symbolization, minimalist abstractions are rendered. In this case, humans were disembodied into some type of representational simulacrum in which they appeared as only bits or bytes of select information. This idea advanced reductionistic representations of humanity by offering a tool that diminished the concept of the human. The disembodiment of humans to mere boxes and circles encoded with information was consistent with reductionist thinking common of this era that encouraged medical thinkers to look at the body more as distinct components rather than as a whole patient.

Within a short timeframe during the "classical era of genetics," pedigree charts gained an iconic status.[58] Though mere lines, circles, and squares, they held a power to persuade viewers to think about heredity within their own family. Following art historian Barbara Maria Stafford, it is precisely these kind of forms—the simplest forms of artistic expression—that represent "ideal forms," the very forms that "should be imposed on disorderly biota" in order to clarify the desired image to be represented.[59]

Thanks to the efforts of all of those who have contributed to our better understanding of the "mapping cultures of twentieth-century genetics," we have learned to see and to read new meaning in the design of linkage and genomic maps.[60] As a form of visualizing meaning, pedigree

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[56] For an overview of the social construction of genetic disease, see Yoxen (1984) in contrast to Child's(1999) history of ideas approach.

[57] Ludmerer (1972), p. 59.

[58] For coverage of other icons related to heredity, see Nelkin and Lindee (1995) and Rheinberger and Gaudillière (2004).

[59] Stafford (1991), p. 3. Further exploration into the semiotics and symbolic significance of the components of pedigree charts would be most helpful, though it lies beyond the scope of this paper.

charts are a kind of mapping as well. Like maps, they artfully produce a linear image that both spatially and temporally delineate patterns of connectedness between generations. They provide a means of orientation and direction; they concisely depict phenomena in relationship to each other; they convey meaning through the power of synopsis; and they are perspectival in that what features are included depended upon the aims, needs, interests, and mindset of the pedigree chart designers.

Curiously, these little mini-exhibitions of knowledge served both individual and societal needs. On one family's pedigree chart, each individual was highlighted as was his or her interconnectedness with everyone in an entire family, at least regarding a particular trait or disease. These charts seemed to introduce labels of either normality or deviance upon potentially all members of the family represented therein. But the ERO also used vast collections of pedigree charts as a form of collective data, expanding their apparent range of observation, in a manner that supported their overarching efforts of societal reform. Such efforts were aimed, in part, to convince American society that eugenics was working well within mainstream science of the era. Turning specifically to Laughlin, we find that he relied upon both the scientific and the simplistic ways that pedigree charts conveyed information as part of his rhetorical strategy to persuade various audiences about the potential that eugenics held for individual families, for the nation, and for the world.

As an example, Laughlin found the pedigree chart to be useful in his persuasive proposals to gain support for what he viewed as the best means of eliminating the social burden created by the "socially inadequate." The "conscious striving for race betterment on the part of the socially inadequate," he argued, "is impossible . . . . Therefore society must control their reproduction." It ought to be a "eugenic crime," he claimed, to "turn a possible parent of defectives loose upon the population."[61] As secretary to the Committee to Study and Report on the Best Practical Means of Cutting off the Defective Germ Plasm in the American Population, Laughlin issued the committee's report detailing ten possible "cures" of the problem.[62] Ranging from segregation to euthanasia, the committee strongly favored reproductive sterilization as the "least objectionable" and the "most cost-effective" solution.[63] Pedigree charts were, so Laughlin argued, an "obvious" choice to unambiguously document and visualize the "practical application" of eugenics schemes.[64]

With considerable rhetorical skill and sheaves of pedigree charts, Laughlin convinced many states to adopt a model law that he had drafted to serve as the official legislative organ to involuntarily control the reproduction of their institutionalized populations. By 1921, the year before the publication of Laughlin's *Eugenical Sterilization in the United States*, 3200 individuals

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60 See the companion volumes of Rheinberger and Gaudillière (2004), and Gaudillière and Rheinberger, (2004).

61 As cited in Kevles (1985), p. 108. See Laughlin (1920) for an example of his rhetorical prowess in promoting sterilization.

62 Other committee members and consultants included prominent New York lawyer, Bleeker Van Wagenen, Johns Hopkins physician, Lewellys F. Barker, Henry Goddard, the "psychometrician" at the Vineland Training School in New Jersey who introduced IQ testing into the US, Johns Hopkins geneticist Raymond Pearl, and Louis Marshall, leader of the American Jewish Congress.

63 Reilly (1991), p. 60.

64 Laughlin (1912), p. 121.

across the nation were reported to have been sterilized. That number tripled by 1928, and by 1938, nearly 30,000 met this fate. More than half of the states in the US adopted Laughlin's law, with California, Virginia, and Michigan boasting of their lead.[65]

Laughlin also used pedigree charts to secure the staunch support of the U.S. judiciary. In a precedent-setting case, that of Buck v. Bell in 1927, Supreme Court Justice Oliver Wendell Holmes, Jr. upheld the Virginia Statute and claimed, "It is better for all the world if, instead of waiting to execute degenerate offspring for crime, or to let them starve for their imbecility, society can prevent those who are manifestly unfit from continuing their kind." In specific reference to the reputed feeble-mindedness of Carrie Buck and her ancestors as attested on pedigree charts, Justice Holmes deemed in words that have continued to ring loudly, "Three generations of imbeciles is enough." Following this pronouncement, Buck was reproductively sterilized against her will but in accordance to the highest law in the land.[66]

Popularizing Eugenics

Laughlin spearheaded several efforts to popularize eugenics beyond the confines of the ERO. After witnessing the success of the first international congress on eugenics in London in 1912, Laughlin facilitated two additional international congresses; one held at New York City's American Museum of Natural History in 1921 and another at the same venue in 1932. Although aimed primarily at professionals, these conferences drew international attention to U.S. efforts to curb the reproduction of "degenerates" and promote the proliferation of the genetically well endowed.

Eugenicists devoted considerable effort to enhance public awareness about eugenics. Princeton geneticist and cytologist Edwin Grant Conklin noted that the "widespread ignorance" regarding heredity was profound. "Any general reform," he argued, "must rest upon enlightened public opinion . . . the schools, the churches and the press can do no more important work for mankind than to educate the people, after they educate themselves, on this important matter."[67] Campaigns centered around educating the public in order to foster a general "eugenic conscience."[68] Effort must be expended, another eugenicist argued, such that the public gains a sensitivity in favor of eugenic fitness similar to what they have against incest and miscegenation.[69]

As the ERO was actively involved in educating the public, Laughlin worked diligently to keep the message of eugenics paraded before the populace. As a public servant, he oversaw the design of a multitude of easy-to-understand handouts which, using simplistic diagrams and brief accompanying text, were used to relay particulars about the genetic principles underlying human eugenics for the lay public. He distributed these handouts freely to thousands of individuals who

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65 Reilly (1991), p. 97.

66 Court records were used as the basis of Smith and Nelson (1989). Stephen Jay Gould (1984) has briefly addressed Carrie Buck's plight , and much of the sentiment of this case, though not all factual, was portrayed in the 1994 made-for-TV movie, "Against Her Will: The Carrie Buck Story." The 1994 Worldview Pictures Production documentary, "The Lynchburg Story: Eugenic Sterilization in America" is considerably more accurate in its presentation of this case.

67 Conklin (1922), p. 308.

68 Walter (1914), p. 251.

69 Ibid., p. 252.

contacted the ERO. As part of his routine, Laughlin would ask people to complete two family pedigree charts which he included in his mailings. He urged the recipient to be as accurate and complete as possible in identifying all the hereditary traits in each family member according to the list he enclosed. If desired, the ERO was "glad to supply . . . small rubber stamps" of squares and circles, free of charge, to ease the completion of the charts. He urged people to "recast" the chart "two or three times" before drawing up a final copy, to incorporate all "new kinsmen . . . discovered" in the process.[70] After completing both forms identically, the recipients were to return one of them to the ERO for "secure filing" where it would remain "permanently available for reference by persons with legitimate concern" for such records.[71] The other, he suggested, should be kept for their own family records. His actions were aimed at providing families with a tool that expanded the genealogical tree recorded in family bibles, helping them to better visualize the genetic traits present in their family's recent past. This task also fulfilled Laughlin's self-serving interest of supplying data to the ERO beyond that generated by the field workers.

Similar letters were sent to community clubs and organizations as well as to libraries. Here again Laughlin distinguished the typical genealogical family tree from a pedigree record of familial traits. By completing ERO charts, he noted, one can "trace the descent and recombination of natural qualities in the family tree in true pedigree fashion." He closed his form letter to libraries acknowledging their help in "aiding pedigree study of the human family" by "securing valuable permanent records which otherwise would not be prepared, or if prepared, would be lost to the family and the state."[72]

College courses at the time, as well as their accompanying textbooks, devoted increasing coverage to human eugenics. By the late 1920s, nearly 400 U.S. college courses were taught on eugenics.[73] Laughlin directed a series of letters to professors of biology, sociology, and psychology urging them to adopt his pedigree charting methods. Professors were asked to supervise student's completion of the ERO's standardized pedigree forms, and Laughlin left it up to the professors to collect the forms to return to the ERO or to "eliminate" any of the pedigree charts that were, according to the professor, "inaccurate or scantily prepared."[74] Professor U.G. Weatherly of Indiana University claimed that this project "furnished the very best possible kind of laboratory material." There "could be no more effective method of getting young people in contact with the serious problems of family inheritance," he added. Students are "led not only to take a vital interest in the family history," but this pedigree analysis gave them "a sound and impelling interest in the future fate of their own groups and of the race."[75]

In another effort, Laughlin oversaw the ERO's sale of sets of lantern slides that cold be easily used to deliver pre-organized lectures. One section of these sets, some 21 slides, illustrated family pedigree study, whereas another set of 23 slides showed "Pedigrees of Defectives." This non-profit ERO venture was available for anyone "interested in eugenics studies."[76]

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70 Davenport and Laughlin (1915), p. 9.
71 Harry Laughlin Papers, "Family-Tree Folder," p. 1. For a discussion of the confusion over various attempts in analyzing these pedigrees, see Harry Laughlin Papers, (1937).
72 Harry Laughlin Papers, "Letter to Libraries", p. 2.
73 Allen (1983), p. 116.
74 Harry Laughlin Papers, "Memorandum of Suggestions to Instructors".
75 Harry Laughlin Papers, "Family Pedigree Study as College Laboratory Work".
76 Harry Laughlin Papers, (1938), title page.

In addition to his public outreach through mailings and lectures, Laughlin supported public exhibitions as a means to further educate people regarding the benefits of eugenics. In a 1921 exhibition, Laughlin provided an overview of the usefulness of human pedigree study in a case study devoted to the naturalist, John Burroughs. In selections of the text that accompanied this exhibit, we find a rationale for pursuing pedigree study.

> With the materials called inborn traits—physical and mental—nature casts new human personalities by the process of segregation and recombination in heredity. Here also the laws of chance hold good, but the whole problem of human inheritance is so complex that at present only an ancestral trait here and a quality there may be safely wagered, by a definite chance to enter a given offspring. The task is further complicated by the fact that in heredity there is occasionally a new value—a mutation the geneticists call it, not previously present in any form. In such cases the same does not accord with the usual known rules. Nevertheless the Science of human pedigree-analysis is making headway.[77]

In what was undoubtedly his single greatest success in educating the masses, Laughlin organized a eugenics exhibit around the theme "Pedigree-study in Man" as part of the Chicago World's Fair held in 1933 and 1934. Consistent with the Fair's "Century of Progress" theme, Laughlin incorporated many recent eugenic advances within his exhibition.[78] He created a series of panels which, when viewed according to a specific order, presented the principles of human heredity as a puzzle which exhibit goers could solve based upon their own personal and family experience. Since "no one was stationed permanently at the eugenics exhibit," it was "necessary that the charts be self-explanatory and well adapted for conversation among mutually interested visitors."[79] To ensure that his exhibit caught the attention of every age and social class, he employed a variety of practical laboratory set-ups. Some stations were set up with the Midwestern farmer in mind, invoking parallels between human stock and live stock breeding and crop production. The socially elite were catered to with a "Test for Instinctive Appreciation of Quality and Elegance." In this test, ten animal fur samples of varying quality were placed on a table. Using score cards, fair goers were asked to "consider quality and elegance in relation to the appeal [that the furs made] to you personally," and then to rank the samples from best-liked to least-liked. Their findings were then applied to corresponding pedigree charts that outlined how certain favorable traits in a human population could best be propagated.[80]

Part of the effort to improve general eugenic knowledge was aimed at approaching marriage in a more discriminating manner. If young people, "before picking out their life partners . . . are taught to realize the fact that one marries not an individual but a family, then "better matings will be made."[81] Others advocated that stricter marriage laws were essential to reduce the future threat of heritable bad habits. As the popular sexual hygiene manual, *Safe Counsel or Practical Eugenics*, advocated, one of the "simplest and most effective methods of improving the human race" was by

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77 Harry Laughlin Papers, (1921), p. 1.
78 The "Century of Progress" theme was selected in attempt to "demonstrate to an international audience the nature and significance of scientific discoveries and the methods of achieving them." History Files—A Century of Progress, 1998.
79 Laughlin (1935), p. 161.
80 Harry Laughlin Papers, (1932).
81 Popenoe and Johnson (1922), p. 164

requiring a "certificate of freedom from transmissible disease before a marriage license could be issued."[82] The authors noted that such laws existed in a few states, but that they "have never been, and are not now systematically enforced." Nothing prevented persons forbidden to marry in one jurisdiction from doing so in another. Others noted that the marriage laws as they existed were somewhat contradictory to eugenics aims. For instance, "sexual offenders" were often "forced" to marry in order to "legalize the offense" and "save the woman's honor."[83] Implementing a new "health certificate plan" for a "eugenic marriage license" would require a "clean bill of health, both mental and physical, from every applicant for a marriage license, both male and female—that certificate to be signed by a *reputable physician* who would not dare risk his professional reputation without a rigid, thorough and final examination. And let us make it a felony to go outside the jurisdiction of the state to evade the letter of the law."[84]

ERO efforts also warned that unfit marriages would bring about distasteful and unproductive offspring. Laughlin's exhibit at the Chicago World's Fair incorporated pedigree charts showing how both desirable and undesirable traits could be passed along family lines. By placing two pedigrees side by side, he drew particular contrasts between the presidential Roosevelt family and the "degenerate" Ishmael family. Similar to the Jukes and the Kallikaks, the Ishmaels from Indiana were used as a representative family of over 1,750 individuals in which eugenicists traced the linear passage of "defective germ-plasm."[85] By studying the passage of ancestral lineage, viewers were urged to drop any lingering views that marriage was purely a human choice and adopt the more socially desirable belief, at least according to the eugenicists, that responsible Americans pursued marriage mindful of eugenics.[86] Laughlin wanted to convey through pedigree charts that bearing children should be envisioned more as a social privilege than merely as an individual right.

Pedigrees and Hereditary Disease Clinics

New York University Professor Rudolph Binder argued in 1923, that eugenics would be "more readily adopted by a community which knows the value of good health." Moreover, communities that held a "high ideal of health" and in which physicians worked towards preventing disease via improvements in sanitation and hygiene, and towards "producing a finer type of man," would eventually come to view disease itself as "something abnormal."[87] Shifting the focus of medical practice from cure to prevention and to the elimination of disease became a rallying point for a number of health care reformers in the 1930s. Indeed, many came to view achieving these goals through eugenical means as the panacea for disease control.

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82 Jefferis and Nichols (1922), p. 16

83 Walter (1914), p. 251.

84 Jefferis and Nichols (1922), p.17. Claims that pedigrees "ought to be as obligatory as a birth certificate or a marriage license" were still being made through the end of the 1950s. See Montagu (1959), pp. 297-98.

85 Rev. Oscar C. McCulloch (1888) traced the lineage of this family's "degenerates" in "The Tribe of Ishmael: A Study in Social Degeneration." As cited in East (1929), p. 233.

86 For Laughlin's own account of the success of this exhibit, see Laughlin (1935). For a comparable assessment of the eugenics exhibition at the Second International Congress of Eugemics in 1921, see Laughlin (1923).

87 Binder (1923).

Laughlin's interest in the eugenic control of disease continued to flourish. His correspondence indicates a growing interest in various methods to apply eugenical research to a wider range of health care reform measures. By doing so, Laughlin created the need for even more family pedigree assemblage and analysis. No longer were the institutionalized viewed as his only target population; rather, he now expanded his purview to cover the entire U.S. population. The realm over which eugenics ruled was, in the eyes of many, expanding. The role that ERO field workers and institutional physicians had once played in gathering pedigree data would now fall upon the shoulders of every family physician.

Laughlin faced one major problem—few family physicians, in his opinion, had sufficient practical knowledge to apply eugenics to their own patient populations. The 1910s campaign to restructure American medical education by providing all medical students a sound working knowledge of human genetics and eugenics was not realized by the 1930s.[88] Having personally witnessed Davenport's crusade for this reform, Laughlin knew well the previous strategies that had been employed. Therefore, instead of trying to reintroduce previously ineffective stratagems, Laughlin looked for a new approach. After considerable exploration, he concluded that a human genetics clinic would best fit the public's need and serve his own agenda as well. A clinic would serve as a training center for physicians, a gathering point for geneticists and public health workers to share information about best approaches for preventing disease, as an outlet to provide direct patient care, and as a counseling center for patients who were concerned about marriageability issues. Laughlin devoted considerable efforts towards forming such a clinic which he hoped would flourish and, like his successful eugenics sterilization law, become the model adopted throughout the States.

Eugenicists' broad support of a national genetics clinic signified their vision to become more directly serviceable and in control of the campaign against disease. Eugenics-trained clinicians could expand and maintain a national database of familial pedigrees as well as provide hereditary counseling services to an increasing number of inquiries from individuals regarding marriagability. Eugenicists viewed the growing demand for such services as the lay public's acknowledgement of their expert ability to accurately predict the likelihood of disease on future matings.

Publications from such a clinic, Laughlin argued, would alert physicians nationwide to the potential hereditary background of many diseases. Through intimate professional knowledge about their patients, physicians who knew the clinic's latest findings would be even better able to judge the reproductive fitness between potential marriage partners. In this way physicians would become increasingly powerful figures at the forefront of promoting eugenics.

A human genetics clinic would also, it was argued, provide an organized interdisciplinary team or network of professionals collectively working towards the betterment of humanity. Moreover, an interdisciplinary approach was viewed as the ideal method to obtain a greater understanding of the hereditary predisposition thought to underlie a multitude of chronic diseases. By leading the charge to reduce the incidence of an increasing number of diseases found to be caused, in part, by hereditary predisposition, the clinic was viewed as central to improving civilization.

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[88] For examples of the drive to enhance eugenics education within the medical school curriculum, see Jordan (1912) and Davenport (1912).

With an abundance of pedigree charts at his disposal, Laughlin directed his initial attention regarding a clinic towards adding a genetics component to physician George Draper's highly successful Constitutional Clinic at Presbyterian Hospital in New York City. Pedigree charts of Draper's patients were studied with the aim of identifying particular "types" of constitutional makeup. For example, individuals with peptic ulcer were "subjected to study as one group; all with gall bladder disease as another; and those with pernicious anemia, diabetes, acute rheumatic fever, etc., into others." It was by focusing upon differences in the constitutional makeup between different "types" of patient classes that Draper believed physicians could best build a more accurate perception of the pathogenesis of particular diseases as well as more readily acquaint themselves with the best measures to prevent disease in different constitutional "types."[89]

Appearing not to have forged the connections he desired with Draper's Clinic, Laughlin gathered more pedigree charts and attempted to gain support for his clinic on another front. As a member of the National Research Council's Committee on Human Heredity, Laughlin worked to secure Rockefeller Foundation funds to support, among other ventures, the establishment of a genetics clinic. Again, his efforts were rebuffed.

At this point, Laughlin divested further efforts to achieve his goal through two different private ventures. With the primary support of investor Wicliffe Preston Draper, Boston Lawyer Malcolm Donald, U.S. Supreme Court Justice, John Marshall Harlan, and president of the American Eugenics Society, Frederick Osborn, Laughlin helped co-found a group in 1937 whose initial plans included the establishment of "The Institute of American Eugenics." One component of this Institute provided for the foundation and maintenance of a "marriage clinic" to which "persons seriously interested in the inheritance of human racial and family-stock qualities could present their specific problems for advice and information in accordance with the known facts on human heredity."[90] The work of this newly-founded group, who initially considered naming themselves The Eugenics Fund, Inc., or The Genetics Fund, veered in slightly different directions. This group, eventually named the Pioneer Fund, attained many of its initial eugenical goals under Laughlin's directorship. It failed, however, to garner the support needed to found a eugenics-based clinic.[91]

Exemplifying his characteristic fortitude, Laughlin sought yet another pathway to gain support for his clinic. James E. Eddy, founder of the Institute of Forest Genetics in Placerville, California, shared Laughlin's vision of enabling eugenics to be better used in the fight against chronic disease. What was needed, Eddy argued, was a Clinic of Human Heredity. He discussed his plan with California Institute of Technology geneticist, T.H. Morgan who regarded the idea as "excellent" and suggested that it should be "started and carried out in connection with some established laboratory such as that at Cold Spring Harbor." He cautioned Eddy to ensure "permanent [financial] support," arguing that it was one thing to start a clinic of this kind but quite another to "ensure its future support."[92]

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89 George Draper outlined his overall views of basic human types in a number of publications, among the earliest being "Man as a Complete Organism—In Health and Disease" (1934).

90 Pioneer Foundation, "Notes on Getting the Work Underway".

91 The Pioneer Fund's current director, Harry F. Weyher, outlined this organization's somewhat controversial history in "Contributions to the History of Psychology: CXII. Intelligence, Behavioral Genetics, and the Pioneer Fund" (1998).

92 T. H. Morgan (1938).

Eddy had also shared Morgan's views of a Cold Spring Harbor base and approached Laughlin about the possibility of establishing the clinic in close proximity to the ERO. Laughlin quickly joined Eddy's campaign for a clinic and drafted an "Outline of the Organization, Staff and Service, Proposed for 'The Clinic of Human Heredity'" which he presented to John C. Merriam, President of the Carnegie Institute in July 1937. The team proposed a 100,000 cubic foot clinic to be situated near the ERO on Carnegie property. The building would consist of the clinic's headquarters, an office, a laboratory as well as archives and library space for pedigree analysis. Staffing would include "one eugenicist-in-charge," one investigator "skilled in the diagnosis and measurement of human traits," one geneticist "skilled in the rules of inheritance of human traits," one field worker, one secretary-stenographer who would also act as archivist/librarian, and one janitorial caretaker. After an initial $70,000 investment for the building and equipment, the team proposed the clinic could be run on $20,000 per annum.

One well organized clinic would, it was argued, become the "model for similar clinics, many of which would be required to serve the whole field effectively, and which . . . could be established in universities, medical schools, . . . social centers, and possibly [stand] independently" as well. Team members anticipated patients (or clients) "who are faced with or who are especially concerned with a particular problem in human heredity" to first "supply the evidence from several near-kin with a description of the presence or absence [of a trait] or the degree of development of the same . . . [or "allied"] trait in each named near-kin."

After analysis of the evidence, the "findings would be reported to the inquirer." The findings, it was noted, do "not necessarily [need to] include advice," but they should state "as accurately as possible the behavior of Nature in reference to the inheritance of the particular subject-trait" as well as the "probabilities of the particular trait being transmitted along certain branches of a specified family tree." The proximity of the clinic to the ERO was suggested because "the world's stock of knowledge of rules of inheritance of a given trait are on hand and available for critical application to the specific [hereditary] problem."

The team admitted that "hundreds" of such inquiries had already been answered by the ERO, but that with time and labor constraints, the practice was generally discouraged. A "competent clinic" organized to meet such demands from the public and the medical profession was, they concluded, sorely needed. The team considered whether the staff should offer their services to the public for a small fee or in exchange for completed pedigree information. "First-hand pedigrees of human traits" were, it was noted, of "great use to the archives of human heredity." Such records, when procured by field workers, were claimed to "cost much more" than by acquiring them in exchange for free clinical services.[93]

Merriam's support would be critical for the birth of this clinic. His response, however, was not all that Eddy, Goethe, and Laughlin hoped for. Merriam argued that since the clinic would have "as its normal function a broad relation to health and medical problems," it might best be "connected with a great university hospital or with some independent institution of the hospital-research laboratory type." He acknowledged that the pedigree data assembled by the ERO was indeed "indispensable" for such a clinic, but he envisioned that rather than adding a clinic on their

[93] Harry Laughlin Papers, "Outline of the Organization, Staff, and Service, Proposed for 'The Clinic of Human Heredity'" n.d.

own grounds, the ERO could better establish links with an existing clinic whereby the latter could "obtain use of [the ERO] materials without serious interference with the progress of the [existing ERO] research program." He saw such a relationship to be of advantage to both participants but argued it would be wiser to keep the two participants "sharply separate as to responsibilities and administration."[94]

Laughlin and his co-organizers discussed establishing ties with The Johns Hopkins Hospital in Baltimore. Despite their persistent efforts along these lines, the Human Hereditary Clinic they envisioned never materialized. On the surface, Carnegie President Merriam's doubts were never successfully overcome. Furthermore, Merriam retired from his post and was succeeded by Vannevar Bush in January 1939. Laughlin immediately apprised him of the plans for the clinic, but the new president put him off until he became more familiar with overall Carnegie operations. Like an increasing number of medical science the Carnegie Foundation began to distance itself from anything labeled eugenics.

The pedigree chart proved to be a valuable tool for the developing field of human genetics in several important ways. It offered a concise and clear way of demonstrating a perceived hereditary linkage regarding a particular disorder or disease. Laughlin's coordinated gathering and distribution of family pedigree information was designed, in part, for the eugenic attempt to maintain a healthy reproductive stock within the U.S. population. As such, his use of these charts further substantiated the "hardening" that had occurred in beliefs about the nature of heredity during the late nineteenth century. In particular, the regular appearance of these tools strengthened "hard hereditarian" claims that inherited defects and disease were solely dependent upon a non-malleable nature.[95] As such, alteration of the reproductive stock of the American people during the Progressive Era became intensely focused upon nature rather than nurture. More investigations remain to be undertaken to more fully appreciate the roles whereby these valuable tools have secured a place of permanence in the field of human genetics.

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94 Merriam, John C. (1938).

95 Carlos López-Beltrán (1994) described that this malleable view existed in the "soft hereditarianism" beliefs of the early nineteenth century in contrast to the more objective qualifications of a nature-based, "hard hereditarianism" later in the century.

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Biohistorical Narratives of Jewish History. Contextualizing the Studies of Wilhelm Nussbaum (1896-1985)

Veronika Lipphardt

Towards the end of the 19th century, anthropologists in Germany, Great Britain, France, Russia and elsewhere regarded "the Jews"—persons who were considered to be Jews—as a fascinating object of research. A complex assemblage of social, political and cultural factors led to this focussing of attention. The aim of this paper is to highlight *scientific* factors: It seeks to demonstrate how scientists began to tell Jewish history in biological terms, in accordance with tremendous theoretical and practical changes in the life sciences around 1900.

For physical anthropologists, one difficult problem was to find a well defined group to study. To investigate the essential features of a biologically coherent group, one had to make sure that all persons under study belonged to the group "by nature." In the light of Darwin's theories, this meant "reproductive isolation," a genealogical cohesion for many generations. Anthropologist Bernhard Blechmann from Dorpat was sure that, with the Jews, he had found a group which had doubtlessly been homogenous and isolated for a very long time:

> It is quite a mysterious fact—and acknowledged by most experts—that the Jewish tribe, from its emergence 4000 years ago up to today, has scarcely undergone any changes, and that no other racial type can be traced back through the millenias with as much precision as the Jewish.[1]

Commenting on the persistence of the alledgedly "pristine and pure" Jewish race, Blechmann's remark was—inside and outside the scientific community—hardly unique. In the late 19th century, Jews were generally seen as hardy, indestructible, obstinate, tenacious, brash, ruthless and resolutely self-serving.[2] Jews were considered an isolated group, clinging to conservative traditions, refusing to accommodate and change their way of life, and resisting all kinds of environmental influences. Although pejorative, such stereotypes also resonated ambivalent appreciation of admirable and outstanding characteristics, as, for example, assertiveness—thereby rendering the Jews even more harmful.

Although historians have shown in detail how these notions easily spread as a "cultural code of anti-Semitism"[3] and were taken up by National Socialists later, their persistenc in scientific practices and discourses has not been traced yet.[4] While important studies on Zionism and racial theory have appeared recently[5], it is less well known that from the beginning of the 20th century onward the "Jewish race," or the "biology of the Jews," was a topic of serious study. Many scientists

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1 Blechmann (1882) p. 1-2.
2 Driesmans (1912/13) p. 158.
3 Volkov (2002).
4 Touching upon this aspect, see: Efron (1994); Kiefer (1991); Hödl (1997); Gilman (1991); Gilman (1984); Doron (1980); Falk (1998); Hart (1999); Hart (2000), especially Chapt. 4 "The Pathological Cycle;" Essner (1995); Lilienthal (1993); Bacharach (1980).
5 Especially Falk (2006).

up to the 1930es claimed that the Jews were an isolated, unmixed, and persistent type and thus the "ideal object" for investigating human heredity and race.[6]

In German-speaking countries, the "biology of the Jews" was discussed by Non-Jewish and Jewish scientists after 1900.[7] Among the latter, secular "integrationists," as I call them, clearly outweighed Zionists and religious Jews, especially after World War I. In addition to theoretical speculations, most scientific publications drew on empirical data and employed all kinds of contemporary techniques, such as anthropometry, statistics, genealogy, psychiatry, pathology, and serology. Contemporary theories of heredity informed many of those investigations. The transferrability of Lamarckian, Darwinian, Weismannian and Mendelian concepts onto the "biology of the Jews" was hotly debated. Indeed, this scientific debate on the "biology of the Jews" became a forum for discussions on human heredity and races. The identity politics and harsh polemics which pervaded this debate are, though certainly a very interesting and important aspect, not the main focus of this paper. Instead, I want to show how concepts of heredity were used in empirical studies on Jews and how methods of genealogy became important tools in this context.

Neolamarckism and Neodarwinism are certainly the most obvious concepts to be considered, and indeed they dominated many arguments of the debate. However, I want to concentrate on concepts that were associated with Mendelism, mainly because Mendelism offered empirical approaches as well as theoretical inspiration.

After presenting some general thoughts on what I call *biohistorical narratives* and their representation in the debate, I will discuss the example of Wilhelm Nussbaum who pursued research in the "biology of the Jews" between 1933 and 1935.

Biohistorical narratives and the projection of experiments onto history

Investigations and explanations of biological diversity are inevitably accompanied by stories about the historical emergence of the diversity studied. Plants and animals do not take much interest in the stories biologists tell about their ancestry, and they do not leave behind historical records and documents. In the case of human diversity, these stories describe historical events using biological terms. Such stories may be called "biohistorical narratives" because they integrate many historical "facts" with a few biological mechanisms, such as selection, evolution, adaptation, cross-breeding, and environmental influences.

Biohistorical narratives are not confined to the domain of science—quite the contrary: They constitute integral elements of the identity building of many nations, families, ethnic groups or other social entities—in addition to or intertwined with other narrative identity constructions.[8] However, since genetics and evolutionary biology have become the predominant source of knowledge on diversity and heredity, most of those rather mystic narratives need to be aligned

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6 Among others: Andree (1881); Blechmann (1882), p. 2; a rather crititical account: Fishberg (1913), S. 9. See also: Hart (1999), p. 270.

7 Lipphardt (2006). The distinction between "Jewish" and "Non-Jewish" scientists in this paper is in accordance with their self-ascriptions.

8 Recently, many studies on narrative identity constructions from all fields of humanities have been published. Crucial for this trend: Hobsbawm and Ranger (1983); Anderson (1992).

with modern genetics in order to be consistent with contemporary understanding of "how life works." To explain why children resemble their parents, families draw on their understanding of modern genetics. To explain, for example, how the early ancestors of modern Europeans became European, geneticists tell stories about historical events that shaped what today we know as ethnic diversity or human populations. While narratives of inheritance—for example in families—concentrate on a few generations and identifiable individuals, narratives of diversity can stretch over centuries and large masses of living beings.

Let us return to the so called "biology of the Jews."[9] One reason why the Jews were considered an "ideal object" for research in heredity was their well documented history. Many religious and historical texts, of both Jewish and non-Jewish origin, supplied a great variety of biohistorical narratives about Jews. At the beginning of the 20th century, the following narrative of Jewish history prevailed in scientific publications:

Allegedly, the Jewish race had resulted from an ancient cross between three oriental racial types (Amorites, Semites and Hethites) and could thus not be considered a pure race, but a race mixture.[10] After the destruction of the Temple, Jews were dispersed throughout Europe—a story of migration into various geographic environments. Because alledgedly they did not intermarry with non-Jewish societies, the ancient race mixture became a "pure stock" that reproduced only within its own community—it was called an "inbred" or even "incestuous" race. Variations between the dispersed Jewish groups were explained as local adaptations, either induced by climate or other environmental factors. In the Middle Ages, so the narration continues, ghetto life had tremendous selective effects upon the biological make-up of this race, and emancipation in modern times obviously was supposed to lead to race mixture and adaptation.[11]

According to this narrative, Jews were ideal for testing key concepts of biology: variation, geographic and reproductive isolation, selection and so on. Both Jewish and non-Jewish scientists drew on these narratives, yet by combining single narratives very differently and with different motives and outcomes. The dominant narration given above was subject to minor alterations: For example, in terms of "compatibility," it made a difference whether the oriental race mixture was regarded as closely related or alien to the "European race mixture." While Non-Jewish authors tended to blame Jews for voluntary social isolation, Jewish authors explained isolation with the discrimination by the Christian surrounding. Whether the selection effects of the ghetto time had been harmful or enhancing for the genetic make-up was a contentious topic, as well as the question whether the negative genetic effects could be altered or not by exercise, education, and positive environmental influences, such as equal opportunities and social acceptance—or climate and hygiene.

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9 I borrowed this term from Franz Weidenreich, who tried to found a "Wissenschaftliches Institut zur Erforschung der Biologie der Juden" in 1934. Weidenreich Papers, American Museum of Natural History (AMNH).

10 It was Prof. Felix von Luschan who first published on Jews as a "Rassengemisch;" Luschan (1892). The "Rassengemisch"-hypothesis came to be the standard doctrine in the "biology of the Jews" in the beginning 20th century.

11 For an interesting version of the narration, see: Auerbach (1907a); Auerbach (1907b). As PhD-student, Auerbach published an article against the "Rassengemisch"-thesis of his academic teacher Felix von Luschan; later, in the 1920es, he integrated the notion of a "Rassengemisch" into his narration of Jewish history.

It is barely surprising that Neodarwinism helped to support notions of inalterability and was supposed mostly—but not only—by Non-Jewish authors, while Neolamarckism, as a narrative of personal adaptability and hereditary flexibility, prevailed in the narratives of some Jewish biologists. But there were many exceptions to this rule, and although there might be a tendency towards Neodarwinism among Zionists, as suggested by other authors, the dividing line cannot be drawn easily. Biographical factors played an important role in this context. For a biologist, a biological theory was more than just a working hypothesis: It had to explain all kinds of striking phenomena in his social world as well, especially at a time when biological theory did not provide the coherence of the later Great Synthesis. Certainly, biologists agreed upon some "prominent examples," serving as "test cases" or "touchstones" for biological theories: the mule as a proof of hybrid infertility, or the Axolotl for Neolamarckian inheritance. Vice versa, such "prominent examples" could be the target of publically performed deconstruction of scientific antagonists.[12]

Often, however, "well known" and "obvious" phenomena of human heredity or social life were at the center of those strategies of exemplification. And hence, according to their own social experiences, some authors—from Jewish or Non-Jewish or "mixed" families—considered the example of the Jews a very important test case for any theory of inheritance. It is this specific interaction between personal narratives and scientific theories which was at work in their scientific inquiries.[13]

Mendelian genetics provided not only new terms, metaphors and theoretical frameworks with which to interprete the history of the Jews, but also an applied empirical methodology. Anthropologists constantly complained about an inherent problem of human genetics: No experiments were allowed, no pure line inbreeding technology applicable. But exactly for this reason, the Jews seemed to allow for an alternative approach. For to investigate the "biology of the Jews" along Mendelian lines, the research object had to meet certain requirements: It had to be a pure line—that is, an inbred group—which had not undergone mixture with other groups. Projects could be designed to demonstrate the inheritance of certain characteristics within this isolated homogenous group or to analyse the results of so-called "bastardisations" between Jews and non-Jews. Either way, it was necessary to take extensive notes on families, pedigrees, inherited characteristics, and any striking feature. Variation within the isolated group was admitted, but considered to be insignificant compared with the enormous differences between Jews and non-Jews. For some anthropologists, purity was not necessarily a feature of the group itself: it was rather visible in contrast to other groups.[14]

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[12] For example, the Neo-Lamarckist Kammerer was famous for his amphibian experiments. When a colleague claimed in 1926 that Kammerer had manipulated his specimens, not only Kammerer, but Neo-Lamarckism in general was discredited.

[13] Others considered this example a rather marginal or irrelevant one, not worthy of any serious scientific discussion. At the time, however, "being objective about 'the Jewish question'" implied an active, scientific approach rather than the so called "ignoring" or "denying" attitude which was suspected to be driven by interest. This runs contrary to today's intuition to render the latter as the only "serious scientists" and those who were interested in studying the Jews as "pseudoscientists" (which expresses a moral judgement I agree to; but it omits the alledgedly "serious scientists" and their motives from historical investigation, which I find asymmetric). My claim is that in both cases individual factors on the socio-cultural level help to explain the respective attitude.

[14] Lenz (1914/15); Auerbach (1920/21); Auerbach (1919); Auerbach (1930); Gutmann (1925).

The notion of the Jews as a pure and unalterable race turned into an indispensable presupposition for empirical research. Conversely, the operational sequence of Mendelian experiments had been projected onto Jewish history: The supposed reproductive isolation of the Jews led researchers to discriminate the "Jewish line" from the "Non-Jewish line" and render the children of intermarriages as F1-generation. Although both lines showed considerable variation, the distinction seemed much clearer than any distinction between so-called European groups. And that seemed to make sense because European history was, at least if contrasted with intercontinental constellations, narrated as a story of exchange, mutual relations, and kinship between Christians.

To give an example of such a projection, I would briefly like to draw on the botanist Redcliffe Salaman's study of the Jewish facial expression.[15] The facial expression of the Jews was generally said to display a melancholic and permanently suffering condition and to be "durchschlagend," persistent, inheritable, and distinguishable—in Mendelian terms: dominant. To scrutinize these assumptions, Salaman took photos of children from Jewish-Christian couples in Great Britain and showed them to assistants (who were not familiar with his research design), asking whether the photo showed a Jew or a non-Jew. The assistants he had recruited were all Jewish—and Salaman regarded this as methodological advantage:

> Most of my observers were quite ignorant of the purpose of my examination and of the results I expected, whilst none were conversant with Mendelian or other theories of heredity. All who have assisted me have been themselves Jews and I have noted a distinct tendency on their part to claim, wherever possible, a Jewish type or face for the children they have examined, and also, as I shall show, the results are entirely in the opposite direction, yet what error there is, is distinctly towards increasing the number of supposed Jewish faces in the offspring of mixed marriage.[16]

In spite of their "tendency," the assistants identified a large majority of the faces as non-Jewish. Even though they had been looking for Jewish faces, they were unable to detect the "Jewishness" of the "mixed offspring." Salaman drew the conclusion that "the Jewish facial type […] is a character which is subject to the Mendelian law of Heredity," and that "the Jewish features have been shown to be recessive to the Northern European."[17] This, in reverse, seemed to prove that the Jews had indeed been an inbreeding group for the longest time, because otherwise the facial expression—according to Salaman—would simply have disappeared over the centuries.

> […] complex as the origin of the Jew may be, close inbreeding for at least two thousand years has resulted in certain stable or homozygous combinations of factors which react in accordance with the laws of Mendel.[18]

German reactions to Salaman's study were very ambivalent.[19] On the one hand, rejecting old stereotypes of Jewish persistency, ineradicability and "dominance," and then claiming "recessiveness" instead, evoked notions of the Jews as being less aggressive and more submissive,

[15] Salaman (1911). On Salaman's study, see Falk (1998).
[16] Salaman (1991) p. 280.
[17] Salaman (1991), pp. 285, 288.
[18] Salaman (1991) p. 290.

adaptable and integratable. On the other hand, "recessiveness" connoted the subtle danger of hidden and invisible enemies and maneuvers. For Zionists, it may have been difficult to accept such a proof for the "defencelessness" of Jews against "dissolving" into the so-called European population.[20] This, again, shows how strongly influenced by personal believes the multiple interpretations of such scientific findings could be. The next subchapter will examine an exceptional and drastic case of those interactions between personal and scientific agenda.

Wilhelm Nussbaum and the "Arbeitsgemeinschaft für Jüdische Erbforschung und Erbpflege"

After the Nazis assumed power in 1933, discussions and investigations on the "biology of the Jews" came to an end in Germany.[21] However, Wilhelm Nussbaum, a young Jewish gynaecologist who had trained as an anthropologist with Eugen Fischer and Otmar von Verschuer until 1933,[22] set up an institution in Nazi Germany that over the course of eight months investigated more than 1100 Jews. The "Arbeitsgemeinschaft für Jüdische Erbforschung und Erbpflege" was founded in the summer of 1933 and existed until March of 1935 (fig. 1).[23] Nussbaum received considerable support from Jewish institutions and was able to conduct his work with the permission of state authorities. The very interesting political implications of this story will be discussed elsewhere; this paper shall concentrate on the way Nussbaum organized his research.

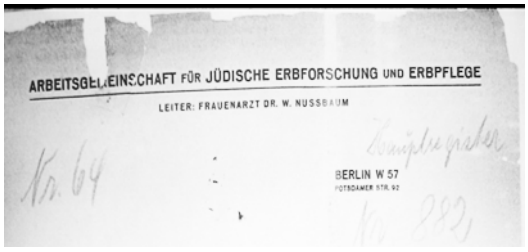


Figure 1. Letterhead of the "Arbeitsgemeinschaft für Jüdische Erbforschung und Erbpflege."

19 For the discussion of Salaman's study of the "Jewish facial expression" and the alledgedly dominant inheritance of the "Jewish type," see: Fishberg (1913) pp. 176-194; Till (1913); Feist (1925) pp. 187-188; Kaznelson (1913) p. 489; Marcuse (1921) p. 327; Wagenseil (1923/1925) p. 88; Auerbach (1930) column 1178; Michelson (1929) pp. 65-70; Iltis (1930) p. 67.

20 Theilhaber (1911).

21 With exceptions: Walter Dornfeldt, a student of Eugen Fischer, published an anthropological study in 1940 (Dornfeldt 1940). In Austria, anthropologists examined Jews who had been imprisoned before their deportation to concentration camps. In Auschwitz, skeletons of prisoners were collected for research purposes (Rupnow 2006).

22 On Eugen Fischer and Otmar von Verschuer: Lösch (1997); Schmuhl (2005).

23 All references in this subchapter relate to material in the William Nussbaum Collection, Archive of the Leo Baeck Institute, New York. I have worked with the collection in 2004. The collection has since been completely reorganized and not been accessible during that time. It is being microfilmed at present (Feb 2007) and will be accessible in summer 2007. Until then, the location of the material cited in this paper within the collection cannot be provided. The new finding aid is already available online: Guide to the Papers of William Nussbaum (1896-1985), 1773-1975 (bulk 1932-1935), AR 10750, processed by Michael Simonson, October 2006, http://findingaids.cjh.org/?fnm=WilliamNussbaum&pnm=LBI (last accessed 7.3.2007).

Nussbaum was well aware that managing a scientific undertaking of this sort under such political conditions was quite a challenge. The most important thing for him was an elaborate inscription regime, a "Bezifferungssystem," as he termed it: "The *Bezifferungssystem* for such investigations must be simple, manageable and consistent. I have set up such a system."[24] And indeed, Nussbaum's system contained preprinted questionnaires and examination forms, pedigrees and report sheets that were filled out for each of the hundreds of probands. With the help of assistants, photos were taken, collected and registered; hundreds of lists, charts, calculations, graphs, tables and diagrams were derived from them; manuscripts and papers summarized findings and implications; and thousands of letters to and from Jews in Germany were sent to gather more information.

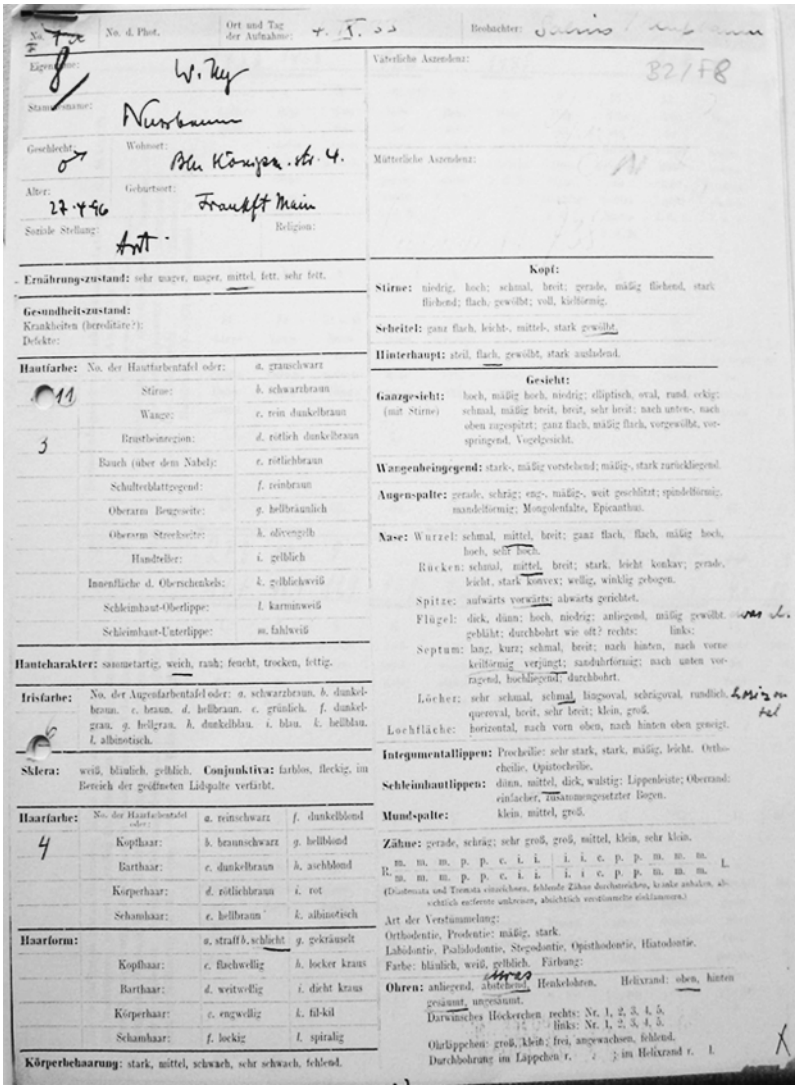


Figure 2. Examination form from the Nussbaum Collection.

24 Nussbaum, Wilhelm, manuscript, untitled ("Die erbbiologische Betrachtungsweise…"), undated, 18pp., here: p. 3 (author's translation).

The system's backbone was a central register where each proband was listed by name or by place of origin and supplied with a number. Other registers were derived from the central register, such as a family register or a twin register. Nussbaum's interest in twins dated back to his PhD-time with Fischer: He had planned to conduct a twin study according to Verschuer's methodology before 1933. Each proband underwent medical examination and was measured according to anthropometrical standards. The data were recorded on an examination form; of course one was filled out for Nussbaum himself (fig. 2). The blank form, published by Verschuer, sought more than just detailed anthropometric information. It also reported on nutritional and health conditions, illnesses, social status, religion, the form of genitals and so on. On the back, a wide space was left open for "special observations."[25]

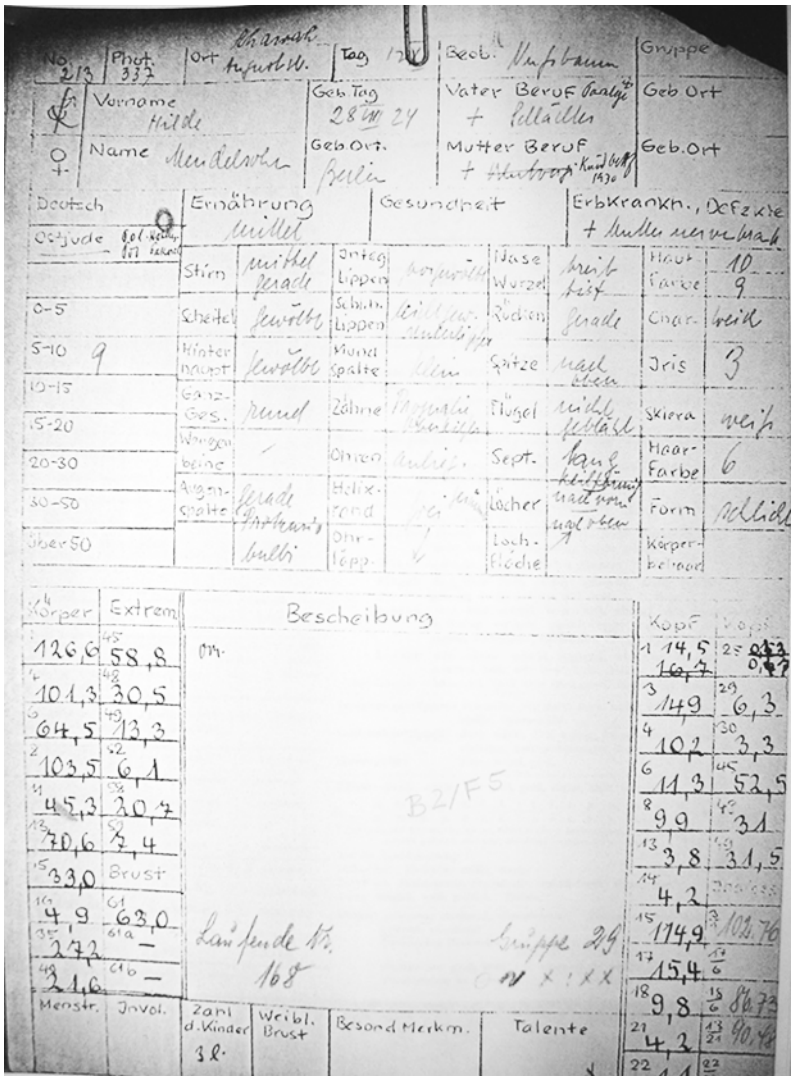


Figure 3. Handwritten examination form devised by Nussbaum.

[25] In Nussbaum's form, it contains a general description of the bodily condition of the proband; for other probands, psychic pecularities or abnormalities were noted.

Obviously, the form did not suit Nussbaum's needs: he devised a hand-written one (fig. 3). On this form, Nussbaum included a special entry for hereditary diseases—in this case it says "neurasthenic"—and three entries for the geographic origin of the proband, one for East European Jews, one for Germans and an empty one for any other. On each form, the register number from the main register was noted. The parents' register numbers were printed in their name fields (unless the proband was an orphan), and the family and pedigree register number were displayed there too. A large white field was used for manifold purposes in other cases, such as indicating whether the proband was a "Mischling," a "Langschädel," or had mental problems. Numbers referring to other documents were also printed in this large field, as, for example, the "group number" which will be explained below. For gynaecological information—menstruation, births, menopause etc.—as well as the proband's peculiarities and talents Nussbaum included extra fields.

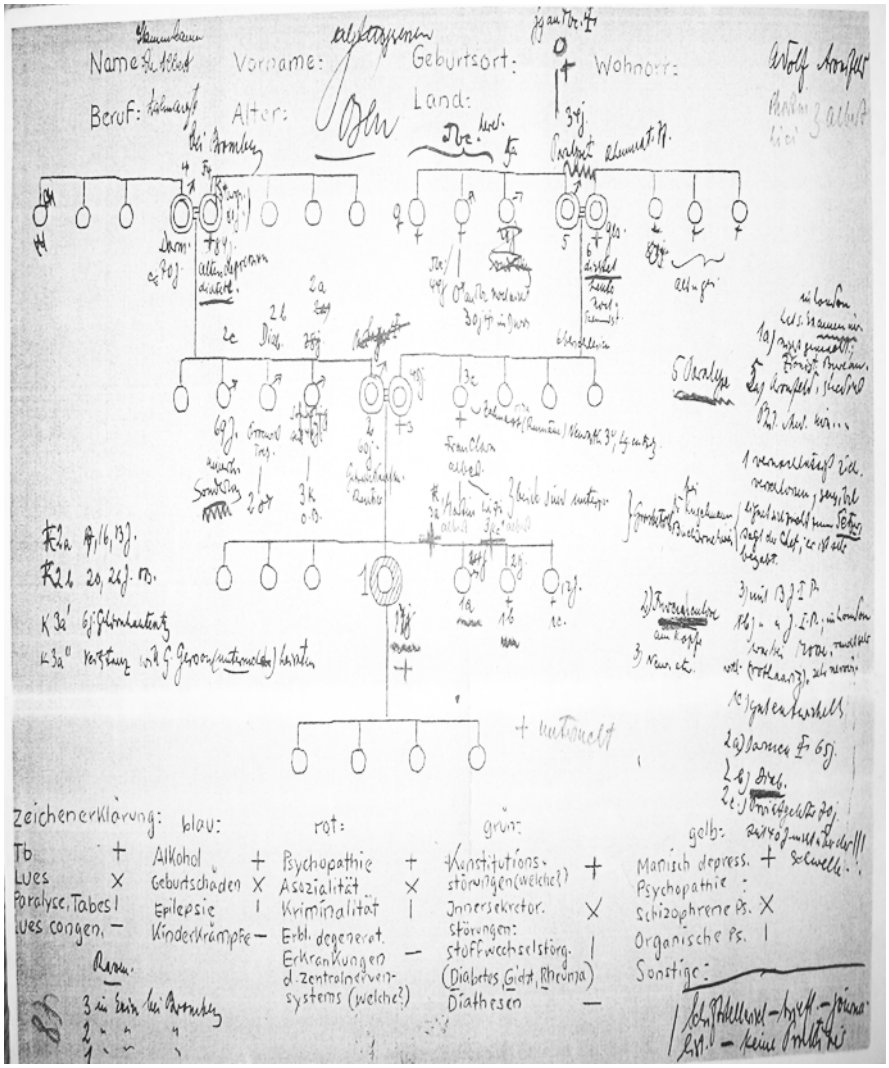


Figure 4. Pedigree form from Nussbaum Collection.

Certain probands underwent more thorough investigation than others, and additional forms needed to be filled out. There were three different psychogramm forms, one for children and two for adults. There were two very detailed forms for twins. Pedigree forms and "family forms" were filled out for each family (fig. 4). As can be seen from the legend and additional notes, Nussbaum noted any peculiarity which ran in the family—talents, habits, likings and quirks. From pedigrees such as these, he derived trait pedigrees, such as the one for homosexuality (fig. 5) or the one for "recessive enervation" (fig. 6).

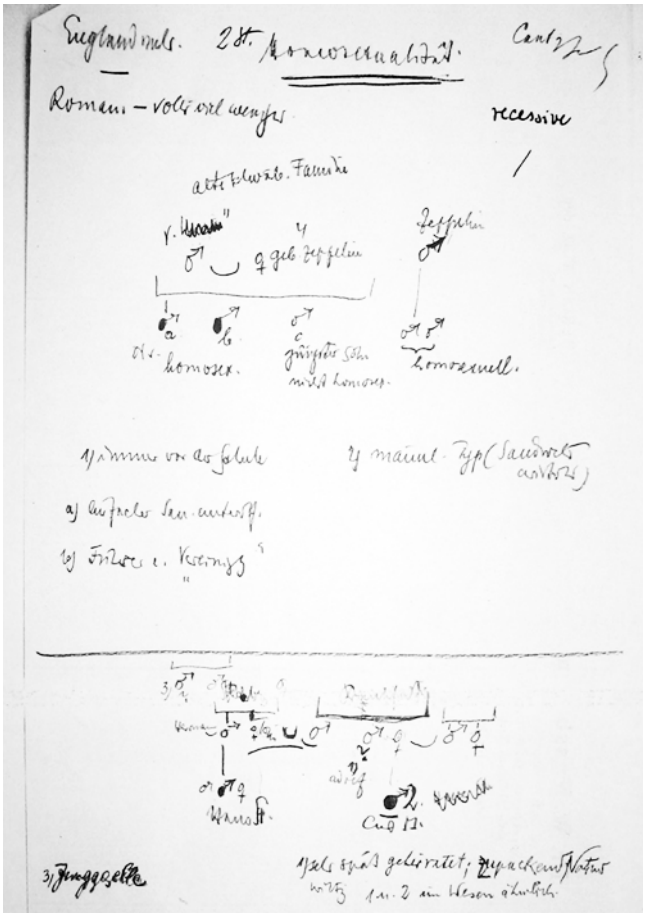


Figure 5. Pedigree for homosexuality from Nussbaum Collection.

All the forms were linked with one another by references, numbers and symbols. Each proband could easily be traced through the system by just following the references. Proband groups could be sorted according to many aspects, as for example origin: Berlin Jews and South German Jews, together representing German Jews; and German Jews together with East European Jews made up the European group, in contrast to the Sephardim.

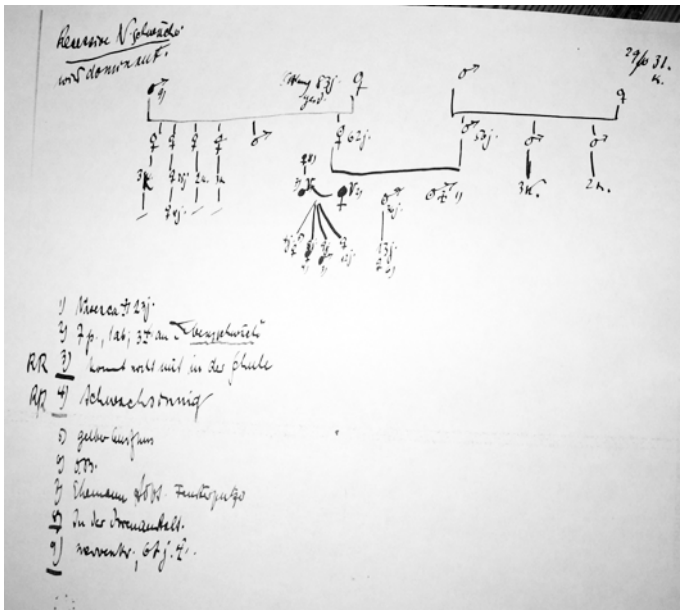


Figure 6. Pedigree for "recessive ennervation" from Nussbaum Collection.

To analyse this mass of information, Nussbaum devised hundreds of documents which represent a stepwise refining process of information with several intermediary analytical steps, such as sorting, counting, calculating, comparing etc. The table titled "Central European physical characteristics in Jews" was, for example, the result of many calculations for those values Nussbaum had gathered from the probands' forms; it was meant to demonstrate that Jews were not a foreign race, but had become a central European "Bevölkerungsgruppe" (fig. 7).

Zentraleuropäische Körpermerkmale bei Juden.

	Ostjuden n = 295	Berliner Juden n = 156	Würzburger Juden n = 111	insgesamt n = 562
Lang- u. mittelschädlig	14%	32%	22%	23%
~~Lang-~~normal- kurzschädlig	62%	78%	74%	71%
Schmal u. mittelgesichtig	38%	67%	58%	54%
Grade Nase	80,5%	82%	69%	77%
Schmale Nase	67%	77%	92%	79%
Grade u. aufwärtsgerichtete Nasenspitze	65%	85%	81%	77%
hellägig (blau – grau)	45,5%	52%	50,5%	51,5%
blond-braunhaarig	83,5%	84%	64%	77%

Figure 7. Table on "Central European physical characteristics in Jews" from Nussbaum Collection.

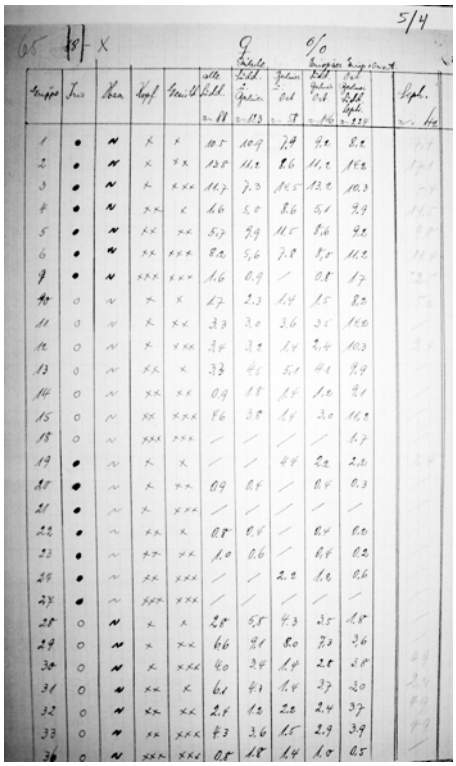


Figure 8. "Gruppenformel" from Nussbaum Collection.

Very curious documents are those that refer to what Nussbaum called the "Gruppenformel" or "Rassenformel." Nussbaum had selected four characteristics for a special analysis: eye color, hair color, head shape, and face shape. Each character was supposed to occur in two or three variations, and Nussbaum assumed that theoretically there were 36 combinations (fig. 8). Each proband's examination form was supplied with one of those 36 "Gruppenformel" that reported on his or her specific combination of characteristics.

Then Nussbaum analysed which combinations appeared in the various "geographical" groups he had examined, in East European Jews, Sephardim, German Jews etc. He found that certain combinations appeared in none of the groups, others only in one or two groups, and some in all groups. He did what every student of human diversity does: He sought clear lines of demarcation between ethnic groups. Whereas Salaman had sought the historical dividing line between the "pure inbred Jewish race" and the Europeans, Nussbaum sought diversity *within* the Jewish "Bevölkerungsgruppe." However, apart from that, he also analysed his data on twins and compared "Jewish twins" and "Aryan twins" (fig. 9).

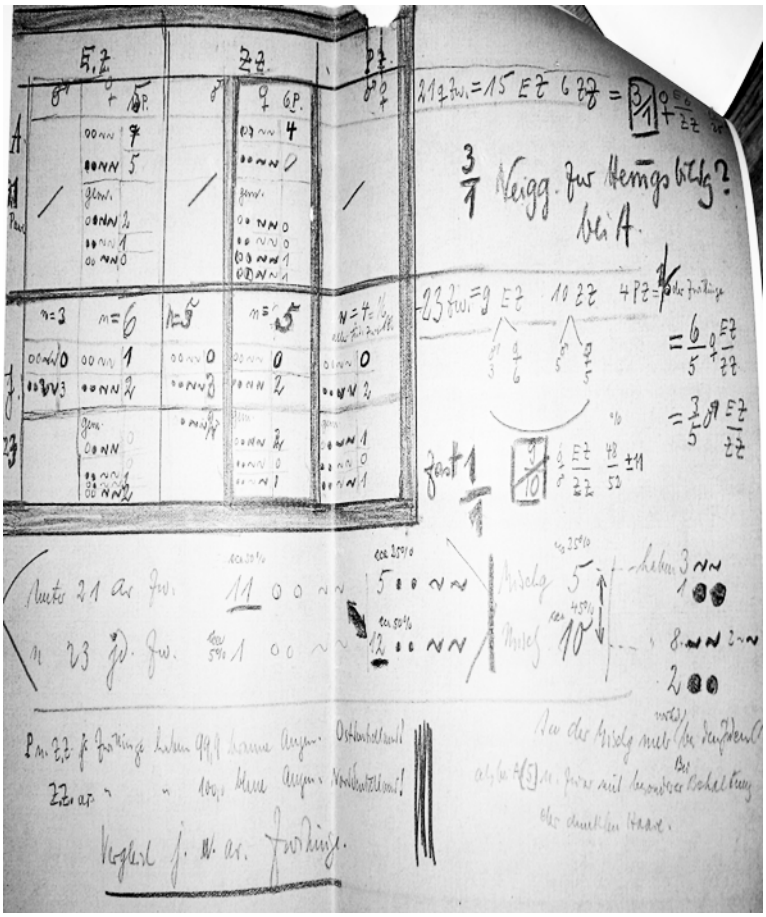


Figure 9. Comparison of "Jewish" and "Ayran" twins from Nussbaum Collection.

He also, but not only, tried to determine Mendelian patterns in the inheritance of those characteristics. Other than Salaman, he was not interested in "pure groups," but rather in the inheritance of single characteristics in families. As many scrawled notes and drafts show, he tried to apply Mendelian methodology whenever he suspected Mendelian ratios to appear (fig. 10). It seems that he sought for an ultimate scientific legitimation for what he was doing, a finding that would have rendered his work valuable in the eyes of famous geneticists, but without success.

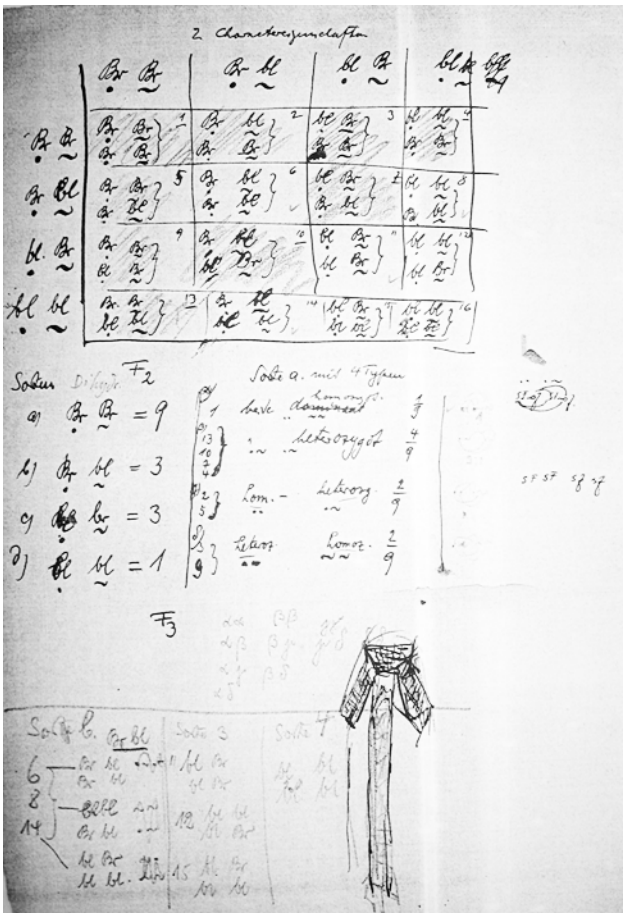
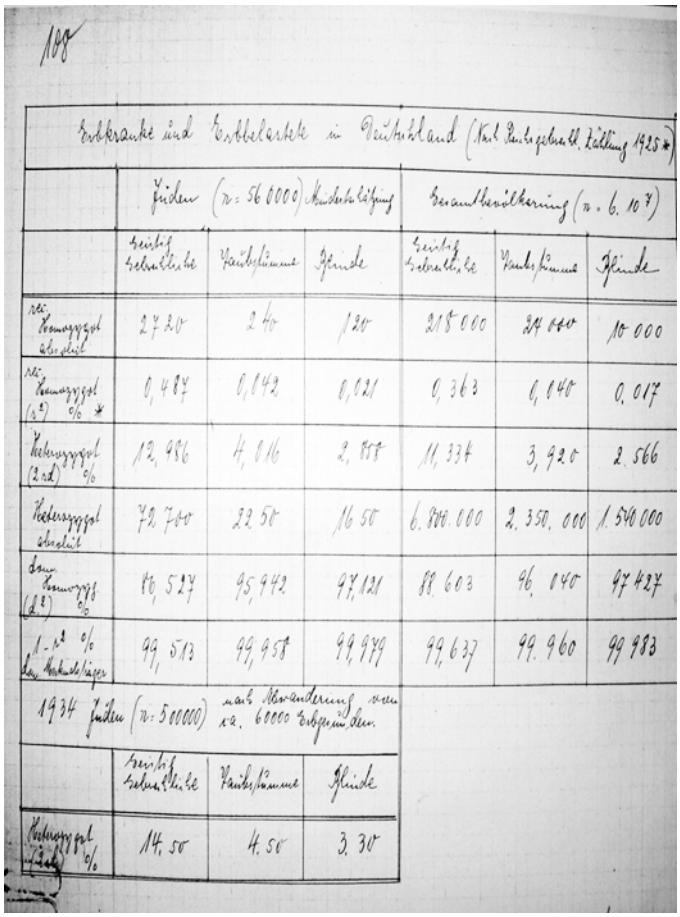


Figure 10. Calculation of Mendelian ratios from Nussbaum Collection.

Beyond these efforts, Nussbaum supported a rather liberal kind of eugenics and examined patients in Jewish charity institutions for blind, deaf and "feeble-minded" persons. One table compared the percentage of those diseases given in the *Reichsgebrechlichenzählung* in 1925 with an estimation for 1934, allegedly yielding alarming results: The percentage of heterozygotic carriers of those diseases among Jews seemed to increase (fig. 11/12). Nussbaum saw the Nazi segregation laws as the most dangerous threat to the Jewish community: According to him, the new political situation obviously caused more inbreeding than ever before.[26] Besides, Nussbaum saw healthy Jewish citizens leaving the country in much higher proportions than those with hereditary defects. Both events, he concluded, increased the occurrence of heritable diseases among Jews in Germany. Nussbaum turned the dominant biohistorical narrative about the Jews upside down: They were *now* being forced to be the inbreeding group that they had *never* before been. In order to avert such dangers of degeneration, Nussbaum set up a marriage counselling service for Jews (fig. 13/14).

[26] Nussbaum, Wilhelm, manuscript, untitled ("Die erbbiologische Betrachtungsweise…"), u.d., 18 pp., here: p. 16 (author's translation).



Erbkranke und Erbbelastete in Deutschland (Nach Reichsgesundh. Zählung 1925*)

	Juden (n = 56 000) Mischbevölkerung			Gesamtbevölkerung (n = 6. 10⁷)		
	Gesamt Erbkranke	Familienzahl	Gemeinde	Gesamt Erbkranke	Familienzahl	Gemeinde
rez. Genmorgogt absolut	2720	240	120	218 000	24 000	10 000
rez. Genmorgogt (2) % *	0,487	0,142	0,021	0,363	0,040	0,017
Krankheitsgogt (2nd) %	12,496	4,016	2,088	11,334	3,920	2,566
Krankheitsgogt absolut	72 700	2250	1650	6 800 000	2 350 000	1 540 000
Gen Genmorgogt (2) %	96,527	95,942	97,121	88,603	96,040	97,427
1-2 % der Krankheitsträger	99,513	99,958	99,979	99,637	99,960	99,983

1934 Juden (n = 500000) nach Abwanderung von ca. 60000 Erbgeschädigten.

	Gesamt Erbkranke	Familienzahl	Gemeinde
Krankheitsgogt (2nd) %	14,50	4,50	3,30

Figure 11. Table "Erbkranke und Erbbelastete in Deutschland" from Nussbaum Collection.

Nussbaum was also busy publishing articles, giving lectures at Jewish institutions, writing letters to potential supporters, and launching new campaigns in order to get more information, such as the addresses of twins. When he published a call for pedigrees dating back to the early 18th century, hundreds submitted pedigrees and provided additional information on their families.[27] Nussbaum's intention was to find out about the geographical distribution of Jews in Central Europe in Early Modern times, but he also offered a certain kind of orientation: Many hoped Nussbaum could help them overcome the shock of the "Ariernachweis"-policy of the Nazis. Their growing interest in genealogy, and their need for positive identification, run parallel to a new interest in Jewish culture among German Jews after 1933.

[27] Arthur Czellitzer, a doctor and geneticist, worked along similar lines like Nussbaum and tried to convince German Jews to be proud of their origin, ancestry and heritage; Czellitzer (1934).

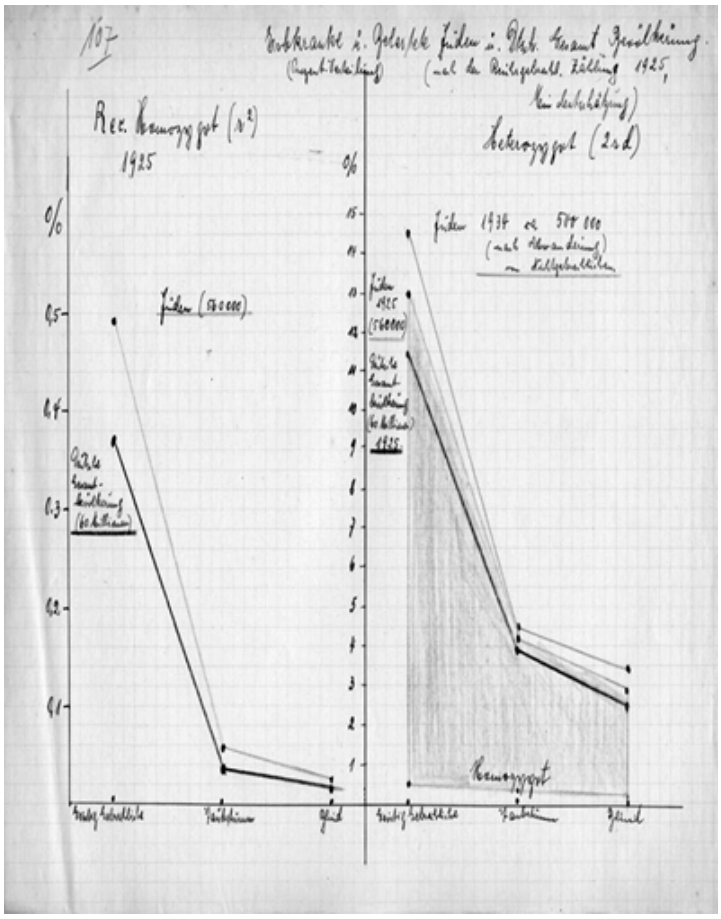


Figure 12. Graph "Erbkranke u. Belastete Juden in Dtsch." from Nussbaum Collection.

Nussbaum wanted to convince Jews in Germany that his work was of outstanding importance and could help the Jewish community. He gained much support by numerous Jewish institutions, such as the *Jüdische Frauenbund*, the *Jüdische Kulturbund* and the *Reichsvertretung der Deutschen Juden.*[28] His manuscripts and lectures contain biohistorical narratives taken from scientific discourse, and they powerfully resonated with biohistorical narratives that were embedded in what Nussbaum saw as Jewish traditions, including those of emancipation and integration. Backed with genealogical and anthropological data, he offered a remarkable alternative biohistorical narration: According to Nussbaum, the Jews—an ancient oriental race mixture of three types—had fully adapted to the European surrounding by environmental influences, education and intermarriages since the Middle Ages.[29]

[28] Leo Baeck helped Nussbaum with his emigration with a very positive reference letter.
[29] For a similar account, see Fishberg (1913).

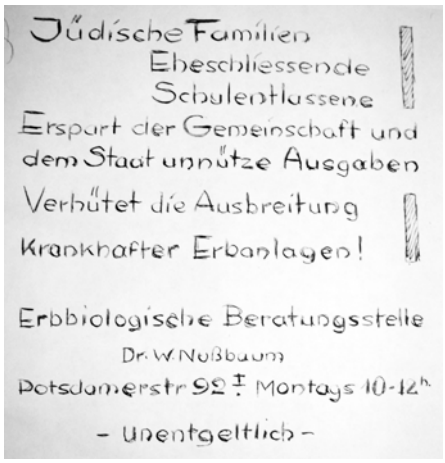


Figure 13. Advertisment for eugenic counselling from Nussbaum Collection.

Although some of Nussbaum's aims and perspectives come out clear from the archival material, it leaves many questions unanswered. The most confusing aspect is probably the rhetoric style of many of his texts: Some passages echo the biopolitical language of the Nazis, and it is hard to imagine that Nussbaum could succeed with this imitation when seeking support from Jewish institutions. On the other hand, he was dependent on the acceptance and support by German authorities as well. It remains unclear whether he tried to avoid censorship, or whether he really embraced that rhetorical mix of Darwinism, genetics and racial theory. He was obviously fascinated by biology, to an extent that might be called religious, but at the same time he seemed to have been aware of the dangerous political situation. It is thus difficult to say what Nussbaum's intention really was. Certainly, he was convinced that his endeavours were the only salvation available to German Jews. He clearly considered race biology and eugenics to be the best weapons for defending Jews from Nazi persecution. Whether he deemed it possible that his institution could win a sovereign position within Nazi Germany, remains unclear.

Figure 14. Advertisment for eugenic counselling from Nussbaum Collection.

But apart from that, Nussbaum was also pursuing a number of scientific objectives, some of which were demonstrated above. My suggestion is that Nussbaum did not devise all of these objectives from the outset, but that they changed over time. He surmised how difficult it would be to acquire such a sample in the future, because he saw people leaving the country. Long-term investigations were out of the question. What Nussbaum decided to do was to collect as much information as ever possible in the shortest time-span possible, even if the usefulness of much data remained unclear to him at the time. He recognized how important it was to link all the various inscriptions, in order to acquire a very dense system of information. He assumed that later on, after the examinations were completed, the data would reveal many regularities and "striking effects" of great interest.

Nussbaum was obviously aware that the unfinished nature of his project was also the best strategy for coping with his awkward situation: Any challenge to his work, be it from Jewish, state, or any other institutional or private source, could be mitigated because he could provide a convincing biohistorical narrative derived from his data. That data could be interpreted in countless different ways; any of the various steps of analysing data offered new directions for interpretation. For example, Nussbaum gave a lecture on the inheritance of gynaecological traits in twins in London 1934.[30] In 1948 he lectured in Brussels on his "Gruppenformel."[31] His inscription system was extensive, flexible, and all-encompassing, but its comprehensiveness would only be appreciated in the future, once methods to interpret the data correctly would become available. I think this "deferred science" is one of the most remarkable aspects about genealogical and many other sorts of inscriptions.[32]

His project also helped Nussbaum to emigrate and work with Franz Boas, who had been looking for a young German-Jewish anthropologist, trained under his opponent Fischer, to disprove race theories. Boas and the Warburg family supported Nussbaum with a stipend and a research position in New York.[33] The data Nussbaum had collected in Germany were integrated into a large-scale research project on bodily conditions of children of various ethnic groups that Boas and Shapiro had initiated in New York in 1935.[34]

It remains unclear just how serious Nussbaum was about his own rather moderate eugenic views and whether he may simply have used them to avoid conflicts with German state authorities. It was not unusual for German-Jewish doctors to promote liberal eugenics before 1933. However, in a Boasian context, these ideas had no place. After emigration, Nussbaum never wrote about eugenics again.

Although Nussbaum's inscription system resembled the research strategies he had been taught to use at Fischer's laboratory, Nussbaum modified all the forms to suit his own unique needs. Thus he gathered more, and at the same time more *specific* information than the published forms of his

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30 Unpublizierter Bericht über den internationalen Kongreß für Ethnologie und Anthropologie in London.

31 Anthropological Studies on German Jews (1933/34) 16pp., manuscript, undated; printed abstracts of Congress papers.

32 The rhetoric of incomplete data/methodology and hence the deferral of prospective benefits is also among the most consistent characteristics of positivist science.

33 See Franz Boas Papers, American Philosophical Society Archive, Philadelphia, Correspondence Boas-Nussbaum.

34 See Harry Shapiro Collection, American Natural History Museum, Box 68, folder: Research data, Negroe infants, White infants, Hebrew Orphan Asylum.

former supervisors allowed. The specific information he sought was designed to account for the unique situation of the probands: Jews in Germany between 1933-1935, a time when biohistorical narratives on Jews were not only part of a cultural code, but also deployed as arguments in the discrimination and persecution of Jews.

Concluding remarks

Looking back from the perspective of today, it might seem irritating that Jewish anthropologists joined in the biological debate on Jews, a debate that also circulated narratives compatible with Nazi ideology. John Efron, who has studied Zionist doctors mainly, has argued that participating in the debate was a form of active resistance and self-assertion, and that racial discourse was so universal at the time that, for a trained scientist, no other concepts and terms came into question than those of biology.[35] This is a convincing explanation, however, there are more differentiations to be made. Racial discourse was not homogenous; biology provided more concepts than race; and Efron does not explain why Jewish scientists agreed to pejorative accounts of the Jewish people. Furthermore, his argument captures only the socio-political agenda of the scientists he studied, but not their scientific agenda. And it certainly fails to capture the complex and manifold agendas of a non-Zionist like Wilhelm Nussbaum.

Michael Bernstein's concept of *side shadowing* is helpful in this context.[36] In his analysis of literary narrativions of the life stories of Holocaust victims and survivors, Bernstein criticizes what he calls *back shadowing*:

> a kind of retroactive foreshadowing in which the shared knowledge of the outcome of a series of events by narrator and listener is used to judge the participants in those events *as though they too should have known what was to come.*[37]

With such a narrative strategy, Bernstein criticizes the repression of the "value of the quotidian, the counter-authenticity of the texture and rhythm of our daily routines and decisions, the myriad of minute and careful adjustments that we are ready to offer in the interest of a habitable social world."[38] He suggests to practice a strategy he calls "sideshadowing: a gesturing to the side, to a present dense with multiple, and mutually exclusive, possibilities for what is to come."[39]

> Sideshadowing's attention to the unfulfilled or unrealized possibilities of the past is a way of disrupting the affirmations of a triumphalistic, unidirectional view of history in which whatever has perished is condemned because it has been found wanting by some irresistible historico-logical dynamic. […] Instead of the global regularities that so many intellectual and spiritual movements claim to reveal, sideshadowing stresses the significance of random, haphazard, and unassimilable contingencies [...].[40]

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35 Efron (1994).
36 Bernstein (1994).
37 Bernstein (1994), p. 16.
38 Bernstein (1994), p. 121.
39 Bernstein (1994), p. 1.

Bernstein's critique suggests that one should not project today's knowledge about the Holocaust back into pre-1933 Germany. Post-war Historians have, with much success, traced the ideological roots of Nazism back to Enlightenment times. But that does not mean that before 1933, it should have been predictable how those traditions would lead to genocide. What is even more important in this context is the wide frame of possible futures that was open for the imagination of the contemporaries: None of the Jewish scientists who participated in the debate knew what racial biology would be used for under the Nazis, or that biologists would support genocide. Instead, they imagined all kinds of futures for racial biology. For some of them it seemed a promising professional career; or they aimed to prove that, by pure scientific evidence, racism had no future at all. Science itself was full of unassimilable contingencies, had various possible futures, and it was not foreseeable which of those would come to pass.

For Nussbaum, many different hopes and aims were connected to his scientific efforts. Even the research design of his study, including Mendelian methods, was set up flexible enough to serve various, contradicting aims he pursued all at the same time. He lived in a "present dense with multiple, and mutually exclusive, possibilities for what is to come," even if he knew that most of those possible futures were dangerous and unhappy for him and his family. Seen against the backdrop of his situation, it was not opportunistic, but a desperate attempt to make the best of an unpredictable future.

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[40] Bernstein (1994), p. 3-4. "To concentrate on the sideshadowed ideas and events, on what did not happen, does not cast doubt on the historicity of what occured but views it as one among a range of possibilities, a number of which might, with equal plausibility, have taken place instead. The one that actually was realized, though, exists from then on with all the weight afforded by the singularity of what we might call its event-ness." p. 7.

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William Bateson's Pre- and Post-Mendelian Research Program in 'Heredity and Development'

Marsha L. Richmond

The rediscovery of Mendel's work in the spring of 1900 sparked a flurry of new activity in biology. Within a short time, many researchers all over the world began breeding experiments to see whether this new approach might be the long-sought breakthrough in understanding the basis of heredity. William Bateson (1862-1926) was in the vanguard of these investigators. Having studied variation for over a decade as a means of studying evolutionary change, Bateson remarked, soon after reading Mendel's 1865 paper, that "we are in the presence of a new principle of the highest importance," only a year later to proclaim that because of this work "the whole problem of heredity has undergone a complete revolution" (Bateson, 1900, 60; Bateson and Saunders, 1902a, 4). Although certainly not everyone shared this view, with hindsight Bateson's prediction seems prescient indeed. Mendel did in fact revolutionize modern biology.

Historians of genetics have long agreed that the year 1900 marked a significant watershed in understanding the problem of heredity. Indeed, the literature on this period predominantly focuses on the period after Mendel's rediscovery and particularly the decade after 1910, which witnessed the rise of "Morganian genetics," or the Mendelian chromosome theory of heredity. Yet, in order to appreciate the full extent of the impact Mendel's work exerted on early twentieth century biology, it is helpful to have a better understanding of the kind of work on heredity that was being pursued immediately prior to the rediscovery. That is, we need to compare and contrast the work on heredity in the pre-Mendel years with that in the immediate post-Mendel period. Bateson is a particularly good subject for such a comparison, given that he was arguably the one who did more to promote Mendelism in the English-speaking world than any other biologist. Contrasting his 1890s publications with those after May 1900 thus provides a particularly good indication of the importance of Mendel's rediscovery: it easily allows us to see the ways in which Mendel's work transformed Bateson's previous inchoate research program in "variation" into a targeted study of the "physiology of heredity," or what in 1906 he christened "genetics" (Bateson, 1907, 91).

A brief (and albeit somewhat schematized) sketch of Bateson's situation circa 1900 helps clarify this claim. Although not one of the "re-discoverers" of Mendel, Bateson was perhaps better positioned to appreciate the significance of Mendel's laws of heredity than were either Hugo de Vries, Carl Correns, or Erik von Tschermak (Kottler, 1979; Lenay, 2000; Saha, 1984; Rheinberger, 2000; Stamhuis, Meijer, and Zevenhuizen, 1999). For more than a decade he had been focusing on discontinuity in nature, cataloguing cases of variation that represented alternative rather than gradualistic change. In 1894 he published an encyclopedic compendium of notable cases of variation in his *Materials for the Study of Variation* (Bateson, 1992). The next year he began a new phase of this project, undertaking an experimental investigation of variation through carrying out hybrid crosses. For five years he collected data without discovering any patterns or underlying process that could explain his findings. When directed to Mendel's paper, Bateson at once realized that the laws of heredity Mendel formulated based on the inheritance of discrete character-pairs

in hybrid crosses could explain his own findings of the persistence of alternate characters rather than their blending. Bateson thus became an immediate and ardent convert to Mendelism. He changed his experimental design to reflect Mendel's method of crossing and back-crossing, and began reinterpreting his previous results in the light of "Mendelian" analysis. He also began to proselytize, trying to entice many more workers to become committed disciples. In this he was successful: by 1906, Bateson was recognized as a leading figure in the new field, serving as the head of an active band of followers, not simply in Cambridge but in England and abroad (Olby, 1985, 2004; Falk, 1995).

There is, however, a certain irony in this turn of events. Prior to 1900 Bateson operated on the fringe of British biology. He was somewhat of a pariah in Cambridge, the seat of Balfourian post-Darwinian evolutionary morphology, not so much because he abandoned the search for phylogenetic progenitors but because he so brazenly regarded this approach as worthless (see Ridley, 1985; Geison, 1978; Blackman, 2003; and Hall, 2004). He also was regarded as a maverick among the Darwinians owing to his well publicized views about the discontinuous basis of evolutionary change and vocal challenge to the all-sufficiency of natural selection. Championing Mendel's laws served to propel Bateson from the periphery of British biology to a place within its inner circle, gaining not just national but also international prominence (Lock, 1906, viii). Just how did such a remarkable transformation—in both theory change as well as scientific stature—come about?

A full-scale biography of Bateson remains a great desideratum in the history of genetics. Nonetheless, there is an abundant corpus of literature that leaves few aspects of Bateson's career untouched. One area that remains hazy, however, is the work he did during the interregnum between the publication of *Materials for the Study of Variation* and the rediscovery of Mendel. This is precisely the focus of the present paper, which aims to examine the work Bateson carried out in the 1890s and compare it with that conducted during the first two years after finding Mendel. It aims to gauge critical changes that occurred in Bateson's technical procedures, standards of analysis, and problem orientation in order to assess more fully the changing architecture of knowledge that marked his dramatic shift from a study of variation to the new Mendelian program in "genetics." In so doing it highlights the importance of his long-time scientific collaboration with women biologists, which has not to date been sufficiently appreciated. Contrasting Bateson's study of variation before and after 1900, I argue, allows us better to recognize the continuities with previous practice as well as new modes of conceptualization wrought by Mendel, and to highlight the main features that shaped the new epistemic space Bateson carved out for the new field of genetics.

Bateson's Study of Variation

The Influence of William Keith Brooks

Bateson, by his own admission, noted that his interest in studying the origin of variation was sparked by his association with the American zoologist William Keith Brooks during the summers they worked together in 1883 and 1884. In his contribution to Brooks's memorial volume, Bateson

provided an insightful profile of how Brooks's rather novel understanding of variation influenced his own thinking and, by implication, his subsequent career in biology. It is worth quoting this passage at length:

> For myself I know that it was through Brooks that I first came to realize the problem which for years has been my chief interest and concern. At Cambridge in the eighties morphology held us like a spell. That part of biology was concrete. The discovery of definite, incontrovertible fact is the best kind of scientific work, and morphological research was still bringing up new facts in quantity. It scarcely occurred to us that the supply of that particular class of fact was exhaustible, still less that facts of other classes might have a wider significance. In 1883 Brooks was just finishing his book "Heredity," and naturally his talk used to turn largely on this subject. He used especially to recur to his ideas on the nature and causes of variation, and to the conception which he developed in "Heredity," that the functions of the male and female germ cells are distinct. The leading thought was that which he expresses in his book (p. 312) that "the obscurity and complexity of the phenomena of heredity afford no ground for the belief that the subject is outside the legitimate province of scientific enquiry." He deplored the fact that he had no opportunity for the requisite experiments in breeding, but he saw plainly that such experiments were the first necessity for progress in biology.
>
> To me the whole province was new. Variation and heredity with us had stood as axioms. For Brooks they were problems. As he talked of them the insistence of these problems became imminent and oppressive. It all sounded rather inchoate and vaporous at first, intangible as compared with the facts of development which we knew well how to pursue, but with the lapse of time the impression became strong that Brooks was on the right line. That autumn I went home feeling that though in technique we were a long way ahead of Johns Hopkins—I had the pleasure of showing off the Jung microtome, then the latest thing in progress, to the admiring Baltimore men—yet somehow Brooks had access to novelties of a more serious description. (Bateson, 1910, 6-7; see also Bateson, 1922, 55-56)

Although a professor of morphology, Brooks looked to variation for clues about the workings of evolution. Written only two years after Darwin's death, Brooks's 1884 book, *The Law of Heredity. A Study of the Cause of Variation, and the Origin of Living Organisms* was not only dedicated to Darwin but paid homage to *The Variation of Animals and Plants under Domestication* (1868). Indeed, Brooks offered a revision to Darwin's theory of heredity, to counter objections to pangenesis and reflect recent research in cytology (Brooks, 1883; Benson, 1979).

Brooks noted that Darwin's theory of pangenesis, which posited that the ovum contains "not the perfect animal in miniature, but a distinct germ for each distinct cell or structural element of the adult," had been undermined empirically by Francis Galton and theoretically by Lamarckians, and hence required modification (Brooks, 1883, 78). Galton had tested pangenesis experimentally by infusing rabbits with the blood of different varieties (and hence, presumably, containing different pangenes) and found they were not transformed as was to be expected on the theory of pangenesis (Pearson, 1914-30, 2: 160-73; Gillham, 2001). For their part, Lamarckians favored more rapid response to environmental change than natural selection operating to alter pangenes seemed to allow. Brooks characterized his theory as lying "midway between that accepted by Darwin and that advocated by Semper and other Lamarckians," and thus offering a good compromise. "If the hypothesis of pangenesis could be so remodelled," he wrote, "as to demand

the transmission of only a few gemmules from the various parts of the body to the reproductive elements, instead of the countless numbers which are demanded by the hypothesis in its original form, we should escape many of the objections which have been urged against it" (Brooks, 1883, 80). These few gemmules, he assumed, would be collected by the ovum, which thus served a conservative role in heredity. Variation and adaptation arose from the male element's "peculiar power to gather and store up germs," allowing for faster response to changes in the environment (Ibid., 82, 84-85). Hence Bateson's statement that for Brooks "the functions of the male and female germ cells are distinct."

Brooks obviously supported a "particulate" view of heredity suggested by pangenesis, pointing to his view of "the egg as containing material particles of some kind to represent each of the hereditary congenital peculiarities of the race." Yet in understanding how variation could come about, he referred to the "physicalistic" view of forces operating on matter proposed by St. George Jackson Mivart (1827-1900), quoting at length from Mivart's *On the Genesis of Species* (1871):

> It is quite conceivable that the material organic world may be so constituted that the simultaneous action upon it of all known forces, mechanical, physical, chemical, magnetic, terrestrial and cosmical, together with other as yet unknown forces which probably exist, may result in changes which are harmonious and symmetrical, just as the internal nature of vibrating plates causes particles of sand scattered over them to assume definite and symmetrical figures when made to oscillate in different ways by the bow of a violin being drawn along their edges. The results of these combined internal powers and external influences might be represented under the symbol of complex series of vibrations (analogous to those of sound and light) forming a most complex harmony or a display of most varied colors. . . . Also as the atoms of a resonant body may be made to give out sound by the juxtaposition of a vibrating tuning-fork, *so it is conceivable that the physiological units of a living organism may upset the previous rhythm of such units, producing modifications in them—a fresh chord in the harmony of Nature—a new species.* It seems probably, therefore, that new species may arise from some constitutional affection of parental forms—an affection mainly if not exclusively of their generative system. (Ibid., 87)

Qualitative change in the gemmules thus ultimately derived from forces operating on matter to cause some kind of physical rearrangement. Brooks indicated that his view of variation well accorded with Mivart's: "a new variation is caused in essentially the manner which Mivart suggests as probable. The accumulated influence of surrounding conditions, organic and inorganic, does upset the previous rhythm of the physiological units of the living organism, and causes them to give rise to gemmules, and the tendency of the corresponding units of the offspring to vary, is directly due to this constitutional affection of the parental forms" (Ibid.). This way of conceptualizing variation had major implications for the understanding of species change.

If variation arose from environmental changes affecting the physiological activity of the cells of an organism and causing them to throw off altered gemmules, then the possibility of sudden, abrupt changes of form was likely. This presented a challenge to the assumption of gradualistic evolution. As Brooks stated:

> There are many reasons for believing that variations under nature may not be so minute as Darwin supposes, but that evolution may take place by jumps or saltations. According to our

> view a change in one part will disturb the harmony of related parts, and will cause their cells to throw off gemmules. A slight change in one generation may thus become in following generations a very considerable modification, and there is no reason why natural selection should not be occasionally presented with great and important saltations. (Ibid., 328)

In his book, Brooks, then, despite paying homage to Darwin, offered significant revisions to the tenets of Darwin's theory of evolution and hereditary theory of pangenesis (see Endersby, 2003). Ten years later, Bateson joined suit, also by means of publishing a work dedicated to studying "the nature and causes of variation."

From Morphology To Variation

Historians have mainly focused on Bateson's morphological training as having promoted his deviation from neo-Darwinian gradualistic evolution. As Peter Bowler stated, "the particular research problems that had engaged Bateson as a morphologist must have predisposed him to see discontinuous variation as more important" (Bowler, 1992, xxi). Yet it was shortly after working with Brooks at the Chesapeake Zoological Laboratory that Bateson decided to change his line of morphological investigation, abandoning the search for ancestral forms he had previously pursued. In taking up Brooks's suggestion that studying variation was a better means of understanding the process of evolution than tracing phylogenetic relationships, he explicitly rejected the morphological research program that Francis Balfour had championed at Cambridge (Olby, 2004; Hall, 2005). This had serious implications for his career, both in terms of altering his scientific methodology as well as hindering his ability to garner institutional and financial support for his work.

In 1886 and 1887, Bateson undertook a research trip to the Aral Sea and Egypt, with the aim of investigating "the relation between the variations of animals and the conditions under which they live" (Bateson, 1889). He was disappointed to find no clear-cut evidence to support this claim. Rather, the shells of the mollusk *Cardium edule,* living in the brackish water of the Aral Sea, presented only slight differences from the forms inhabiting the much saltier water of the Mediterranean. He regarded the results of this study as negative evidence, showing "that, while such variations do occur in certain species, in the majority they do not." (B. Bateson, 1928, 35). According to his wife Beatrice Bateson, "[h]e always regarded these expeditions as failures," and yet ultimately as putting him on the right road after all: they "proved very stimulating: he had to make good: if he had followed a false clue, the greater the need to find the right one" (Ibid., 27).

Bateson's sense of failure reinforced a growing conviction that variation was not produced by the affect of external stimuli acting on organisms, but rather by the operation of some unknown mechanism internal to the organism, an idea, as we have seen, that was not dissimilar to Brooks's views. As Bowler points out, the germ of this conception was already apparent in Bateson's oft-cited 1886 work on the ancestry of the chordata. There he identified a tendency in nature toward the repetition of parts, by which means he explained the origin of (segmented) chordates from an (unsegmented) invertebrate, *Balanoglossus*. "The duplication of an existing structure was self-evidently a discontinuous process," Bowler noted, "and he suspected that it would occur whether or not the results were useful. In effect, evolution would be driven by a process arising from within the organism, forcing the species to evolve in a certain direction whatever the environment to

which it was exposed" (Bowler, 1992, xix; Hall, 2005). Although Bateson made no explicit mention of Brooks's and Mivart's ideas about the basis of variation, he was obviously moving toward looking internally rather than externally for causal factors prompting organic change.

By his own admission, upon concluding this study Bateson experienced an epiphany, a kind of personal "revolt from morphology." As he described it: "On finishing these investigations I became dissatisfied with this mode of attacking biological problems and resolved to seek a new field of inquiry." As a result, some time in 1885 he embarked on "work of an entirely different kind" (B. Bateson, 1928, 31). The main problem he set for himself was to identify "the nature of the forces by which the forms have been produced and fixed. . . . Hence, if we seek to know the steps in the sequence of animal forms, we must seek by studying the variations which are now occurring in them, and by getting a knowledge of the modes of occurrence of those variations and, if possible of the laws which limit them" (Ibid., 33-34). He increasingly came to believe in "the Discontinuity of Variation" as a "new point of attack on the problem of Species," and conceived of variation from a physicalistic standpoint not unlike that expressed by Mivart and Brooks. The underlying elements of his thinking moved him in certain directions, "from observation of Discontinuity to Meristics, Symmetry and the Repetition of Parts, and to tentative suggestions of Rhythm, which he never put aside from his considerations of the forms of life" (Ibid., 56). These were topics present in all of Bateson's publications in the 1890s.

One of the first fruits of Bateson's new line of work on variation appeared in 1890, in a short paper entitled "On Some Cases of Abnormal Repetition of Parts in Animals." This brief description of cases of "abnormal repetitions of normal structures" reveals his acute interest in meristic phenomena, or repetitive patterns in nature. While apologizing for the descriptive nature of this work, he nonetheless pointed out its relevance, stating that "the key to some of the problems of variation is to be sought by an analysis of this class of facts, yet such an analysis can only be attempted after a wide survey of the whole ground" (see Bateson, 1928, 1: 113-23). Another paper presented the same year to the Cambridge Philosophical Society continued with this theme. He exhibited a number of insect specimens he had collected and reported on "about 220 recorded cases of extra legs, antennae, palpi or wings, and particulars" in various species of insects. He concluded by offering his views about the "mode of occurrence of these structures," but unfortunately these remarks were omitted from the published abstract of his talk (Ibid., 1: 125).

Until this point Bateson had kept pretty close to the vest about the new conceptual reorientation prompted by his new direction of research. By 1891, however, it was clear that he was beginning to deviate both from mainstream morphology and also from core neo-Darwinian tenets. The first public admission of his new "epistemic space" came in a seemingly descriptive paper discussing cases of floral symmetry. Coauthored with his sister Anna Bateson (1863-1928), a graduate in botany at Newnham College, Cambridge, this paper discussed the irregular forms of corollas (the petals of flowers) in four species, *Linaria spuria, Veronica buxbaumii, Gladiolus* hybrids, and *Streptocarpus*. Despite its seeming descriptive nature, this paper in fact harbored well considered general reflections on the nature of variation and its role in evolutionary change.

The authors began by focusing on variation without discussing its cause, noting that such an attempt should wait "until a much fuller knowledge of the modes of Variation shall have been

attained." They did, however, address the evolutionary significance of irregular corollas, stating that such cases appeared to be connected "with their adaptation to the purposes of cross-fertilisation, and that their perfection and persistence have consequently been achieved by the agency of Natural Selection" (Bateson and Bateson, 1891, 386). While granting a significant role to natural selection, they did not believe selection operated on a series of small variations, resulting in gradual evolution. Rather, they envisioned the kind of variation important in evolutionary change as discrete and discontinuous in nature, as opposed to the continuous variation the neo-Darwinians assumed. They indeed speculated about the kind of processes that might result in discontinuous as opposed to gradual variation:

> The success of any attempt to comprehend the nature of the forces which are at work in the production of Variation will depend very largely on the precision with which we shall be able to answer these questions [about whether the series of ancestors of new forms is continuous or discontinuous], and to determine the degree of continuity which is present in the process of Evolution. For if, on the one hand, the transition from form to form shall be found to occur by insensible and minimal changes which are so small that no integral change can ever be perceived, we should recognise an analogy with the continuous action of mechanical forces; but if it should appear that the series is a discontinuous one, and that there are in it lacunae which are filled by no intermediate form, the analogy would rather hold with the phenomena of chemical action, which is known to us as a discontinuous process, leading to the formation of a discontinuous series of bodies, and depending essentially on the discontinuity of the properties of the elementary bodies themselves. (Bateson and Bateson, 1891, 387-88)

Evolution, in other words, may result from the selection of discontinuous rather than continuous variation. In proposing a kind of causal juxtaposition of continuous variation as based on the operation of mechanical forces versus discontinuous variation derived from chemical combination, the authors seemingly deviated from both Brooks's and Mivart's more morphological emphasis on physical forces as the source of organic variation. They found the idea of elements combining in different proportions to produce discrete chemical compounds a better analogy for understanding sudden qualitative change in living forms. In this they were unusual, for few biologists in the late nineteenth century speculated about the chemical basis of heredity; rather, following Darwin, most thought in terms of some kind of particulate inheritance (Robinson, 1979). Throughout his career, however, Bateson often invoked chemical analogies to illustrate his views about hereditary change.[1]

Continuing along these lines, if it were found, the authors reasoned, that many variations were indeed discontinuous, then "the necessity for supposing each structure to have been gradually modelled under the influence of Natural Selection is lessened, and a way is suggested by which it may be found possible to escape from one cardinal difficulty in the comprehension of Evolution

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[1] See, for example, Bateson and Saunders, 1902b, 147: "Remembering that we have no warrant for regarding any hereditary character as depending on a material substance for its transmission, we may, with this proviso, compare a compound character with a double salt, such as an alum, from which one or other of the metals of the base can be dissociated by suitable means, while the compound acid-radicle may be separated in its entirety, or again be decomposed into its several constituents. Though a crude metaphor, such an illustration may serve to explain the great simplification of the physiology of heredity to which the facts now point."

by Natural Selection" (Bateson and Bateson, 1891, 388). The "difficulty" to which they refer was the origin of complex structures like alternative forms of flowers, and specifically the problem of explaining the selective value of incipient stages of useful structures.

The question of what adaptive advantage a new character would represent at its earliest stage of formation that could trigger natural selection was first posed by Mivart in *Genesis of Species* (1871) and answered by Darwin in the 6th edition of *Origin of Species* (1872; Gayon, 2003, 243-44). The Batesons returned to this issue in the context of flower morphology, noting, "it cannot be supposed that the mechanism was at all periods of its evolution so beneficial as to be selected . . . in short, that the evolution of a special contrivance for adaptation is not compatible with constant and perpetual usefulness." Rather, in all the cases of irregular corollas they analyzed the new form appeared to be an instance of a "sudden variation" rather than a gradual change from one form to another. Moreover, unlike meristic phenomena, in species exhibiting flowers with irregular corollas, the "change of symmetry [was] attained not by an alteration in the number of parts, but by the selection of a different morphological plane about which the symmetry is developed." Such a change could only have come about by a sudden alteration in the basic morphology of a plant's petal structure. "It is easy," they claimed, "to conceive the steps between forms differing in the degree of expression of some character, such as size or intensity of coulour, but in trying to pass from a form with one kind of symmetry to a form with another we often cannot even conceive the transitional steps." (Bateson and Bateson, 1891, 388-89; 417). What, they implied, could be the possible selection value to cause a 2-petaled flower symmetrical form to generate a 3-petaled asymmetrical flower? (See Figure 1.)

In this way the Batesons thus declared their allegiance to discontinuous variation as the predominant force in evolution. Darwin, they noted, was well aware of forms that had characters that did not blend. "Our object now is to show," they stated, "that this principle is widely true of variations which are of the nature of specific changes, and to point out that it may help us to measure the size of the integral steps of Variation" (Bateson and Bateson, 1891, 419-20).

Such a position was not only at odds with contemporary neo-Darwinian tenets, but also challenged the core ancestrian view of the biometricians. Galton's law of ancestral heredity posited that individuals inherited characters proportionally from their remote ancestors as well as their parents. Thus the well known phenomenon of "reversion" could be explained as the reappearance of ancestral traits (Gayon, 1998, chap. 4). Both Galton and W. F. R. Weldon, the authors noted, had recently analyzed forms exhibiting continuous variations in size, Galton studying human stature and Weldon the proportional sizes of the limbs of shrimp. Both attempted to test the applicability of Galton's "Law of Error," according to which "the greater the departure from the normal form, the rarer will be the Variation" (Bateson and Bateson, 1891, 420-21; Galton, 1889; Weldon, 1890). However, such an explanation could not well apply to the cases of floral variation they were considering, which were not "instances of reversion to an ancestral type." Indeed, under their view, they noted, "[i]t is likely that the study of Variation will hereafter lead to and necessitate a revision of the whole question of the nature of Reversion, but this is no part of our purpose at present" (Bateson and Bateson, 1891, 415). Reversion, considered from a discontinuous point of view, rather suggested the persistence of latent traits, not ancestral reminiscence.

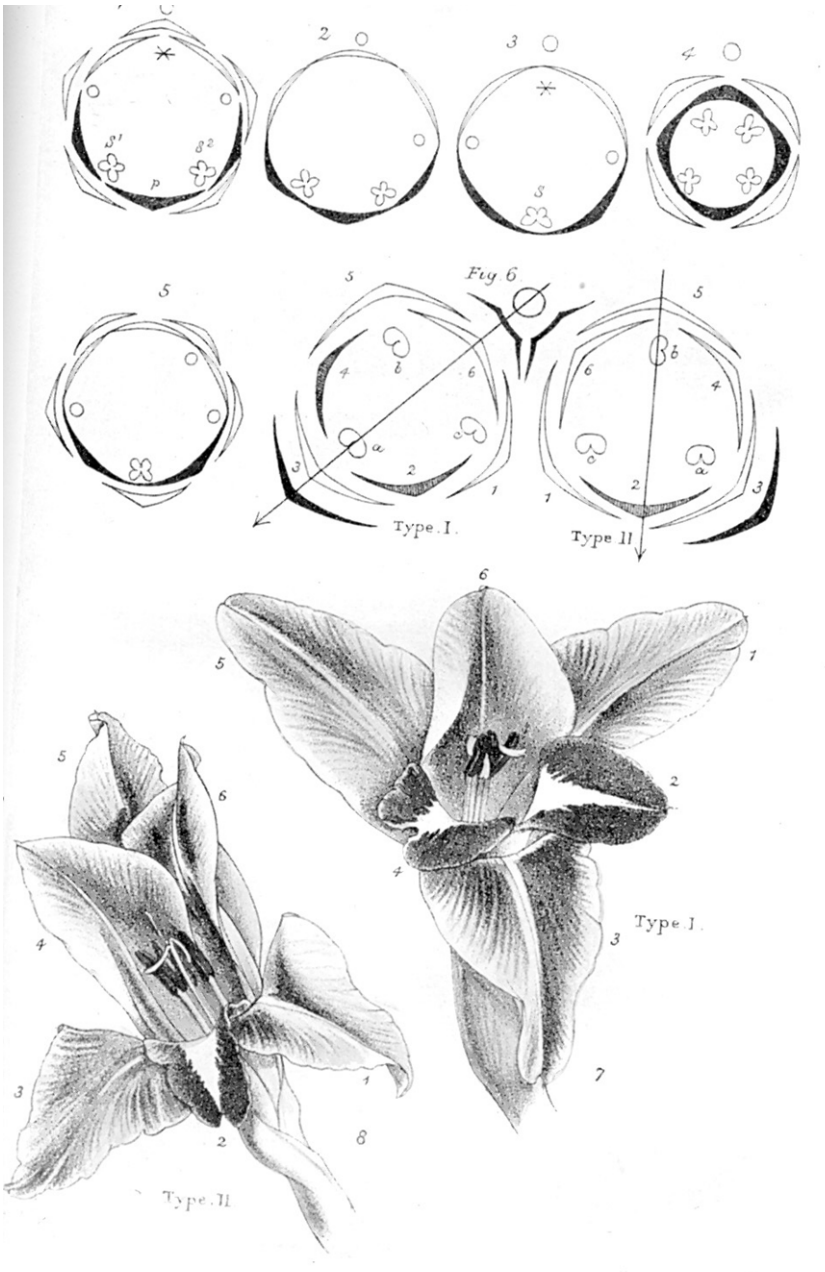

Figure 1. Variations in Floral Symmetry. Table from Bateson and Bateson 1891, Plate LI.

This line of thought led them to another "fact of great importance," namely, that "there are at least two classes of Variation," those representing a "Variation in kind," such as the cases of floral symmetry they studied, and other "Variations in degree," like the phenomena investigated by Galton and Weldon. Variations in kind were discrete and qualitative, exhibiting no transitional forms. There must, therefore, be some underlying mechanism accounting for this property. "It seems, in fact, in cases where changes of symmetry are concerned, that the intermediate forms are, as it were, points of unstable equilibrium, and that the body therefore assumes these forms rarely, as in some instances, or never, as in others" (Bateson and Bateson, 1891, 421). The notion of

"unstable equilibrium" built on Galton's notion of "organic stability" as the basis of discontinuous change introduced in *Natural Inheritance* (1889) (Galton, 1889, 27; Gayon, 1998, 170-74; Gillham, 2001). Variations in degree, on the other hand, were by nature quantitative, and, they argued, "no one as yet has ever indicated the way by which such Variations could lead to the constitution of new forms, at all events under the sole guidance of Natural Selection" (Bateson and Bateson, 1891, 421). Evolution, they thus implicitly argued, did not result from selection operating on continuous characters (as assumed by the neo-Darwinians and biometricians alike) but was rather fueled by the sudden appearance of new "variations in kind," upon which selection could operate. Evolution, in other words, was saltatory, not gradualistic, in nature.

Having made a series of bold theoretical claims about the nature of evolutionary change, the two authors next turned to the question of the best methodology to study evolution. In this context they challenged the efficacy of morphology to deal with this problem. As a "deduction from facts," they reasoned that only variations arising through a continuous process of change will leave traces of their history that can be investigated by means of a "comparative study of form and development," that is, by employing the conventional morphological toolkit. If, as they believed, the kind of variation important for evolution is variation in kind rather than variation in degree, and hence produced through a sudden event, then "comparative morphology [will] cease to be an effectual guide to the history of Descent." As they explained:

> We are therefore disposed to think that the first teaching of the facts of Variation is this: that *comparison* of forms is not likely to be a good guide to the history of those forms; and that there is no evidence that degrees of apparent relationship of form are an indication of degrees of actual relationship by descent; and that nothing short of an actual knowledge of the processes of Variation and a discernment of the changes which are possible to living things from those which are impossible to them, can be of any use in the solution of the problem of Descent. (Bateson and Bateson, 1891, 4)

In this way, the Batesons called into question the value of morphology for investigating evolutionary change. This conclusion, they well realized, "touches the nature and soundness of the received principles by which morphological facts are interpreted" (Ibid., 416). If morphology can only study variation in degree but not variation in kind, its importance as a means of exploring evolutionary change was thus significantly diminished.

Hence, the 1891 paper by the Bateson siblings was not at all a merely empirical contribution to botany. Rather it should be read as a daring theoretical manifesto, offering a radical revision, not just of the approach to variation and heredity, but of foundational concepts guiding modern biological investigation. They challenged such fundamental Darwinian tenets as gradualism and the role played by natural selection. They also applied boundary conditions that restricted the applicability, and hence efficacy, of morphology and biometry to evolutionary problems. In short, the 1891 paper laid out a completely new direction of research as well as a new mode of conceptualizing evolutionary change. William Bateson soon followed up this declaration of principles with an even more extensive avowal of his new, revisionist views of variation and speciation in a monograph devoted to exploring "variation in kind."

Materials for the Study of Variation (1894)

Two years after the paper outlining his maverick views of variation, Bateson's book, *Materials for the Study of Variation, Treated with Especial Regard to Discontinuity in the Origin of Species* (1894), was published. In this book, he extensively catalogued notable cases of variation, paying particular attention to discontinuous variations that appeared to have arisen suddenly and without any apparent adaptive value. His view of the discontinuous nature of evolutionary change shared similarities with the ideas Brooks expressed in his 1884 book. Yet despite pointing fifteen years later to the formative influence Brooks had on his own thinking, it is curious to note that Bateson did not refer to Brooks or his proposed "law of heredity" in his own book on variation.

In *Materials for the Study of Variation*, Bateson emphasized the importance of this topic, proclaiming that "Variation, whatever may be its cause, and however it may be limited, is the essential phenomenon of Evolution. Variation, in fact, *is* Evolution" (Bateson, 1992, 6). In the few pages he devoted to speculating about the cause of variation, he presented a physicalistic description that shared essential features with the views expressed earlier by Mivart and Brooks. Meristic or repetitive variation was, he believed, the result of mechanical changes in the pattern of a developing organism. He explained his view as follows: "Patterns into which the tissues of animals are divided represent positions in which the forces that effect the division are in equilibrium. On this view the lines or planes of division would be regarded as lines or planes at right angles to the directions of the dividing forces; and in the lines of Meristic Division we are perhaps actually presented with a map of the lines of those forces of attraction and repulsion which determine the number and positions of the repeated parts, and from which Symmetry results" (Ibid., 70). As suggested in the 1891 paper, he thus assumes that such variations in degree are the result of mechanical forces operating on living matter to effect change (see Coleman, 1970).

Bowler has rightly noted that the "evidence presented in *Materials* is not, of course, experimental in character. Bateson gathered his evidence for the existence of discontinuity from the study of natural varieties and occasional monstrosities" (Bowler, 1994, xxii). Yet we should not overlook Bateson's statements that emphasize the pressing need for an experimental approach to the problem. "So long as systematic experiments in breeding are wanting," he wrote, "and so long as the attention of naturalists is limited to the study of normal forms, in this part of biology which is perhaps of greater theoretical and even practical importance than any other, there can be no progress" (Bateson, 1992, 76). In so doing, he echoed Brooks's earlier statement that the nature of variation could best be approached by undertaking extensive hybridization experiments (Brooks, 1883, vii). In the conclusion to his book, Bateson reiterated this point, stating: "The only way in which we may hope to get at the truth is by the organization of systematic experiments in breeding, a class of research that calls perhaps for more patience and more resources than any other form of biological inquiry" (Bateson, 1992, 574). In the event, with considerable patience but few resources, he himself took up the call.

Bateson's Hybridization Experiments, 1895-1900

Immediately after publishing *Materials for the Study of Variation,* Bateson initiated a new line of research to study variation experimentally. In part, this appears to have resulted from his doubts

about the persuasive value of simply amassing facts on discontinuous variation. As he admitted to Anna shortly before the work appeared, "Every day almost makes me misgive more and more about this book. Several of the sections of evidence seem very weak now they are actually 'floated and rendered' as the builders say, and half of the best things seem never to have been got in at all" (B. Bateson, 1928, 54). These misgivings intensified after the negative reception given to his book. Adam Sedgwick, Balfour's successor as the head of Animal Morphology at Cambridge, called Bateson's approach "stupid & narrow" and thereafter provided him little institutional support.[2] His earlier mentor and friend, Frank Weldon, viciously attacked Bateson's new research program in a scathing review of *Materials* (Weldon, 1894). Despite his criticism of biometry in the 1891 paper, Bateson found this lack of support and harsh criticism difficult to accept. In 1895, he began a series of hybridization experiments in the hope of providing evidence to support his view that discontinuous or saltatory variations, rather than the small, adaptive variations envisioned by Darwin and the neo-Darwinians, was the basis for evolutionary change. He thus aimed to prove that alternative characters did not, in fact, generally blend but rather were discrete and somehow self-perpetuating.

In pursuing this line of work, Bateson well realized the need for collaborators, but his marginal status at Cambridge worked against this. Even Anna, although sharing his views about variation and evolution, was no longer able to assist with such a study. In 1890, when her mother left Cambridge and thus broke up the family home, she decided to abandon academic biology to support herself as a tradeswoman, using her inheritance to purchase a nursery in a small village in Hampshire, in the south of England.[3] Although William disapproved of this decision, believing it lowered her social status, Anna was realistically confronting her limited options. As a student of botany at Newnham College, Cambridge, Anna had only obtained a second class in both parts 1 and 2 of the Natural Sciences Tripos (1884, 1886). Although this qualified her for a position as a botanical instructor (demonstrator) at the Balfour Biological Laboratory for Women as well as earned her a Bathurst Studentship to pursue postgraduate study, a future career in academic science was not well assured. The reality was that a woman with a degree in science in 1890 had precious few options for employment. Although she had gained recognition among botanists through her publications, her tripos rankings made a secure position at Cambridge unlikely (Richmond, 1997).[4] While many women science graduates looked for teaching positions at a

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2 Sedgwick to Bateson, 9 October 1890: "I also think that yr. views on Zoology—on the morphology side—are stupid & narrow, but that is a very different thing from thinking that yr. work is stupid & unprofitable." Bateson Correspondence, ADD 8634, Manuscripts Room, Cambridge University Library.

3 Anna Bateson obtained second-class honors in the Natural Sciences Tripos, 1884 and 1886. She taught advanced botany at the Balfour in 1886 and was appointed assistant demonstrator in botany in 1887. She held a Bathurst studentship, 1887-1889, which supported post-graduate research. She assisted Francis Darwin in the University Botanical Laboratory, 1886-1890. In 1890, she left Cambridge to establish a nursery in Bashley, Hampshire, that became quite profitable. See Cock, 1979.

4 That Anna Bateson's work had gained attention, particularly among German botanists, is shown by Carl Correns's letter to Bateson, 21 October 1900, who asked him: "Sind Sie mit Miss A. Bateson verwandt, die die hübschen Untersuchungen über die Wirkung von Kreuz- und Selbstbefruchtung bei kleinblüthigen Pflanzen ausgeführt hat? Ich habe diese Arbeit mit grossem Interesse gelesen!" ["Are you related to Miss A. Bateson, who published the wonderful investigation of the effect of cross- and self-fertilization in small-flowered plants? I read this work with great interest!"] Correns refers to A. Bateson, 1888. This same paper was cited by Munich professor of botany Karl Goebel in his essay on the biology of flowers in the 1909 volume commemorating Darwin (Goebel, 1909, 421).

secondary school that offered science instruction, in the 1890s few such positions were open (Perrone, 1993). In the event, while Anna's decision well suited her needs and inclination, it left William without a suitable intellectual confident and experimental ally.

With Anna gone, Bateson turned to another Newnham botanist, Dorothea Frances Matilda (Dora) Pertz (1859-1939) to help carry out an experimental study of variation. A niece of geologist Charles Lyell, Dora Pertz was an accomplished botanist with solid experimental skills (Browne 2004). Bateson designed crosses for Pertz to carry out in *Veronica*, aiming "to test whether there is any difference between offspring raised from abnormal flowers, and the offspring of normal flowers borne by the same plant." Pertz pursued this work over four growing seasons, from 1892 through 1895, self-crossing abnormal flowers and normal flowers and then comparing the proportion of normal flowers to abnormal ones in the progeny. In the joint paper they published in 1898, they noted that normal flowers appeared about 80-90 percent of the time, no matter whether the parents were normal or abnormal (Bateson and Pertz, 1898). These results were disappointing, and thus the approach was abandoned.

In the mid-1890s Bateson entered into what became a highly profitable mutual collaboration with another young Newnham botanist, Edith Rebecca (Becky) Saunders (1865-1945). In many respects, Becky Saunders's background was similar to Anna Bateson's. Saunders took second class honors in Part I of the Natural Sciences Tripos in 1887, but the following year she gained distinction by gaining a first in Part II (botany). She was awarded a Bathurst research studentship, which allowed her to pursue postgraduate research, and served as botanical demonstrator at the Balfour Biological Laboratory for Women. But in 1899, upon the resignation of her friend Marion Greenwood, Saunders was appointed director of the laboratory, a position she held until its closure in 1914, also holding various college positions. Saunders was thus more fortunate than either Anna Bateson or Dora Pertz in being able to pursue an academic career in science. This was fortunate for Bateson. With an extensive knowledge of botany and a strong background in research, Saunders proved to be an excellent colleague. Her independent research conducted on problems of variation ultimately provided critical evidence that supported his views of discontinuous variation (Richmond, 1997, 2001; Creese, 1998).

Using seeds that Bateson brought back with him from a trip to Italy, in the summer of 1895 Saunders initiated a series of breeding experiments on an allotment they rented from the Cambridge Botanic Garden. In the Italian Alps, Bateson had observed two distinct forms of the perennial herb *Biscutella laevigata* growing side-by-side, one with hairy (hoary) leaves and the other with smooth, or glabrous, leaves. He found this especially curious given that the two forms "intercrossed readily" and yet apparently bred true to form: offspring generally exhibited either hoary or glabrous leaves, with relatively few intermediates. Saunders set out to determine how this distinctness was maintained. As she noted in her paper of 1897, "on the supposition that hairiness and smoothness are characters capable of blending freely, it might be expected that offspring derived from a cross between hairy and smooth parents would tend constantly to regress to a mean condition of texture." Since this biometrical prediction was not fulfilled, it appeared this case "might lead to interesting results bearing upon the views which have recently been brought forward with regard to discontinuous variation and its value as a factor in the origin of species"

(Saunders, 1897). The case, in other words, appeared to support Bateson's hypothesis of discontinuous variation.

Presenting her findings qualitatively, Saunders noted that the alternative characters generally persisted in the offspring. Out of 208 plants raised, 127 were hairy, 36 appeared to be intermediates, and 45 were smooth leaved. When she crossed two hairy plants, out of the 76 offspring that matured, 61 were hairy, 13 intermediate, and 2 smooth. These results were thus promising. Hairy and smooth-leaved *Biscutella* appeared to represent two stable discontinuous characters, with only a handful of "blended" offspring appearing in cross-bred plants. Moreover, the hairy character appeared to be "prepotent" over smooth leaves, a fact that Saunders wished to follow up (Ibid., 17, 18).

In the summer of 1896, Saunders set out "to ascertain the nature and amount of the variations occurring among the *offspring of unlike parents*," intercrossing hairy-leaved plants with smooth-leaved ones. The seeds she procured from the offspring of the cross were planted the same year. These results she presented in tabulated form:

Classification of 120 Cross-Bred Seedlings	Surface hairy	Surface intermediate	Surface smooth	Totals
Number of seedlings derived from five hairy plants x smooth plants	4	7	26	37
Number of seedlings derived from five smooth plants x hairy plants	5	32	28	65
Number of seedlings derived from one plant, surface, marginal hairs numerous x hairy plant	12	6	0	18
Totals	21	45	54	120

These data were not as supportive of the discontinuity hypothesis. Saunders attempted to downplay the negative evidence, reporting that the results "show that a blending of parental characters as regards hairiness and smoothness occurs to a certain extent in the offspring of plants of dissimilar types, giving rise to intermediate forms." She could only add that plants exhibiting an intermediate condition early in life often grow distinctly more glabrous with maturity (Ibid., 23).

Saunders's investigation of *Biscutella* illustrates the evolving approach she and Bateson took toward the study of variation. In setting up their hybrid crosses, they looked for data that indicated the persistence of "variations in kind" in heredity. They did not carry out a quantitative and statistical analysis of "variation in degree," as biometricians did in recording the proportion of individuals showing ancestral rather than parental inheritance through the regression to the population mean. In concentrating on the retention of parental traits among the progeny, they rather aimed, as Robert Olby has noted, to predict "the probability that a given transmissible

character of the parents will be possessed by the offspring" (Olby, 1987, 400-401). Olby also tellingly points out that Bateson "was thus concerned not with variation in general, but with those forms of variation which he saw as significant in the origin of species" (Olby, 1989, 308). As Bateson described the approach he and Saunders employed: "Cross-breeding, then, is a method of investigating *particular* cases of evolution one by one, and determining which variations are discontinuous and which are not, which characters are capable of blending to produce a mean form and which are not" (Bateson, 1899, 64). It was thus not blending characters but rather alternative ones that held their attention.

Encouraged by her findings in *Biscutella*, Saunders embarked on a new series of crosses using other species with forms exhibiting alternative variations. To carry out this scheme, however, she needed a larger plot of land. Bateson thus began to solicit outside funding, approaching the Royal Society as a member of its newly reconstituted Evolution Committee. Formed in 1894 as the Committee for the Measurement of Plants and Animals, with Galton as chair and Weldon as secretary, the committee soon encountered differences of opinion over its orientation, whether evolution was to be approached mathematically (as did the biometricians) or biologically. One consequence was the invitation of Karl Pearson (a mathematician) and Bateson (a biologist) to join the committee in 1896 (Froggatt and Nevin, 1971; Provine, 1971; Kim, 1994).

An early initiative of the committee was inviting animal breeders and horticulturists to submit proposals for investigations on heredity "such as relate to the means whereby new races of plants and animals come into existence, and old ones are modified," for which small sums were available to support. Although now a nurserywoman, Anna Bateson was among those submitting a proposal to study heredity in the Lady Slipper orchid, *Cypripedium*. Weldon mentioned Anna's application in a letter to Bateson, saying: "The scheme of your sister's is worth twenty programmes." Although funding was apparently granted, it is not clear whether Anna ever carried out the project (Cock, 1979, 62).

By January 1900, the growing animosity between the biometricians and Bateson came to a head. As a result, Galton, Pearson, and Weldon all resigned from the committee, and Bateson took over as secretary. He took this opportunity to redirect the committee's mission to reflect his own approach. Funding from the Royal Society allowed Bateson and Saunders to expand their experimental work, even if they continued primarily to rely on domestic resources (Richmond 2006). The Society also eventually supported the publication of their findings, although not without considerable debate (B. Bateson, 1928, 60-61).

Using the small grant from the Royal Society to procure a larger plot of land and some assistance, in the growing season of 1897-1898, Saunders thus began a study of inheritance in four new species, all of which exhibited alternate characters. This included: (1) *Matthiola*, the common garden stock, whose hairy and glabrous forms offered "excellent material for statistical experiments upon cross-breeding;" (2) *Lychnis*, which exhibited hairy and glabrous varieties as well as differently colored flowers; (3) varieties of *Atropa* with contrasting flower and fruit colors; and (4) *Datura* varieties in which the fruits borne were either prickly or smooth. By the beginning of the third growing season (1899-1900), Saunders had accumulated sufficient data to conclude that this study supported Bateson's views concerning discontinuous inheritance, but she did not yet feel enough advanced to publish a full account, which indeed was not forthcoming until 1902.

During these years Bateson also carried out breeding experiments in plants and animals. In 1895 he began crossing butterflies and in 1898 initiated extensive cross-breeding experiments in poultry (Bateson, 1897, 1898a, and 1898b; see also Olby, 1985, 125; Cock, 1971, 29-34).[5] However, he encountered technical problems in crossing butterflies and was generally not as successful as Saunders in finding support for his views of discontinuity. He found it hard to interpret his results, which appeared "irregular and puzzling" (Cock, 1971, 6). In the end, he did not publish any of the results of this work until after he learned about Mendel's experiments in hybridization (Bateson, 1902b).

Some understanding of the conceptual basis of Bateson's and Saunders's early research program comes from general remarks he made in several papers published before May 1900. In a paper of 1897, for example, Bateson briefly noted Saunders's preliminary findings, stating that her experiments indicated that "the two characters of smoothness and hairiness do not completely blend, and the offspring do not regress to one mean form, but to two distinct forms. The variety, in short, is not 'swamped by intercrossing'" (Bateson, 1897, in Bateson 1928, 1: 354). In July 1899, in a paper presented at the first international conference on plant hybridization organized by the Royal Horticultural Society, he again referred to Saunders's work. In this oft-cited paper, "Hybridisation and Cross-Breeding as a Method of Scientific Investigation," Bateson described in detail the nature of the investigations he and Saunders were pursuing. He presented a brief synopsis of his views about variation, admitting that "we are far from knowing which kinds of variations may thus be definite and palpable, and which are not." To gain such answers, more extensive data was needed, and he implored practical breeders, and "especially the cross-breeder of plants or of animals," to help provide "first-hand evidence as the *magnitude of variations*." The question of the day, in his view, was "Why do not nascent varieties become obliterated by crossing with the type form?" This required crossing a variety "with its *nearest allies*" and recording "how many of the offspring resembled each parent and how many shewed characters intermediate between those of the parents" (Bateson, 1899, 60-61, 63). This, in short, was precisely the approach he and Saunders were using.

This paper is frequently cited because it presents a vivid statement of Bateson and Saunders's research program just prior to his reading Mendel's 1865 paper. Some earlier historians have interpreted Bateson's statements as anticipating Mendel's experimental approach (see Cock, 1971). Yet, it is clear, judging by the work he had pursued since 1890, that this is mistaken. Both in terms of methodology and conceptualization, Bateson and Saunders were far removed from the approach Mendel brought to his hybridization studies. To be sure, like Mendel Bateson and Saunders crossed forms exhibiting alternative characters and recorded how many of the offspring

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5 See Bateson, 1898, which includes a description of his experimental set-up for butterfly breeding: "We had the pleasure of seeing Mr Bateson's garden in which these experiments are carried out, and admired the simplicity and completeness of the arrangement for these experiments. He finds no difficulty in getting the butterflies to pair and oviposit. The apparatus consists of a box placed in the garden, open to the weather, and covered with gauze. The box is about 30" x 18", and contains a supply of flowers in a glass and of the food-plant growing in a pot. Some shade is provided by a partial covering of canvas thrown loosely over. Mr Bateson has long ranges of these boxes and of pots of the food-plants to which the insects may be removed and on which they are sleeved after oviposition has been completed." A notebook containing records of Bateson's crosses of moths and butterflies is in the Bateson Collection, John Innes Centre, Norwich.

resembled one or the other parent and how many showed characters intermediate between the two. However, they generally did not know the ancestry of the parental generation, and they seldom bred an F_2 generation. Saunders, for example, only did so in *Lychnis*, repeating experiments made by Hugo de Vries. In an F_1 cross between hairy and smooth leaved plants that produced all hairy progeny, the offspring were "backcrossed" with the smooth parent, producing an F_2, "of which some were hairy and others smooth" (Bateson, 1899, 64-65). Neither she nor Bateson generally carried out reciprocal crosses. This largely was because Bateson was operating with a working hypothesis that "in-breeding may have a specific effect in modifying the power of transmitting parental character to offspring" (Bateson and Saunders, 1902a, 3; see also Olby, 1987, 412-13; Cock, 1971, 6). The differences between their work and Mendel's systematic approach could not be starker.

With regard to data collection, Bateson and Saunders recorded the results of their hybrid crosses, but only to note whether the parental character persisted in the offspring or was blended. This reflected the ultimate goal of their research, described by Bateson in 1899:

> How did the one form separate from the other? By crossing the two forms together and studying the phenomena of inheritance, as manifested by the cross-bred offspring, we may hope to obtain an important light on the origin of the distinctness of the parents, and the causes which operate to maintain that distinctness. (Bateson, 1899, 63)

Thus, they solely focused on tracing the inheritance of parental discontinuous characters in the offspring. This explains the small number of crosses made and paucity of data collected in comparison with Mendel. Indeed, Bateson downplayed the amount of data required, telling breeders that only "rough statistics" were needed: "All that is really necessary is that *some* approximate numerical statement of the result should be kept," he noted, and just "a few words" might suffice to describe the outcome of a cross (Ibid.).

The generally qualitative character of their work is particularly apparent in Bateson's discussion of Saunders's results in *Biscutella*. In mentioning the "well-marked discontinuity between the two varieties," Bateson referred to the difference between "the nature of the relationship of the two forms to each other," explaining in a footnote his use of the term *relationship*: "It is used to denote not simply the blood-relationship of the forms to each other, but those physiological relations subsisting between them which are manifested by experimental crossing. The word is thus used in a sense similar to that which it bears when we speak of the chemical relations of one substance to another" (Ibid., 64n.). He spoke of the "transmitting powers" of diverse varieties being unequal, noting that "in each the mechanism of inheritance works differently." Yet he recognized that if "tested by the method of breeding and by study of the transmitting powers, the relation of varieties and species would be shewn in an entirely new light" (Bateson, 1900, 55). Unlike Mendel, Bateson could discern no pattern in his results, let alone any indication of the physical basis of heredity. In short, Bateson and Saunders continued to work within the same hybridizing tradition that Darwin pursued (Olby, 1985; Bartley, 1992). Hence it is clear that despite some tantalizing resemblance, both Bateson's and Saunders's experimental design and interpretation of results were a far cry from the focused experimental analysis developed by Mendel (Balen, 1986, 181). After five years of work, then, neither Bateson nor

Saunders could discern any general patterns to describe the results of their crosses. A. G. Cock described the situation facing Bateson in 1900 as follows: "he had to some extent reached an impasse as far as any explanation of his experimental results was concerned, an impasse which was resolved when he came to learn of Mendel" (Cock, 1971, 7).

Robert Olby has painstakingly and convincingly reconstructed a chronology of the critical events in the spring of 1900. Bateson apparently first read Hugo de Vries's April 1900 paper in French on the "law of the disjunction of hybrids" on 8 May 1900, while on the train to London to read a paper to the Royal Horticultural Society. But he only learned about Gregor Mendel's 1866 paper on the laws of heredity after reading de Vries's subsequent paper published a month later that was directed at German botanists (de Vries, 1900a, 1900b; Olby, 1987). He presumably read the papers of Carl Correns and Erik von Tschermak shortly afterwards (Correns, 1900; Tschermak, 1900). Certainly, it is easy, given Bateson's and Saunders's previous inability to recognize any law-like patterns in their own crosses, to understand the incredible impact these works must have had on them. Having long attempted to gather evidence in support of the hypothesis of discontinuous variation, de Vries's proposal of a "law of disjunction," based on a modification of Darwin's hypothesis of pangenesis, must have been very interesting indeed. Describing crosses between parents distinguished by a single character, de Vries noted that there was no possibility of the progeny evidencing blending heredity because "l'hybride ne saurait tenir le milieu entre eux; car le caractère simple doit être considéré comme une unité non divisible" (the hybrid would not be able to blend, because the simple character must be considered as an indivisible unit) (de Vries, 1900a). Mendel's paper, however, as Olby has noted, provided "the key he needed. It gave a causal explanation for the production of variation which was independent of the environment; it showed how hereditary differences were separated from hybrid mixture because of the purity of the germ cells. The theory offered an algorithm with which to predict the outcome of experiments in crossing" (Olby, 2004). It provided, in short, both the critical conceptual principles and method of analysis that Bateson and Saunders had long been seeking.

There was also another aspect of this flurry of papers that engaged Bateson and Saunders. The data de Vries and Correns presented were based on many of the same species they were studying, namely, *Veronica, Lychnis, Datura, Stramonium*, and *Matthiola.* Not only did these papers provide critical conceptual keys to aid in the interpretation of their findings, but they also may have triggered a desire to publish their own data as soon as possible, given that neither Bateson nor Saunders had as yet published full accounts of their work of the past five years.

The Impact of Mendel

The extent to which the "rediscovery" of Mendel's work prompted a radical reorientation in Bateson and Saunders's research program can readily be gauged from noting the change in tenor and substance between his previous pronouncements and the published version of Bateson's May 1900 paper to the Royal Horticultural Society. He began with the bold statement: "An exact determination of the laws of heredity will probably work more change in man's outlook on the world, and in his power over nature, than any other advance in natural knowledge that can be foreseen," followed by the confident assertion that "these laws can be determined." Repeating a call to horticulturists to conduct controlled breeding experiments, Bateson spoke of the effort to

discover a law of heredity as of great practical importance in helping to predict "the degree with which the purity of a strain may be increased by selection in each successive generation." He mentioned Galton's well-known work on this problem, but noted that Galton's law of ancestral heredity did not apply to cases like those he and Saunders considered, in which "on crossing two varieties the character of one variety is almost always transmitted to the first generation," or those in which "the characters of one variety very largely, though not exclusively, predominate in the offspring," and thus could not be regarded as a general law of heredity. This was little changed from earlier presentations.

It was in this context, however, that Bateson mentioned de Vries's recent "brief account" of his study of variation (citing, in the footnote, both the French and German texts) and pointed out the essential aspects of this work: "The cases are all examples of discontinuous variation: that is to say, cases in which actual intermediates between the parent forms are not usually produced on crossing. It is shown that the subsequent posterity obtained by self-fertilising these cross-breds or hybrids *break up into the original parent according to fixed numerical rule*" (Bateson, 1900, 57; my emphasis). Bateson then referred to Mendel's work, calling his account "excellent and complete" and stating that "the principles which he is able to deduce from them will certainly play a conspicuous part in all future discussions of evolutionary problems." He drew attention to Mendel's use of *dominant* to refer to the prevailing character, and *recessive* to the other, which avoided "the complications involved by use of the expression 'prepotent.'" There could be no doubt, Bateson claimed, that "Mendel's law is a substantial reality": already his findings had been confirmed by de Vries, Correns, and Tschermak. It is clear, he concluded, that "we are in the presence of a new principle of the highest importance." Moreover, the "facts of crossing prove that each ovule and each pollen grain is pure in respect of each character to which the law applies." The direction of future work was thus set: Mendel's "hypothesis of perfect purity in the reproductive cells" required validation and "the subjects of experiment should be chosen in such a way as to bring the laws of heredity to a real test." (Bateson, 1900, 57, 59, 60).

Bateson and Saunders were ideally situated to do just that: they immediately embarked on revising their pre-1900 experimental design to reflect the new orientation of the Mendelian laws and methodology (Cock, 1971, 4-7). By October 1900, they were well under way, having identified new problems as well as reinterpreted their previous data in order to test the general validity and extent of Mendelian heredity.[6] The era of Mendelism had begun.

The earliest publications of Bateson and Saunders after the rediscovery of Mendel well reveal the contrast between their pre- and their post-Mendelian research. These include the co-authored first part of the five-part series (1902-1909) entitled *Reports to the Evolution Committee of the Royal Society* (submitted in December 1901, with additions dated March 1902), and Bateson's *Mendel's Principles of Heredity: A Defense* (preface dated March 1902), which was written in consultation with Saunders.

In the introductory essay to the *Report* entitled "Experimental Studies in the Physiology of Heredity," Bateson and Saunders described their research program investigating discontinuous

[6] That this is true comes from the statement: "After the re-discovery of Mendel's work it seemed desirable to use varieties differing in a pollen-character. Searching for such forms, it was found in October, 1900, that the Sweet Pea, Emily Henderson (referred to as E. H.), a pure white var., usually has pollen distinct from that of normal vars." See Bateson, Saunders, and Punnett, 1905, 80.

characters and the effect of inbreeding "in modifying the power of transmitting parental character to offspring." Since beginning this study in 1895, they noted, "the whole problem of heredity has undergone a complete revolution," and the evidence they had collected on prepotency, the long-held belief that in hybrid crosses one race (generally the "older") would stamp its character on the progeny, "is now capable of different interpretations, and it is clear that to obtain a definite result on this point, a new set of precautions must be used." In the wake of Mendel, Bateson now recognized that prepotency could be interpreted as a consequence of dominance, and reversion—the reappearance of ancestral traits—as the recurrence of latent characters. Although admitting that their investigations were not as yet sufficiently advanced, the authors stated that "we feel that with the re-discovery and confirmation of the principle which will henceforth be known as Mendel's Law, the study of heredity and the cognate problems of evolution must enter a new phase" (Bateson and Saunders, 1902a, 3, 4-5, 5). They could wait no longer to publicize their findings.

After laying out Mendel's basic principles and noting the confirmation provided by de Vries, Correns, and Tschermak, they concluded that "the truth of the law enunciated by Mendel is now established for a large number of cases of most dissimilar characters, beyond question." The key element of Mendel's law in their view was the following: "The essential part of the discovery is the evidence that *the germ-cells or gametes produced by cross-bred organisms may in respect of given characters be of the pure parental types and consequently incapable of transmitting the opposite character*," such that "*there may be, in short, perfect or almost perfect discontinuity between these germs in respect of one of each pair of opposite characters.*" (Ibid., 11, 12; italics in original). This statement is remarkable given that previously neither had ever discussed the cellular basis of heredity, not even, as Brooks had done, referencing the hypothesis of pangenesis. But conceptualizing discontinuous variation as a "variation in kind" easily permitted them to associate the "physiological relations subsisting between them [two discontinuous varieties] which are manifested by experimental crossing" that Bateson spoke of in 1899 with qualitatively different characters in "the germ-cells or gametes" that Mendel proposed.

As Lindley Darden has noted, "That Bateson immediately saw the conceptions as important indicates that they had connections with approaches and problems he had already formulated. That Bateson called them new indicates they differed from some of the conceptions he had held previously. Thus both continuity with old problems and change from old conceptions occurred with Bateson's adoption of the Mendelian approach" (Darden, 1977, 89). Several statements in the separate pieces that make up the first *Reports to the Evolution Committee* support this, indicating the ways in which Bateson and Saunders's previous work differed from the approach taken by Mendel. In the general section discussing "The Facts of Heredity in the Light of Mendel's Discovery," they noted how many earlier breeding experiments now "must be re-stated in terms of Mendel's hypothesis," noting that it "would be a useful task to go similarly through the literature of breeding and translate the results into Mendelian terms. Such an exercise would show that the change which must now come over the conceptions of biology can only be compared with that which in the study of physical science followed the revelations of modern chemistry" (Bateson and Saunders, 1902b, 125). This was particularly true of their own work.

In terms of change to their experimental design, after describing Mendel's use of back-crosses ("crossing the first crosses with pure D and pure R forms respectively"), they noted that in their crosses, "almost all our breedings of cross-breds with pure types have been in the form cross-bred ♀ x pure ♂, but reciprocal experiments are in progress" (Ibid., 10n.) In discussing her botanical experiments, especially comparing her 1897 paper on *Biscutella* with the 1902 account of subsequent crosses, Saunders's noted she had not controlled for the purity of parent plants, and those they originally believed showed complete dominance may have included cross-breeds carrying both a dominant and recessive trait (that is, a heterozygote) (Saunders, 1902, 22). Also, she had not always been careful to prevent unwanted cross-fertilization through the agency of insect pollination. Yet despite these lapses, she believed her results did "follow Mendel's law with considerable accuracy, and no exceptions that do not appear to be merely fortuitous were discovered" (Ibid., 44).

In hybrid crosses between *Lychnis vespertina* (white flowers; hairy) and *L. diurna* (red flowers; glabrous), for example, Saunders recalculated the proportion of hairy (dominant) to glabrous (recessive) in the F_2 generation as 3.2:1 (rather than the expected 3:1). The same was true for *Atropa* (color of fruit) and *Datura* (two pairs of characters: smooth or prickly fruit; white or violet flowers). She included a series of tables to present the data, revising the earlier tabulation appearing in the 1897 paper into categories that reflected Mendelian modes of analysis. (See, for example, Figures 2 and 3, providing data for *Lychnis* crosses.)

Table I.—First Cross-bred Generation obtained by crossing the Hairy and Glabrous Forms in each of the eight possible ways.

Parentage.*	Number of seed parents.	Number of flowers.	Number of offspring.	
			Hairy.	Glabrous.
WG × WH.....	5	6	91	
WG × RH.....	2	3	63	
RG × RH.....	4	6	133	
RG × WH.....	1	4	126	
WH × WG.....	4	12	100	
WH × RG.....	1	1	3	
RH × RG.....	3	11	208	
RH × WG.....	2	9	282	
Total.....	Individuals used more than once.	52	1006	0

* Throughout the paper expressions in the form A × B indicate that A is the seed parent and B the pollen parent.

Figure 2. Table from Saunders, 1902, p. 16.

In *Matthiola*, however, the situation was not as clear-cut as in the other genera, for "the phenomena are much more complex." She initially set out to follow only one character—leaf surface (hoary or glabrous)—using five different types or races. However, she "found that the results differed widely according to the variety, and occasionally according to the individual, with

which the crosses were made," so she expanded her analysis to include other characters as well, including seed color, flower color (white, cream, red, pinkish white, bluish pink), and time of flowering. While several simple cases did appear to "follow Mendelian principles," others did not. For example, she found that hoariness was not always dominant, as expected. In fact, even after considerable effort to come up with a system to present her results, they remained "complicated and difficult to follow" (Ibid., 15, 32). These seemingly aberrant cases required further analysis and indeed continued to occupy Saunders for the next few years.

Table II.—Offspring of Cross-breds when fertilised *inter se*.*

Parentage.	Number of seed parents.	Number of flowers.	Number of offspring.		Totals for each particular kind of union.	
			Hairy.	Glabrous.	Hairy.	Glabrous.
(RH × RG) × (RH × RG)	1 1	2 1	17 82	6 21	99	27
(RH × WG) × (RH × WG).....	1 1	1 1	31 11	12 4	42	16
(RG × RH) × (RG × RH).....	1 1 1	2 1 2	47 62 28	17 14 10	137	41
(RG × WH) × (RG × WH)	1	1	59	14	59	14
(WG × WH) × (WG × WH).....	1 1	1 2	15 37 7	6 16 2	59	24
(WG × RH) × (WG × RH).....	1	1	12	4	12	4
Total	..	..	..	..	408	126
Expected result, 3 : 1; actual result, 3·2 : 1						

* As all the forms employed are dicœcious, fertilisation of the cross-breds *inter se* is necessary where the alternative of self-fertilisation would be possible with hermaphrodite types.

Figure 3. Table from Saunders, 1902, p. 17.

With respect to Bateson, it is interesting to contrast the account he provided of the importance of Mendel's work in 1900 with the revision of this paper included in *Mendel's Principles of Heredity*. This well indicates the rapid conceptual and methodological transformation that he was experiencing by virtue of translating his previous views on variation into a new Mendelian mode of analysis. This contrast was sharpened by the need for him to clarify and "defend" the tenets of Mendelism in the wake of the attack launched by Weldon in the second number of the new journal *Biometrika*, published in January 1902. Weldon downplayed the various accounts of the Mendelian 3:1 ratio of dominants to recessives by pointing to deviations from the expected ratio and claiming these were not simply accidental but indicated the additional operation of ancestral inheritance, not just parental. As he put it, "the degree to which a parental character affects

offspring depends not only upon its development in the individual parent, but on its degree of development in the ancestors of that parent" (Weldon, 1902a, 244, 251). This paper prompted Bateson to respond, drafting *Mendel's Principles of Heredity—A Defense* in only a month.

The most significant modification Bateson made to the text of his earlier paper of 1900, announcing Mendel's laws to the English-speaking public, was an illustration of the union of distinct pairs of characters in a cross between varieties differing in two characters—that is, a dihybrid cross. This material was not included in *Reports to the Evolution Committee*, and hence must have been added in February or March 1902. For this reason, his description is presented in its entirety below:

> Mendel made further experiments with *Pisum sativum*, crossing pairs of varieties which differed from each other in *two* characters, and the results, though necessarily much more complex, showed that the law exhibited in the simpler case of pairs differing in respect of one character operated here also.
>
> In the case of the union of varieties *AB* and *ab* differing in two distinct pairs of characters, *A* and *a, B* and *b*, of which *A* and *B* are dominant, *a* and *b* recessive, Mendel found that in the first cross-bred generation there was only *one* class of offspring, really *AaBb*.
>
> But by reason of the dominance of one character of each pair these first crosses were hardly if at all distinguishable from *AB*.
>
> By letting these *AaBb*'s fertilise themselves, only *four* classes of offspring seemed to be produced, namely,
>
> *AB* showing both dominant characters.
>
> *Ab* showing dominant *A* and recessive *b*.
>
> *aB* showing recessive *a* and dominant *B*.
>
> *ab* showing both recessive characters *a* and *b*.
>
> The numerical ratio in which these classes appeared were also regular and approached the ratio:
>
> 9 *AB* : 3*Ab* : 3*aB* : 1*ab*.
>
> But on cultivating these plants and allowing them to fertilise themselves it was found that the members of the
>
> Ratios
>
> 1 *ab* class produce only *ab*'s.
>
> {1 *aB* class may produce either all *aB*'s,
>
> 3 {2 *or* both *aB*'s and *ab*'s

Ratios

	{1	*Ab* class may produce either all *Ab*'s,
3	{2	*or* both *Ab*'s and *ab*'s
	{1	*AB* class may produce either all *AB*'s,
9	{2	*or* both *AB*'s and *Ab*'s
	{2	*or* both *AB*'s and *aB*'s
	{4	*or* all four possible classes again, namely,
		AB's, *Ab*'s, *aB*'s, and *ab*'s,

and the average number of members of each class will approach the ratio 1 : 3 : 3 : 9 as indicated above. (Bateson, 1902a, 11-12.)

Although this material looks elemental to anyone familiar with Mendelian genetics, it was a novel presentation for those just being introduced to Mendel and different from that in Mendel's 1866 paper. Bateson's formulation provided a clear presentation of the essence of Mendel's hypothesis of the "purity of the germ cells" and the law of segregation—the key features that provided solid theoretical grounding for Bateson's conception of discontinuous variation. Together with the subsidiary assumption of dominant and recessive characters, an explanation was provided for the regular, proportional appearance of parental characters in hybrid offspring, the "blending" of characters in the "heterozygote," and the reappearance of apparently long lost characters, not because of a "reversion" to ancestral traits but because of the reappearance of latent recessive factors. Mendel, in short, provided an explanation for many of the phenomena Bateson had been grappling with for over a decade.

Bateson's development of a schematized representation of Mendel's principles may also have come in response to a table Weldon included in his criticism of Mendel that presented all the possible combinations of characters in hybrid crosses along with their frequency (Weldon, 1902a, 235).

From this analysis, Weldon concluded that Mendel's 9 : 3 : 3 : 1 ratio was an approximation that held only in certain crosses. This was because, he maintained, the "degree to which a parental character affects offspring depends not only upon its development in the individual parent, but on its degree of development in the ancestors of that parent." Hence, since the "law of segregation, like the law of dominance, appears therefore to hold only for races of particular ancestry," Mendel's laws could not be considered to be general laws of heredity (Weldon, 1902a, 244, 251). It is possible that Bateson's presentation of a "mathematized" schema to illustrate Mendel's analysis of hybrid crosses was calculated to neutralize this challenge by Weldon.

Scholars have pointed to the positive as well as negative aspects of the ensuing biometrical-Mendelian controversy that resulted in a series of vociferous public exchanges after 1902 (Nordman, 1992, 68). It seems clear that Weldon's consistent, targeted, and clever criticism of Mendelian terminology, experimental design, and data analysis forced Bateson and Saunders to

think more critically about, and thus sharpen their elaboration of, Mendelian phenomena. For example, Weldon's second major challenge, published in *Biometrika* in November 1902 and entitled "On the Ambiguities of Mendel's Categories," successfully identified Bateson and Saunders' "Achilles heel"; he charged that the criteria both used to characterize "intermediates" in their first *Report to the Evolution Committee* were highly subjective. As he noted: "The confusion between resemblance to a race and resemblance to an individual involved in Mr Bateson's treatment of Mendel's work is one of the many unfortunate results which follow when Mendel's system of dividing a set of variable characters into two categories, and of using these categories as statistical units, is carried too far" (Weldon, 1902b, 44-5, 46). After Bateson and Saunders began to attract more followers to the Mendelian fold in subsequent years, the biometricians' continuing criticism of their research program was difficult to deal with, but it nonetheless forced them to think carefully about their experimental design and interpretation.

Conclusion

William Bateson holds an ambivalent place in the history of early genetics. On the one hand, he is lauded as the champion of Mendel in the English-speaking world, the founder of one of the most important research programs in the first decade of Mendelism, and the founding father of the science of "genetics." After 1910, with the rise of the Morgan school's chromosome theory of heredity, he again became somewhat marginalized owing to his long-time refusal to accept the chromosomes as the seat of the Mendelian factors or "genes." However, both of these stages in his career become more understandable when one juxtaposes them against the earlier period of the 1890s. As we have seen, Bateson came to Mendelism with well developed conceptions about the physical basis of variation (both discontinuous and gradualistic), the limited role of natural selection, and the saltatory nature of evolutionary change. He was not prone to think in terms of particulate heredity, but rather envisioned physical forces and different chemical combinations as effecting changes in organic matter. His ideas seem to have been greatly influenced by Brooks's view of heredity and development, and hence to be intimately linked to late nineteenth-century concepts. The rediscovery of Mendel crystallized previously inchoate conceptions he held about the "physiology of heredity," but his understanding of Mendel was superimposed on existing conceptual categorizations. Such a perspective helps us better understand both Bateson's early Mendelism and later seeming conservatism with regard to genes and chromosomes.

Contrasting Bateson's approach to variation in the 1890s with that after 1900 reveals the tremendous transformation in thought wrought by Mendel's work. While Bateson's earlier study led him along paths similar to the ones Mendel followed, it seems clear that he would have continued to flounder had he not been introduced to Mendel's mode of analysis. Identifying the working hypotheses that fueled his early problematic also highlight differences in his understanding of Mendelism and that of other early Mendelians, especially de Vries and Correns. Ultimately, their conceptualization of variation and heredity prior to learning of Mendel's work shaped their subsequent Mendelian interpretations (Stamhuis, 1996, 2005; Saha, 1984; Rheinberger, 1995).

Bateson's research program was rightly considered unorthodox and even heretical to neo-Darwinians and evolutionary morphologists alike. Even before Mendel's rediscovery, he forced British biologists to confront two opposing approaches to heredity, the biometricians' ancestrian view of heredity based on Galton's law of heredity and his own rival understanding grounded in a qualitative, physiological approach to variation. But there was more to their dispute than simply intellectual property rights. At a time of scarce resources to support the increasingly experimental work in biology, these men were also competing for authority and patronage within the scientific establishment of late Victorian Britain (Farrall, 1975; Sapp, 1987; Marie, 2004). Bateson was fortunate in being able to tap a major new resource within the scientific workforce: the talented pool of women among the first generation to gain university training in the life sciences (Richmond, 1997; 2001; 2006). This gave him a significant edge.

On a personal level, contrasting Bateson's pre- and post-Mendelian work better illuminates radical revisions in his architecture of knowledge, which, in turn, provoked major changes in technical procedures, with the new "Mendelian" regime provoking the adoption of different standards of experimental design and control. This resulted in a new means of presenting data, of analyzing crosses mathematically rather than qualitatively, and application of the new "laws" of heredity to understanding variation. Thus Bateson's former notion of discontinuous variation produced by physical forces or chemical combinations became refashioned into a new Mendelian knowledge regime. Old concepts were translated into new ones: alternative characters became *allelomorphs,* parental traits were either *dominant* or *recessive,* reversion resulted from the reappearance of latent recessive factors, and swamping balanced by the purity of the gametes. In short, Bateson's previous study of the physiology of heredity was refashioned into the new field of genetics. Contrasting Bateson's pre- and post-Mendelian work thus explains how a previously marginal line of work could be transformed into a vigorous research program that emerged as the leading approach to heredity in the decade before the introduction of the chromosome theory of heredity.

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Genetics Without Genes: Blakeslee, Datura, and "Chromosomal Mutations"

Luis Campos

"Now that Shull has left us to go to Princeton I fear the oenothera work will suffer," Charles Davenport, director of the Cold Spring Harbor Station for Experimental Evolution, wrote to Hugo de Vries in 1916. "Still I think that Dr. Blakeslee will keep up with some of it and I hope the opportunity will arise for us to have a man who shall devote a good share of his time to the oenothera. I have not forgotten that in your opening address at this Station in 1904 you recommended this plant especially to our care."[1] Various cytological investigators had struggled for years and would continue to struggle to come to grips with *Oenothera*'s "normal" karyokinetic idiosyncrasies and the sheer complexity of the phenomena it presented (including, at various points, Davis, Renner, Gates, and Cleland). It wasn't until Albert F. Blakeslee's early work at the Station, however, and his even more focused studies on his own chosen model organism, the jimsonweed *Datura*—that these chromosomal shenanigans began to shed light beyond cytogenetics onto the nature of evolution itself. Blakeslee's studies of the jimsonweed and his attention to its *chromosomal* dynamics thus highlight an otherwise largely forgotten early genetical study of the production of non-genic hereditary differences—a "genetics without genes," as it were. Long before the "genetical systems" and other pathbreaking work of C. D. Darlington and later investigators, Blakeslee's work in the 1920s relating mutations to differences in chromosomal number and arrangement provides a compelling example within the history of genetics of how the unstable meaning of mutation (the discovery of viable non-genic alterations in the hereditary material), and the choice of a particular model organism kept "heredity" and "genes"—at least for a time—from any easy and instant equation with each other.

Albert F. Blakeslee

Having begun his botanical career at Harvard under the mycologist Thaxter in 1904, Albert Francis Blakeslee ("Bert") first encountered de Vries' mutation theory while teaching at the Connecticut Agricultural College in Storrs. As he recalled in an autobiographical account, it was in 1909 that he first had "the thrill" of reading de Vries' theory: "[I] thought that if I scoured the country I too might be able to find a species in the process of mutation."[2] The mutation-theory was at the core of Blakeslee's interest in genetics, and both its promise and its unanswered questions sparked his imagination on more than one occasion: "I have always felt that the Mutation Theory was a strong factor in turning my interests and research toward genetics," Blakeslee later remembered. His interest in de Vries' theory remained strong for the rest of his life.[3] Even as late as 1949, Blakeslee continued to say that de Vries was "perhaps the greatest biologist of all time" and that "[t]he mutation theory is one of the corner stones of genetic research."[4]

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1 Davenport to de Vries, March 2, 1916.
2 Blakeslee to de Vries, January 16, 1933.

Blakeslee began to search for possible organisms on which to conduct his research. At first he thought he had found a suitable choice with the yellow daisy known as the Black-eyed Susan (*Rudbeckia hirta*), but he was soon forced to move on to another choice when the daisy proved to be self-sterile and too "reduced in vigor" after two or three crosses to withstand generations of inbreeding—not to mention the generations of inbreeding required for proper detailed research.[5] It was around 1909, while at Storrs, that Blakeslee received from the United States Department of Agriculture "a batch of seeds of *Datura stramonium* as an example of an economic weed." The seed "happened to give both purple- and white-flowered seedling," Blakeslee recalled, "and for several years this species was used to demonstrate Mendel's laws of inheritance," in his teaching.[6] (According to Edmund Sinnott, Blakeslee offered what was "probably the first organized course in genetics in the United States" in 1914-1915.)[7]

On leave from Storrs during the 1912-13 year, Blakeslee went to work at Cold Spring Harbor before finally joining the staff there as a resident investigator in genetics in 1915, replacing the departing Shull. Having devoted considerable attention to genetics in his botany work, it was only natural that he chose to bring his work on the "coarse, weedy plant with its beautiful flowers" with him when he moved.[8] Blakeslee was on the hunt not only for the "the best possible 'Versuchstier,'" as he put it, but for the best possible means to do research with it. Now able to work full-time on genetical problems with better facilities at his command, Blakeslee would over the course of the next 27 years make extensive use of six greenhouses and various agricultural test fields, and ran experiments on a grand scale.

Blakeslee had been drawn to the jimson weed for a variety of reasons including its hardy toughness, the ease with which it could be grown, and the fact that four generations could be grown per year in greenhouse environments. "At first," Blakeslee recalled, echoing newly emerging concerns with *Oenothera,* his own choice *Datura* "seemed to have too many chromosomes, but we kept at it as a side problem since it was so easy to work with." [9] The decision paid off. Blakeslee's assistant, B. T. Avery, found the first novel type in *Datura*—the so-called "Globe" mutant—in the summer of 1915.[10] As he later reported: "The Globe mutant differs from

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3 On the occasion of de Vries' 85th birthday, Blakeslee wrote to de Vries saying "It is a pleasure to have known such a founder of modern genetics who has been an inspiration to my own work" (Blakeslee to de Vries, May 24, 1933). And in a letter to de Vries' wife, Blakeslee recalled: "at the quarter centennial of the founding of the Brooklyn Botanic Garden I pointed out an instance of his wonderful prevision in suggesting in 1904, in an address at the dedication of our Department here, that attempts be made to induce mutations by the use of X-rays and radium. My own researches owe much to him. In a measure, I feel that I have been carrying on the torch which he has laid down." Blakeslee to Mrs. de Vries, May 23, 1935.

4 Blakeslee, "Seventy-Five Years of Progress in Genetics," This lecture, delivered on November 10, 1949, was "one of a series on Development in Some Fields of Science; organized in connection with the 75th anniversary of the founding of Smith College by Sophia Smith."

5 *Ibid.,* p. 4; *cf.* Blakeslee to de Vries, April 7, 1933.

6 Blakeslee, "Lebenslauf," p. 5; *cf.* obituary by Edmund W. Sinnott, 1955.

7 Sinnott, 1955.

8 *Ibid.*

9 Blakeslee, "Lebenslauf," p. 6. Though not in all respects—as Blakeslee later wrote to a colleague, "some of these species [of *Datura*] give very poor germination—sometimes not over a tenth of one percent." Blakeslee to O. L. Inman, December 11, 1934. Blakeslee was also later interested in animal polyploidy, but found this a considerably more difficult task as animals were, as he characteristically put it, "functionally dioecious." Blakeslee to Emmeline Moore, November 15, 1937.

normals apparently in all parts of the plant. It forms a complex of characters readily recognized whether the plants in question have purple or white flowers, many or few nodes, or spiny or smooth capsules."[11] This was no ordinary genetic mutation like those found in *Drosophila*. True to de Vries' theory, much more than one factor had been affected—the entire plant was different from its ancestor, in a whole suite of traits.

Blakeslee became convinced that he had found a new species, and labeled the original new plant specimen as such ("N.S."), including a photograph of the plant in the 1919 paper reporting the discovery. Although the plant proved sterile with other "normal" plants, it could be self-pollinated successfully and with the appearance of progeny that bred true, producing further generations with "depressed globose capsules," Blakeslee concluded that it "seems to have established itself as a distinct new race."[12] He continued:

> This physiological incompatibility between a mutation and the parent species from which it arose suggests that we have actually been witnessing in our controlled pedigrees the birth of a new species which may be capable of maintaining itself in a mixed population uncontaminated by crossing with its ancestral line. The race is relatively vigorous.[13]

In the caption to the photograph included in the paper, Blakeslee put the point more plainly: "Tests have shown that this mutant differs from all others investigated in that it breeds true as a distinct new race. Here we appear to be witnessing the birth of a new species."[14]

As Blakeslee, Avery, and his other assistants bred the "globe" mutants, they rapidly discovered that still "other types appeared as mutants in our cultures, and *Datura* soon became practically our sole object of investigation."[15] As one observer at the Station recalled:

> One new form after another began to appear in his cultures. Some were gene mutations but many were evidently different. These produced some offspring like themselves but threw many normal plants. For an outsider to recognize these forms was difficult, since most of their differences were subtle ones. It was the despair of his colleagues to see Blakeslee go down a row of plants and pick out these mutants unerringly. This he could do partly because of his acute powers of observation and partly because he was personally familiar with his material and did not leave the observing and recording to his assistants alone… The size of the *Datura* cultures increased and in the summer as many as 70,000 plants were grown. Work was actively carried on in the winter, as well, in the six greenhouses and laboratories.[16]

Blakeslee was even able to identify types that while "indistinguishable in gross appearance from each other," nevertheless, "in respect to a whole series of characteristics [are] strikingly different

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10 Blakeslee, "Lebenslauf," p. 5. According to Sinnott, Blakeslee had encountered "one or two Jimson weeds which were different from the typical ones and had begun to study them," while at Storrs (Sinnott, 1954).
11 Blakeslee 1921.
12 Blakeslee and Avery, 1919.
13 Blakeslee and Avery, 1919.
14 Blakeslee and Avery, 1919. As Blakeslee later recounted in 1921, "It may be mentioned that the tetraploid datura was called 'New Species' before its tetraploid nature was suspected. It satisfied the requirements of an independent species. The pollen was relatively good, and the mutant formed a distinct race, self-fertile and fertile *inter se,* while practically sterile with the parent stock." Blakeslee, "Types," 1921.
15 Blakeslee, "Lebenslauf," p. 6.
16 Sinnott, 1955, pp. 9, 8.

from the normal Jimson Weed from which they have been made up to order, as it were, with definite plan and purpose." Blakeslee eventually found three in particular that he thought "perhaps merit the term of synthesized new 'species,' since they satisfy the criterion of breeding true and are more different from the normal type than some of the species which already have been described in the genus *Datura*."[17] He took these newly encountered mutants to be indicative that they had encountered a situation in *Datura* similar to that which de Vries had encountered in *Oenothera*. A year after his initial discoveries, Blakeslee made further explicit reference to the "increasing rôle in experimental evolution" of the de Vriesian "theory of mutations" that had first been laid forth two decades earlier.

Chromosomes Regnant

Unlike the drosophilists who fairly readily shared their stocks and data across the fly room and with other centers of fly research, Blakeslee "kept strict control" of his *Datura* results.[18] But Blakeslee was nothing if not collaborative: having collected the seeds of ten different species of *Datura* from around the world,[19] he engaged in a series of ongoing collaborative ventures over the years, working with (among others) the geneticist Edmund W. Sinnott, an expert in the internal anatomy of the *Daturas* who could recognize most mutants from tissue sample alone (and who also happened to come from Blakeslee's old stamping grounds in Storrs), and J. T. Buchholz, an expert on "the growth of pollen-tubes and the abortion of ovules as problems in developmental selection."[20]

One of Blakeslee's earliest and ongoing collaborations was with the cytologist John Belling, who had joined Blakeslee's group in 1920 and helped him in his "study of the nuclear condition of our mutants."[21] Blakeslee, Belling, and the greenhouse manager M. E. Farnham published a "preliminary report" of their findings in *Science* in 1920.[22] And it was Belling's cytological work—studying the appearance and behavior of chromosomes—that was later held to have given "the greatest possible assistance in the interpretation of the originally baffling phenomenon of mutation in *Datura*."[23] Indeed, it was largely as a result of this "fruitful association" with Belling—as well as the "development of the aceto-carmine staining method" that permitted chromosomes to be "counted directly in smear preparations"—that Blakeslee was rapidly able to establish that "each mutant was the result not of a gene difference but of a third chromosome added to a particular pair of the twelve in this plant." Such mutants were termed "trisomics" or "$2n+1$" types. More generally, this discovery enabled Blakeslee at last to interpret his results on a *chromosomal* rather than a *genic* basis that would presumably have required the joint mutation of a number of different genes at the same time.[24] Blakeslee's mutant plants differed by a whole "complex of

[17] Blakeslee 1932.
[18] Demerec, 1959.
[19] Sophie Satina, undated.
[20] "Department of Genetics," 1922, p. 95.
[21] Blakeslee, 1922, p. 18.
[22] Blakeslee, Albert F., J. Belling and M. E. Farnham, 1920.
[23] "Department of Genetics," 1921, p. 108.
[24] Demerec, 1959.

characters," that were "transmitted collectively," and that segregated "in a very unusual fashion"—and chromosomal observation and analysis was soon to explain exactly how these phenomena came to pass.

While acknowledging that it was "sudden germinal changes, large or small in amount" that were the basis of "perhaps the most fundamental work in modern genetics," Blakeslee noted that "mutations could not be confined to cells associated with sexual reproduction." In an apparent reference to the remarkably productive and groundbreaking work of the drosophilists and other more gene-oriented investigators, Blakeslee emphasized that botany had already applied the mutation concept in ways that extended far beyond the genes that many animal geneticists were most concerned with. *Somatic mutations,* for instance, were those mutations that took place in cells in which sexual processes were not involved. While fairly "less common phenomena in animals," such somatic mutations—or "bud sports" as they were also frequently called—were common in plants and many were even quite well-known. Such instances of mutation were real, and yet they were clearly beyond the ken and the techniques of the drosophilists—no matter how powerful and innovative these investigators were in identifying and mapping mutant genes. Blakeslee argued that these characteristics, including those whose "inheritance could not be established by breeding experiments," had been and should continue to be called "mutations."[25]

Blakeslee also held, therefore, that his new discoveries of polyploidy, trisomy, and the other phenotypic effects of chromosomal alterations were thus novel additional worthy instances of mutation:

> To us, one of the most interesting features of the *Datura* work is the possibility afforded of analyzing the influence of individual chromosomes upon both the morphology and physiology of the plant *without waiting for gene mutations*… Our work so far we believe adds evidence to the conclusion that the mature organism—plant or animal—is not a structure like a child's house of blocks, made up of separate unit characters, nor is it determined by separate and unrelated unit factors. It is rather the resultant of a whole series of interacting and more or less conflicting forces contained in the individual chromosomes.[26]

Blakeslee fully acknowledged that classical Mendelian research up until this time had "dealt almost exclusively with disomic inheritance." [27] But, he noted, "[d]istinct variations, provisionally termed mutations… [have] regularly recurred whenever a sufficiently large number of plants have been subjected to observation," and that these, "[s]o far as investigated… have been found to be connected with a duplication of one or more of the normal chromosomes."[28] Blakeslee's mutant plants thus revealed that *phenotypically distinct* mutations could result from *genically identical types,* simply with different arrangements or numbers of chromosomes.[29] Mutation could thus

[25] Intriguingly, Blakeslee held that the "failure" of a particular mutation in the adzuki bean "to appear more than once in so large a number of individuals indicates that it is a variation genotypic in nature, since it could scarcely be attributed to the reappearance of a character through normal segregation nor be considered a mere modification induced by environmental factors." The sheer rarity of the mutation was an argument for its genotypic, rather than its chromosomal, basis. Blakeslee, 1919.

[26] Blakeslee, 1922, p. 31. Emphasis added.

[27] Blakeslee, 1922, p. 27.

[28] Blakeslee, 1921, p. 255. Blakeslee later realized, of course, that duplication was not the only means. Following Calvin Bridges' work on nondisjunction, he acknowledged that there was room for a "rather novel study of trisomic, tetrasomic and pentasomic inheritance." Blakeslee, 1922, p. 27.

take place at a level that was neither organismic *nor* genic. A mutation, therefore, did not need to be *genic* in order to be *genetic*.

In short order, Blakeslee and his collaborators, colleagues, and competitors identified many other varieties of "chromosomal mutants" over the years—including reciprocal translocation among trisomics, the existence of haploids in higher plants (theretofore unknown), and even mutants with chromosomes arranged in sets and rings (precisely that phenomenon determined to be responsible for the seemingly endless bedeviling of an earlier generation of investigators of *Oenothera*). While the drosophilists had of course acknowledged the phenomenon of nondisjunction at the microscopic level, it was Blakeslee who connected the dots to the effects at the phenotypic level and brought the effects of trisomy, nondisjunction and other chromosomal phenomena into the realm of possible mechanisms for mutation. As Davenport noted: "it has remained for *Datura* to reveal in the hands of Blakeslee and his associates, Belling, Farnham, and others, an extensive system of inter-chromosomal mutation and corresponding somatic change the like of which had been entirely unknown."[30]

The Meaning of Mutation

The wider community of geneticists and other students of heredity were already well aware that it appeared possible to make a definite distinction between the two kinds of mutation thus far readily observed, and whether chromosomal abnormalities were "mutations" became a matter of debate in the field. Although Shull initially seemed to agree with the designation of chromosomal aberrations as mutations—"You go so far in the solution of the change which brings about the occurrence of the Globe mutants that it seemed to me you were justified in applying the more fundamental term 'mutation' as a title of your contribution"—a week later in 1921 he coined a new word for such chromosomal mutations and tried to get Blakeslee to use it. (The word was "anomozeuxis." As Shull noted, "I feel fairly certain that your first reaction to these words will be unfavorable, but they are words which grow easier to say and pleasanter to look at as you become more familiar with them.")[31]

By traditional observable botanical and morphological criteria, and by the simple fact that they bred true, Blakeslee's plants were clearly mutants and any botanist (as de Vries himself had often remarked) would have classified such new organisms discovered in the field as belonging to a new species. By the standards of the drosophilists and some other geneticists, however, these were clearly not new mutants but merely chromosomal aberrants. And yet, as Blakeslee himself reported, "The pure breeding types are more distinct from the original form from which they arose than some of the species of *Datura* which have been founded on single factor differences. Our types we have ventured to call artificial or synthesized 'new species.'"

In the early 1920s, Blakeslee was fully aware of the polyvalent meaning of "mutation" and of the declining influence of De Vries' theory among biologists of all stripes. Having laid out the

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29 Relating the existence of these chromosomal types to geographic distribution patterns also did much to help illuminate the evolutionary history of *Datura* (Sinnott, 1954, pp. 394-8).
30 "Department of Genetics," 1922, p. 93.
31 Shull to Blakeslee, April 26, 1921.

relevant details—from the drosophilist H. J. Muller's work on balanced lethals in the teens to the importance of the study of the behavior, association, and mechanism of chromosomes and chromosomal duplication and polyploidy—Blakeslee asked in 1921:

> What then is a mutation? I do not feel we need to be bound by its application to the evening primrose for reasons of priority, since Waagen… had previously used the term in paleontology in an entirely different sense. I believe, with the idea that mutations must involve a qualitative change, that we shall ultimately confine the term to mutations of genes, although such mutations may later be shown to be as different from our present conceptions of them as are mutations in the Oenotheras from the conceptions in de Vries's classical publication, 'The Mutation Theory.' It may still be desirable to employ the word *mutation* as a collective term to designate the sudden appearance of any apparent genetic novelty—whatever its real cause—until we know better.[32]

Despite claiming that the fundamental meaning of mutation might ultimately be genic, Blakeslee therefore recommended agnosticism on the matter. His own research program, however, was structured around the idea that chromosomal aberrations were not only an *important* source of variation, but were perhaps even the *fundamental* mechanism for the production and maintenance of many "new species" of mutants plants. In fact, Blakeslee spent almost no time whatsoever discussing genic mutations in his writings, confining his attention to the significance of chromosomal mutations alone. In a 1921 article purporting to address the various "Types of Mutation," Blakeslee discussed some of the many varieties of chromosomal mutation, and concluded by saying:

> There is not time at my disposal to discuss mutations of genes... It has not been possible in this brief presentation to give an extended classification of mutations, nor to discuss in detail their possible significance in evolution. It will be sufficient if I have made clear the distinction which must be kept in mind, in any discussion of the subject, between mutations in individual genes and those brought about by chromosomal aberrations. [33]

In all, Blakeslee's approach represented a distinct modification and reworking of de Vries' theory.[34] Although Blakeslee acknowledged that "[s]trictly speaking I should not call chromosomal aberrations mutations when the changes are purely quantitative"—such as in the case of polyploidy—the accompanying table in his article on "Types of Mutations and Their Possible Significance in Evolution" labeled just these forms precisely in that way.[35] The meaning of mutation for geneticists was unstable, and it was unstable even for Blakeslee himself. He was

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32 Blakeslee, 1921, p. 261.

33 Blakeslee, 1921, pp. 262, 265-6.

34 For a case of tetraploidy, for example, *not* to be considered a mutation was as significant an alteration of de Vries' theory as is conceivable, as de Vries himself considered the origin of the tetraploid *Oenothera gigas* to be "the one absolutely typical case of species-formation in all my cultures." He prefaced his remark by saying: "Please tell Miss Lutz that I enjoyed her discovery of the double number of chromosomes in *Oenothera gigas* immensely" (de Vries to Davenport, December 31, 1907). Blakeslee went on to insist, however, that "[t]he occurrence of tetraploidy would therefore be no more a mutation than the doubling of chromosomes at the origin of the sporophyte from the gametophyte ferns." Blakeslee, 1921, pp. 262-3.

35 Blakeslee, 1921, pp. 262-3.

never *opposed* to gene mutation: he was fully aware of the drosophilists' genocentric focus, and gave their understanding of mutation a certain priority (as he once said: "We have seen that chromosomal duplications and related phenomena may simulate gene mutations in their effects upon the individual.") And yet, in his reworking of de Vries' theory, Blakeslee's focus always resolutely remained on understanding the significance of what he called alternately "chromosomal mutations" and "chromosomal aberrations": "What is their possible significance in evolution?"

Blakeslee and Gager

Blakeslee laid out the problem: if plant mutants were due to alterations in chromosomes and not just in genes, then "it should be possible by breeding tests to connect up mutants with as many chromosome sets as there are known Mendelian factors, or factor groups." This, however, was not readily the case, as there were unusual situations (such as various forms of chromosome duplication) where these varied effects also needed to be taken into account. The discovery of what were termed "balanced" and "unbalanced" types—that is, mutative variants with all paired chromosomes, and types where an additional chromosome was left unpaired—provided for a new means of exploring the influence of general mutation. In effect, Blakeslee argued, it meant there was now a means to avoid having to depend on the random appearance of mutations in a population:

> The unbalanced condition gives us an opportunity, never before realized, of analyzing the influence of individual chromosomes without waiting for the appearance of gene mutations. Heretofore, the number of factors determined in the chromosomes has been dependent upon the number of mutated genes available for crossing with the normal type. In the jimsons, however, we may study the sum total of all the factors in individual chromosomes by the unbalancing effect upon the structure and physiology of the plant when a single specific chromosomal set has 1 or 2 extra chromosomes.[36]

Already by 1921, Blakeslee claimed to have discovered three so-called "factor" mutations and twelve "chromosome" mutations in the jimson weed, all of which were "identified by various external characters." But these numbers were to continue to steadily increase throughout the 1920s and 1930s. "Knowing the mechanism to be affected," Blakeslee noted in 1921—that is, the behavior, mechanism, and association of the chromosomes—"we may be able ultimately to induce chromosomal mutations by the application of appropriate stimuli."[37] Radium was one of the first of those stimuli to which Blakeslee turned.

Charles Stuart Gager, the director of the Brooklyn Botanic Garden, was the first to investigate the effects of the rays of radium on plants in 1908. In 1921, Blakeslee began a fruitful collaboration

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[36] "Department of Genetics," 1921, p. 104.

[37] Blakeslee even cited Muller's work on balanced lethals, which he said "strongly suggests that such of the Œnothera mutants as are not caused by chromosomal duplication are due to cross-overs from a balanced lethal condition." Blakeslee, 1921, pp. 257, 260, 262.

with Gager, and described the goals of the collaboration in a presentation to the Botanical Society of America on December 28 of that year:

> to study and compare the *structure* of these mutant forms, both as to gross external morphology and as to internal anatomy; and thus to determine the structural effects produced by a single factor and those produced by a single entire chromosome. In this way it may be possible to begin an analysis of the factorial constitution of each of the chromosomes.[38]

Blakeslee's approach to mutation studies was thus intended to complement other studies in the field, and to better highlight the different ways in which mutations could be produced—both chromosomally and genically, and both by the addition of single triplicate chromosomes to the mix (his current focus), and by other changes that had already been identified (such as rings of linked chromosomes). Phenotypic effects—mutant plants—could result from any of these mechanisms. Although Blakeslee and Gager couched their approach in terms of gene-based genetics, their discoveries were soon to push them ever further toward acknowledging the primacy of chromosomal variation in evolution.

Already by 1921, Blakeslee and Gager encountered a peculiar mutant, "Nubbin," which they noted clearly arose from a "radium-treated parent," and which was likely the particular result of ray-induced "breaking up and the reattachment of parts of non-homologous chromosomes."[39] (As Blakeslee later reported in the *Year Book*, some of the "three chromosomes were fragments, and the fragments of one were attached each to a fragment of the other two.")[40] With its interchanged chromosomes, Blakeslee thought Nubbin was thus "probably the first induced chromosomal mutation." [41] He also held that an albino character might also have been due to radium treatment.[42] In short, Blakeslee believed that the radium treatment certainly increased the proportion of mutants, but he remained open-minded as to whether it could cause new gene mutations—such as the albino mutant—waiting for evidence that such traits acted as mendelizing characters.[43]

By the following year, the two men had begun to compose a draft paper, eventually to be published in the *Proceedings of the National Academy of Sciences.* Production of their paper became bogged down for a period of years, as both the inherent difficulties of the project and Gager's other commitments kept him away from the radium work. By the dawn of 1927, Gager wrote to Blakeslee saying, "I have just glanced the paper through. Apparently, it will need very considerable revision, if not re-writing. Among other things, it might be desirable to mention the results of Mavor on the production of non-disjunction and crossing over… by X-rays, though reference to those papers should, I think, be very brief."[44] James Mavor's results, published in *Science* in 1922

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38 *Ibid.*
39 Gager and Blakeslee, 1923, pp. 75-6.
40 "Nubbin, a type obtained following radium treatment by Dr. Gager in 1921 in which 3 chromosomes were fragments and the fragments of one were attached each to a fragment of the other two, has been of considerable service in the analysis of the cryptic types in nature." "Department of Genetics," 1929, p. 45.
41 Blakeslee, "Lectures, Papers, Etc.," "Control of Evolution and Life Processes in Plants."
42 "Department of Genetics," 1922, p. 98.
43 Blakeslee also acknowledged, however, that some mutations were not expected to be mendelizing. Blakeslee to Gager, January 14, 1923.
44 Gager to Blakeslee, January 3, 1927.

under the title "The Production of Non-Disjunction by X-Rays," had indicated that the phenomena of nondisjunction first identified in *Drosophila* by Bridges (the cause of various heritable traits though not specifically a *genic* mutation) could also be produced artificially.[45] Fully aware that some of D. T. MacDougal's earlier successes with induced mutation had come into question, Blakeslee and Gager were concerned that their own work not fall prey to the same criticisms. Though certain that they had discovered two radium-induced mutations, Blakeslee nonetheless advocated caution: "It seems to me that in view of the trouble which McDougall [*sic*] got into with his induction of mtations [*sic*] it behooves us to be extremely cautious, perhaps unnecessarily so, in claiming much for our preliminary experiment."[46] All in all, he concluded, "I am wondering if we ought not to do a little more work with the radium and get more than an isolated capsule effected [*sic*] before we get out a formal paper."[47]

After years of delay, their joint paper "Chromosome and Gene Mutations in *Datura* Following Exposure to Radium Rays" finally appeared in the *Proceedings of the National Academy of Sciences* in February 1927.[48] While they acknowledged that when they first presented their results in 1922 they had not yet "a sufficient body of data in regard to the mutability of untreated parents to permit us properly to evaluate the significance of the results," they now claimed to have accumulated "considerable" data regarding *both* "gene and chromosomal mutations in closely comparable normal material which can be handled as control to the treated material."[49] Finding great surprise in their success, they reported that they had discovered a variety of what they called "chromosomal mutants" mostly of the $2n+1$ form—having a complete diploid set of chromosomes with an additional chromosome.

Although these types of chromosomal mutants had first been mentioned in the *Anatomical Record* as early as 1923, what was significant in Blakeslee and Gager's new publication was the sheer rate of production of these mutants.[50] While overall they had discovered some 73 "$2n+1$" forms from 15,417 progeny in the controls (a rate of 0.47%), in one case they found "[a] percentage of 17.7 chromosomal mutants in over 100 offspring from a single capsule"—a rate they described as "enormously greater than [that] we have ever obtained before or since." They concluded: "In view of the above figures, we believe the radium treatment was responsible for the increased proportion of chromosomal mutations, as also for the appearance of the compound chromosomal type Nubbin."[51] (Recall that drosophilists had, at this time, discovered about 400 visible mutants from their study of some 20 million flies—Blakeslee and Gager's results were thus by all standards remarkable.) The end result of their collaboration was clear. There was no longer any doubt that the radium could transmute species, and that it did so in at least two different ways: gene mutants (as the drosophilists had found) and chromosomal mutants.[52]

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45 Mavor, 1922.
46 Blakeslee to Gager, January 14, 1923.
47 Blakeslee to Gager, January 14, 1923.
48 Gager and Blakeslee, 1927, pp. 75-79.
49 *Ibid.* p. 75
50 Gager and Blakeslee, 1923, p. 424; Blakeslee, 1923, p. 389.
51 Gager and Blakeslee, 1927, p. 78.
52 "[I]t is our belief that most, if not for all, of these three types of results"—the compound chromosomal type Nubbin, the chromosomal mutants, and the gene mutants—"the radium treatment may be held largely responsible," they concluded (*ibid.,* p. 79).

Much of Blakeslee's work in the 1920s thus centered around identifying the various kinds of "apostles" and "acolytes," as he termed these different varieties of "chromosomal types." He mapped out the theoretical possibilities of combinations, and charted which ones he observed and with what frequency. And he found these chromosomal types to be related to phenotypically distinct and self-perpetuating "new species" of *Datura.* He invented a whole terminology for these new chromosomal types, to categorize the cytogenetic differences: "primaries" were 2n+1 trisomics with an additional but unmodified chromosome; "secondaries" were such trisomics with two like ends, the result of further chromosomal interchange; and "tertiaries" were trisomics with ends from two different chromosomes. He invented diagrammatic karyotypes, explaining these processes of chromosomal interchange and the creation of mutant chromosomes, which in turn were responsible for chromosomally mutant plants, and he related these diagrammatic karyotypes to the phenotype.

Blakeslee and Gager established that "synthesized pure breeding types, which correspond to synthesized new 'species'" resulted from radiation treatment. Blakeslee was firmly convinced that these synthesized pure breeding types—the result simply of chromosomal and not gene mutation—were indeed new species in an evolutionary sense: they bred true, generation after generation, and presented themselves as new types to the botanist.[53] Although one of the first to strongly advocate polyploidy, Blakeslee was also aware of other effects that were clearly the result of *gene* mutations—although the direct relevance of these for evolutionary processes (the emergence and maintenance of new species) was not as readily apparent. (These visible effects included altered pollen tube growth, the non-germination of pollen, and the early or late abortion of pollen grains.) Outside the world of drosophilists, it was not at all clear that gene mutations were in any way more fundamental to the nature of evolution and the origin of species than the chromosomal mutations Gager and Blakeslee were uncovering.

Blakeslee's emphasis on the significance of chromosomal mutation was long-standing. He had written to MacDougal as early as 1923 saying, "I feel very strongly that a study of the chromosomal distribution is likely to explain irregularities in behavior in other plants than the *Datura* and that chromosomal changes in number have been responsible for evolution."[54] In the wake of Gager's work and the widespread realization of the complexity of *Oenothera*'s chromosomal system, Blakeslee was also aware however, and most especially at the Boston meeting in 1922, "that I have been obliged to caution people with whom I have talked about the *Datura* work from being over-enthusiastic and thinking the chromosome irregularities would explain phenomena which appeared to be explainable on ordinary factorial basis."[55] Enthusiasm for chromosomal mutations as the basis for evolution apparently outstripped enthusiasm for gene mutations in some quarters.

Both chromosomal and gene mutations were important for Blakeslee.[56] They were not equally important for everyone else at the time. Gager and Blakeslee had published their paper on "Chromosome and Gene Mutations in *Datura* Following Exposure to Radium Rays" in the February 1927 edition of the *Proceedings of the National Academy of Sciences*. By July 22, *Science*

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53 Blakeslee to Gager, September 5, 1933.
54 Blakeslee to MacDougal, February 15, 1923.
55 *Ibid.*

published results on the induction of mutations in *Drosophila* under the provocative title "Artificial Transmutation of the Gene."[57] The author was none other than one of the archetypal figures in the history of genetics, the ever-priority-conscious Hermann J. Muller. History was about to be rewritten—and Blakeslee and Gager's successes with radium were about to be written out of the picture in favor of Muller's experiments with X-rays, and his focus on the gene as "the basis of life."[58] Blakeslee's work was rapidly overshadowed as Muller's own remarkable successes—a 150% increase in genic mutation—hit the headlines, contributing to the establishment of mutation as a fundamentally genic phenomenon. Chromosomes were important, certainly, but they had been dethroned.

Conclusion

Recognition of the importance of chromosomes—and not just genes—in the phenomena and study of heredity was widespread, especially in botanical circles, in the early twentieth century. Blakeslee's work linking questions of mutation to questions of chromosome structure, directly influenced by de Vries' own focus on plants, thus provides a counternarrative to the dominant tale of gene-centered Drosophila genetics, and recovers a history otherwise lost in the afterglow of Muller's 1927 experiment. Mutation meant many things to many people, even among "geneticists." While Muller regularly racked his brain trying to make further distinctions between "true" gene mutations and the smallest conceivable changes in chromosomes, in order to discover the "basis of life" as it kept on slipping through his fingers, Blakeslee was a more ecumenical mutationist concerned to study the effects of both gene *and* chromosomal mutations, recognizing polyploidy, trisomy, and various forms of multiple linkages and translocations all as distinct and proper forms of chromosomal mutation with definite, observable, inducible, and manipulable phenotypic effects. Moreover, while some plants deal well with polyploidy and trisomy and other vagaries of chromosomal interchange—and these include *Oenothera* and *Datura*, for whom these mechanisms are chromosomal normalities, not abnormalities—fruit flies simply do not. The choice of experimental organism mattered for the meaning of mutation in this period. Muller's meteoric rise to fame after 1927 conspired with his focus on the fruit fly, the X-ray, and the gene to eclipse chromosomes from their rightful place in the story of evolution until the later "genetic systems" of Darlington. Although largely forgotten today, Blakeslee's work on the jimsonweed led him to a vision of a more pluralistic genetics. Not just producing karyotypes and mechanistic explanations for de Vries' oddities, Blakeslee had in fact, sometimes even against the grain of his

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56 This was in distinct contrast to some other earlier investigators. In an article for the *American Naturalist* in 1910 entitled "Mendelian Phenomena Without De Vriesian Theory," William Spillman had proposed four distinct types of "variation": the Mendelian recombination of characters; fluctuation due to the environment; the discontinuous hereditary "irregularities in the distribution of chromosomes… amenable to the action of natural selection" (or as he also labeled it, in light of new understandings of what was going on cytologically with *Oenothera*, "de Vriesian mutation"); and what he called "fundamental change in… the germ plasm," this last of which he believed to be "by far the most important type of evolutionary change."

57 Muller, 1927.

58 I have addressed Muller's rewriting of history elsewhere; see Campos, "*Mutatis Mutandis:* H. J. Muller and the Meaning of Mutation," forthcoming.

own inclinations and earliest pronouncements, initiated productive new ways of doing "genetics without genes."

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Cited correspondence is archived in the Blakeslee papers and the Davenport papers at the American Philosophical Society in Philadelphia, Pennsylvania ("APS"); and in the Blakeslee papers at the Cold Spring Harbor Archives ("CSH").

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Seeing, Breeding and the Organisation of Variation: Erwin Baur and the Culture of Mutations in the 1920s

Alexander von Schwerin

This paper seeks to introduce the research on mutations of the German physician, botanist and geneticist Erwin Baur (1875-1933). It traces Baur's experimental studies on the heredity of plants from 1903 onwards, particularly focusing on the snap dragon (*Antirrhinum majus*). A sophisticated approach to the detection of mutations evolved out of these studies around 1920. In the mid-1920s, Baur managed to create a sudden blast of mutations in his experimental object. The crucial invention was a special system of breeding. In this respect, Baur's experiments were special since in the 1920s mutation research had become dominated by manipulative trials.

The artificial induction of mutations turned out to be the more spectacular result in the perspective of the contemporaries. Highlighting the practical and conceptual trajectory of Erwin Baur's research on mutations, this paper suggests that this view is limited on the conceptual impact of mutations. However, the impact of mutations and the techniques directly related to them were not limited to the very field of mutation research. They increasingly became a technical boundary between variant interests. Baur and other geneticists held not only a fundamental interest in the causes of the variation of organisms, but mutants bound together agricultural interests, evolutionary commitments and eugenic sentiments. Last but not least, mutants were tools and became part of the growing technical spectrum of biological and biomedical research.[1] Instead of reducing variation, geneticists became involved in broadening variations for multiple purposes.[2]

Starting the story: A new type of mutation as a tool for innovative research

In 1934 two leading German geneticists, Alfred Kühn and Nicolai Timoféeff-Ressovsky, utilized a simple distinction when speaking to a mixed auditorium of biologists and physicians at the "scientific week" in Frankfurt (Main). "Good mutations" were those mutations that produced quite visible and striking changes in an organism. Correspondingly, "bad mutations" resulted in nearly *invisible* changes.[3] By using this distinction, Kühn and Timoféeff-Ressovsky resumed the common view of experimentalists in hereditary research. "Good mutations" were "good" in a pragmatic sense because they were *useful* for ordinary genetic research, such as the mapping of genes or the analysis of traits. Of course when scanning hundreds of flies under the microscope, it was easier to detect a mutant of the *Drosophila* fly with striking morphological deformities such as

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1 For the history of the institutionalisation of experimental animal breeding see Rader, Mice 2004.

2 This approach towards a history of the formation of a mutational dispositive supplements, see Christophe Bonneuil's history of the generation of genetic pureness as an "experimental/combinatory/industrial time-space". Same preprint.

3 Timoféeff-Ressovsky, Verknüpfung 1935, pp. 101 f.

missing wings rather than "small changes" such as slight variations in the structure of the wings or of the mean life time.[4]

However, small changes were "bad" only from the perspective of common genetic practice. The message of Kühn and Timoféeff was actually that small mutants had a special value for research. These mutants were not only the proper material of evolution, but were also useful for innovative genetic research. "Small or weak and variably manifesting" mutations were good as a tool for innovative research such as that on the physiology of genes.[5] Kühn argued that "today the complicated cases are more important for us because they pave the way into the effective gearing ("Wirkungsgetriebe") of the genes."[6]

Speaking of "small mutations" ("Kleinmutationen"), Kühn and Timoféeff-Ressovsky suggested that there was a special class of mutations. However, the term "Kleinmutationen" was not coined by them. In using it they referred to another German geneticist: Erwin Baur. Baur (b. 1875) belonged to the first generation of Mendelian geneticists in Germany and had died in late 1933. Until then, he had managed the large Kaiser Wilhelm Institute for Breeding Research at Müncheberg near Berlin. Baur was known for his style leading the institute like a business.[7] He and his assistants held close relations to farmers and the agricultural industry—seed breeders, breeders of poultry and rabbits and the coat manufacturing industry.[8] Baur was also actively engaged in research politics and had been a notorious promoter of human genetics and eugenics.[9] Less well known are his studies in mutations, though these were quite well esteemed by geneticists at that time.

To be sure, "Kleinmutationen" were by definition somewhat unusual in genetics. They were not new in terms of their mode of inheritance and were actually alterations of a hereditary factor, or a so-called factor mutation. Small mutations were noteworthy because of their effects. Geneticists usually referred to those mutations that were not initially noticeable as "recessive" mutations. In contrast to dominant alleles, they became visible only when they became homozygous. Still, in the case of small mutations the manifested effects were only slight, thus, small mutations were somewhat of a subclass of recessive mutations. But natural kinds are always on the move. The distinction between "recessive" and "dominant" genes was fading in the twenties. Timoféeff-Ressovsky classified mutations only phenomenologically since there was a "complete scale" of mutations "beginning with quite visible morphological changes to all kinds of small physiological changes," that is "from 'big' to very 'small' mutations."[10]

Small mutations opened a new space that fell between changes induced by mutations and the realm of non-hereditary modification. However, a special situation was necessary that made this

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4 Timoféeff-Ressovsky's models in the late 1920s were flies with slight changes of the wings and with reduced viability. Timoféeff-Ressovsky, Verknüpfung 1935, pp. 95-99.

5 Timoféeff-Ressovsky, Verknüpfung 1935, p. 102; Schwerin, Experimentalisierung 2004, p. 172. "Physiological developmental genetics" was coined by Kühn who tried to study the physiological and chemical steps that were induced by a hereditary factor. Rheinberger, Ephestia 2001, pp. 542-544.

6 Comment by Kühn in Timoféeff-Ressovsky, Verknüpfung 1935, pp. 117 f.; for Kühn on the significance of mutation research see also Kühn, Genwirkung 1934, p. 218.

7 Harwood, Styles 1993, pp. 214-218; Harwood, Ökonomie 2002.

8 Schwerin, Experimentalisierung 2004, pp. 56-83.

9 Lösch, Rasse 1997, pp. 168-175; Schiemann, Baur 1935.

10 Timoféeff-Ressovsky, Verknüpfung 1935, p. 102.

space possible. Since small mutations were not easy to handle and required special experimental efforts, the question arose as to how these mutations could become something like a natural kind.

Erwin Baur: settling as a botanist within the space of heredity

Baur was psychiatrist by education.[11] He was however interested in biology. When he was studying in Kiel, a city on Germany's eastern coast, he received private lessons from the botanist Johannes Reinke and worked at the marine zoological institute. He finally succeeded in getting an assistantship at the botanical institute of Berlin`s university in 1903. Baur said that he was deeply impressed by the rising experimental trend in biology at that time.[12] One of those experimental idols was the botanist Hugo de Vries, whose "Mutation Theory" had been widely discussed at the time. From the perspective of de Vries' mutations, changes of an organism's form occurred in a single large and sudden step. Baur admired the experimental courage of de Vries, but he was not quite convinced by his concept of mutations.

When Baur started work he was not especially interested in mutations. However, the first problem he had to tackle at the institute in Berlin led him straight into the ongoing biological debates about the reasons for the variation of organisms. The well-known phenomenon that had puzzled the Berliner botanists for some time was the mixed-colour of leaves that were typical for some domestic plants. De Vries had presented these plants as an example for his concept of mutations calling them the "ever sporting species."[13] In the institute's garden was a variety of the snapdragon, *Antirrhinum majus,* that showed variegated leaves.

When Baur began experiments with one variety of *Antirrhinum* called Aurea, he was determined to show ordinary botanists the potential of the new experimental methods. He criticised the studies of de Vries and others following him as weak because they confused non-hereditary modifications and real hereditary variants.[14] It became a mission for Baur and his assistants to show the methodological pitfalls of contemporary studies in heredity and Mendelian genetics using statistics without distinguishing the genetic status of variants.[15] Thus, the early Mendelian geneticists seemed to intervene as methodologists in the first respect.

Baur was not interested in mutations in and of themselves, but his ideas on mutations were influenced by his methodological efforts and work on Aurea. Baur was convinced that the effects of mutations were not as big as de Vries suggested, but evident in the range of the effects of a Mendelian factors. This idea was in accordance with other geneticists. However, Baur's view on mutations was special in a certain respect; he was convinced that there were even smaller mutations than common Mendelian traits like the colour of blossoms. This conviction derived

11 For a detailed biographical sketch of Baur's early life see Schiemann, Baur 1935.
12 Baur, Einführung 1911, p. 1.
13 Baur, Untersuchungen 1907, p. 443.
14 Baur, Untersuchungen 1907, pp. 443, 448 and 450. Baur showed that the new forms of Aurea were the result of the segregation of mixed characters and the influence of the environment, respectively. In the example of Baur the "ever sporting varieties" of de Vries were only special cases of modification. Baur, Untersuchungen 1907, p. 447.
15 This critique showed Baur to be an early follower of the Danish geneticist Wilhelm Johannsen who strengthened the distinction between non-hereditary variation and heredity. Baur, Untersuchungen 1907, p. 449.

from Baur's critique of the confusion with modifications and hereditary factors. He suggested that the reason for the difficulties of distinguishing these types of influences was that the effects of modifications and factors largely overlapped. This assumption rested on a certain idea of how hereditary factors functioned. As a by-product, this idea informed Baur's view of mutations.

When Baur tried to deduce the cause for the variegation of the leaves of Aurea, he turned to the physiological studies of the botanist Georg Klebs. Klebs was successful in systematically showing the influence of the environment on the development of plants.[16] Baur concluded that the appearance of an organism is the result of both the influence of a Mendelian trait and a reaction to the environment. Referring to a formulation of Klebs, Baur specified that the Mendelian factor determined only the range of reactions of an organism to the environment.[17] In 1908, he explained this view when he presented physicians with the basics of Mendelian genetics: "When we see the colour of a blossom or some other outward appearance of a plant, we always see only a result of the reaction of this special individual to the outer conditions."[18] On this basis he then continued to explain the difference between changes due to the environment (modification) and the heritage (mutations). Sometimes variations are not due to environmental influence, but rather to "what has been so often recalled mutation in the past years […]. However, the case of the newly-appeared, deviating characteristic rests on a change in the mode of reaction—*even if it is only a very small one*—that means commonly that the change is hereditary; we might then speak of a mutation."[19]

The effects of mutations might only be a smart shift in the norm of a plant's reaction. This view was nothing other than the translation of Johannsen's statistic scale of continuous modification in a functional and reactive relationship of Mendelian factors and the environment. However, this environmental perspective of hereditary effects drove Baur to emphasise that mutants were not generally recognisable phenomenologically because they could be just as small as the slightest modification.[20]

Baur performed most of these early experiments on *Antirrhinum* near his home where he had leased some property.[21] However, Baur's occupation at the university's institute was also relevant. The experience that Baur had gained working with microorganisms at the zoological institute in Kiel met the interests of the botanists at the Berlin institute working with bacteria and fungi.[22] Since the relationship of "Erbeinheiten und Außeneigenschaft"—the environmental influence

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16 Baur, Untersuchungen 1907, pp. 448 f. Klebs was not a Mendelian geneticists but he also criticised de Vries. Klebs, Studien 1907, p. 99. In his view the variations of plants were not due to chance; instead he tried to show experimentally that the plants reacted to the different conditions of the environment. Klebs, Studien 1907, pp. 31 u. 102.

17 Baur, Untersuchungen 1907, p. 449. The formulation used by Baur was close to the concept of the "norm of reaction" formulated one year later by Woltereck that was rather influential in German genetics. Harwood, Culture 1996.

18 Baur, Ergebnisse 1908, p. 286. Emphasis by AS.

19 Baur, Ergebnisse 1908, p. 286. Emphasis by AS.

20 Baur, Ergebnisse 1908, p. 286. Thus, Baur turned de Vries' theory around: large changes of a trait could simply be modifications, and, vice versa: small changes could be mutations.

21 Baur also held lectures and university courses at that site in Friedrichshagen near Berlin. Schiemann emphasises that this large venue was of quite a bigger scale than the facilities of the university and was a definitive resource for Baur's move from "pure botany to experimental genetics." Schiemann, Baur 1935, pp. 65 f. and 70 f.

22 Baur got his "Habilitation" for a work about myxobacteria in 1904. Schiemann, Baur 1935, p. 63.

and the distinction of modifications and hereditary characters—had become Baur's main scientific problems, he asked two doctoral students to test claims that extreme conditions or the treatment with poisons, temperature and other agents would induce mutations in bacteria and fungi—Claims which appeared to be quite popular at that time.[23] Actually, they became a junction between hereditary research and bacteriology since bacteriologists were under the proponents of that view.[24]

40 Mendelian traits and 642 races of the snap dragon: an experimental system on the edge of Mendelian genetics, agriculture and evolutionary theory

This early research led Baur into the virulent discourse on the scope of Mendelian genetics. Baur had already attended collected variants of *Antirrhinum majus* when he was working on variegated leaves, but he stepped fully into that field after he had finished that work in 1908. He did not hesitate to outline what was at stake: he sought to show that the appearance of *Antirrhinum* was completely influenced by Mendelian factors.[25] The attitude of Baur was the same he would adopt in the 1920s: to defend Mendelian genetics against those who tried to limit Mendelian validity. He remarked that experimental geneticists were usually too compliant critics when they regularly admitted that a trait was non-Mendelian; but more than ever one shouldn't give up the claims since geneticists knew about the complicated relation between Mendelian factors and the environment.[26] Obviously, the idea that heredity was disguised by the influences of the environment encouraged far-reaching claims. In his university lecture on hereditary research, Baur suggested that not only common racial traits of plants are in accordance with the Mendelian laws:[27] "It looks like the slightest differences between races and species are in accordance with Mendelian laws."[28]

This was the context when Baur started his the analysis of *Antirrhinum majus* published as "Vererbungs- und Bastardisierungsversuche mit *Antirrhinum.*"[29] He was not the only one at that time who used *Antirrhinum* as a genetic model. The American botanist Ms. Muriel Wheldale had published extensive breeding experiments in 1907, and de Vries had done some work with *Antirrhinum* as well.[30] However, Baur's aim was to go as far as possible and to include increasingly more traits into the analysis.

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23 Baur, Vererbungsversuche I 1910, p. 34; Schiemann, Baur 1935, p. 63. Baur was convinced that environmental conditions could induce mutations, referring to earlier experiments of the American zoologist Tower on the Colorado buck. The experiments that were performed by Elisabeth Schiemann and Franz Wolf produced no clear results. However, Baur was satisfied because the experiments seemed to contradict the claim of some bacteriologists that extreme environmental influences result in *adaptive* and not arbitrary mutations. Baur, Einführung 1911, pp. 203 f.

24 For a short review of the literature see Wolf, Modifikationen 1909; Baur, Einführung 1911, p. 204

25 Baur, Vererbungsversuche 1910, p. 53.

26 Baur, Vererbungsversuche 1910, p. 93. Baur made the criticism that many people would think that the Mendelian laws are only valid for bastards because they were called "Spaltungsgesetz der Bastarde." Baur, Ergebnisse 1908, p. 288.

27 Baur, Ergebnisse 1908, p. 288.

28 Baur, Einführung 1911, p. 182.

29 Baur, Vererbungsversuche 1910; Baur, Vererbungsversuche II 1912; Baur, Untersuchungen 1924.

30 Baur, Vererbungsversuche 1910, pp. 88 f. See also Richmond, Birth 2007

Baur took the first variants of *Antirrhinum* from the university's garden. He then searched the nurseries near his house and later, systematically, the seed companies around Berlin; he also collected wild *Antirrhinum* variants on his hikes through the countryside.[31] The variants Baur had bought or collected became "Stammpflanzen," the units he intended to analyse.[32] He started with the most prominent racial traits such as the colour and form of the blossoms, but he widened successively his scope looking for the colour and form of leaves.[33] In 1908, Baur was confident that the 250 races of *Antirrhinum majus* he was able to distinguish were the product of the combination of Mendelian differences.[34] In 1910, Baur specified 13 "Erbeinheiten" and estimated that there were all together about 40-50 of them.[35] This number, he added, would be enough to predict the appearance of a race by looking at the genetic formula. And Baur was sure that the countless races of the species *A. majus* were "just combinations of these few differences that behave like Mendelian units."[36]

The involved number of plants was successively increased. From 1909 on, Baur was allowed to use a part of the university's garden where there was space for 25,000 individuals.[37] In 1911, Baur changed from the university to the agricultural university of Berlin ("Landwirtschaftliche Hochschule") and became the head of the newly founded Institute of Heredity Research. First based at Berlin's city centre with no extensive possibilities to grow plants, Baur managed to get a field and barracks in the nearby city of Potsdam.[38] Now Baur and his workers could double their breeds and grew about 50.000 single plants each year.[39] Until 1919, the number of analysed genetic units had increased up to 40 causing the characteristic differences of 642 races.

Baur's project could also be linked to the explanation of the evolution of species—a question that had also been addressed by de Vries. Baur began making this connection in 1911.[40] He was quite convinced that Mendelian heredity was a key to understanding the process of evolution, but he was also ambivalent. In 1911, Baur claimed: "The faith of selection theory depends on whether it can be shown that mutations are frequent enough in order to enable an effective process of selection or not."[41] Thus, Baur was quite aware that the analysis of mutations would be a big task for future genetic research.[42] However, Baur admitted that at the basis of his environmentalist view there was a major practical obstacle. "It is possible and probable that small mutations, which have curves of modification that overlap with those of the wild type, will be overseen in most of the cases."[43]

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31 Baur, Untersuchungen 1924, pp. 2-4.
32 In 1912, he cultivated 642 individuals as "Stammpflanzen." Baur, Vererbungsversuche II 1912, p. 202.
33 Baur, Vererbungsversuche 1910, p. 34.
34 Baur, Ergebnisse 1908, p. 288; Baur, Vererbungsversuche 1910, p. 39.
35 Baur, Vererbungsversuche 1910, pp. 50 f. and 91.
36 Baur, Vererbungsversuche II 1912, p. 202.
37 Baur, Wesen 1908, p. 333.
38 Schiemann, Baur 1935, pp. 79 f.
39 Baur, Untersuchungen 1924, p. 1.
40 Baur, Vererbungsversuche 1910, pp. 34 and 53.
41 Baur, Einführung 1911, p. 265. Early in the lecture, Baur was sceptical as to whether mutations were frequent enough to cause the "'individual variability' of a species." He presumed that the witnessed variations of plants were due mostly to modifications, while variations of animals were due primarily to the new combination of factors. Baur, Einführung 1911, p. 190.
42 Baur, Einführung 1911, p. 202; see also ibid., pp. 186 and 188.
43 Ibid., p. 266.

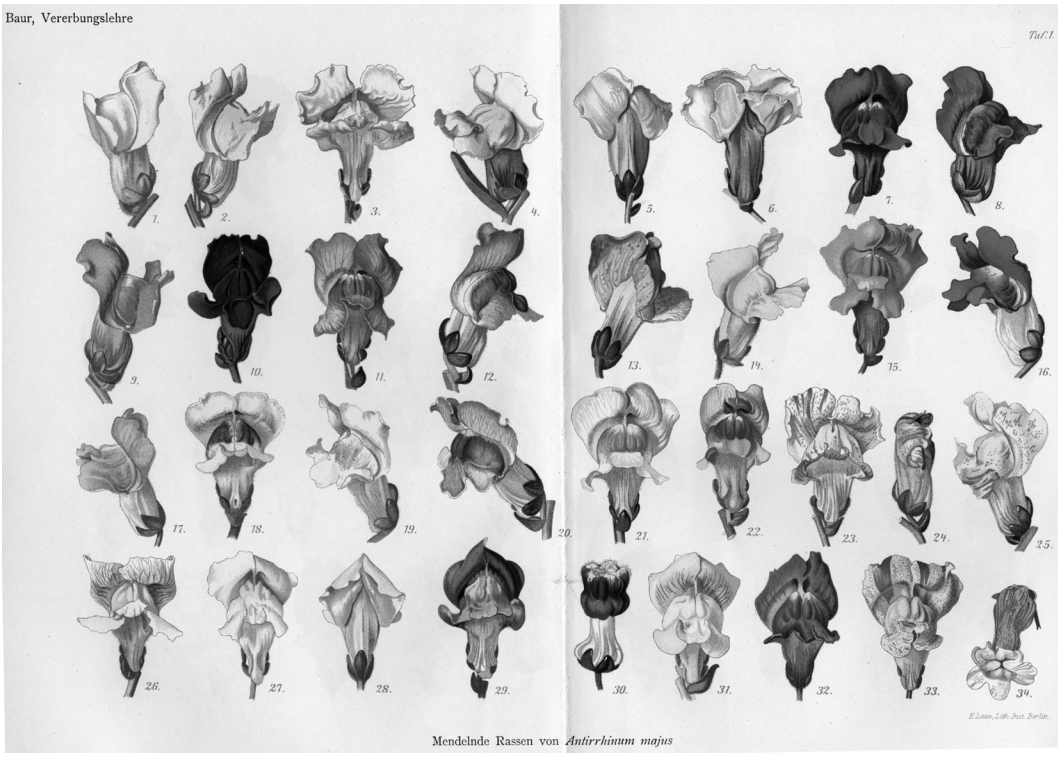

Figure 1: The chart shows painted variants of the blossoms of the snap dragon, *Antirrhinum majus*, which Baur analysed genetically. Source: Baur, Einführung 1911, table 1.

While evolution and mutations were more a topic for the future, the application of Mendelian genetics to agriculture was already then acute and would become even more so when World War I began. Baur foresaw the upsurge of rationalised animal and plant breeding and compared himself and his colleagues to the chemists who deliberately combined atoms and molecules.[44] The result of the genetic analysis was that "once identified genes become more available, I can work with the hereditary formulas exactly as the chemist works with his atoms, molecules and his formulas."[45] With respect to the Mendelian methodology it made no difference to speculate about hereditary changes as material for evolution or to envision them as material for the breeder.[46]

Mutations coming through the backdoor

Baur's general strategy to analyse the genetic composition of the snap dragon was a mixture of inbreeding and cross-breeding. The basis of his experiments formed his "Stammpflanzen"-system. "Stammpflanzen" became those plants Baur wanted to analyse.[47] The plants selected to

44 First he did so in 1910. Baur, Vererbungsversuche 1910, p. 90.
45 Baur, Vererbungsversuche II 1912, p. 202.
46 This equation should become problematic only later when Baur began to distinguish pathologic and valuable mutations.
47 Baur, Vererbungsversuche 1910, p. 35 f.

become a "Stammpflanze" were grown in pots for a number of years and served as source for seeds and reference for comparison in cross-breeding experiments. "Stammpflanzen" were the living standards in the ongoing experiments. The "Stammpflanzen" turned out to be homozygous in most of their genetic factors because most of the wild or commercial breeds had been inbred for some time.[48] In the perspective of Baur, the "Stammpflanzen" represented the varieties of *Antirrhinum* that is the tableau of races. Entering the experimental phase, Baur seeded about 1,000 seeds, growing a blooming bed of the cross-generation (F1) that should reveal a Mendelian ratio. However, the genealogic chart presented by Baur does not show this progeny, but only schematically details the steps of his breeding strategy (figure 2). A single plant or few plants were selected for another experiment or to establish new "Stammpflanzen" by self pollination. The breeding strategy was to create not a genealogic tree but an ever increasing net. Step by step, the system of mutual references expanded and each new experiment would reveal a new detail of the genetic constitution of even a distant ancestor or "Stammpflanze."

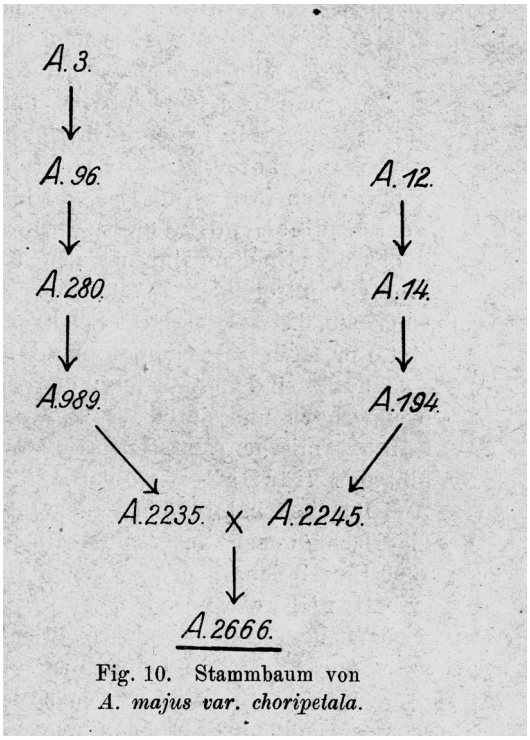

Fig. 10. Stammbaum von *A. majus var. choripetala.*

Figure 2: This genealogic chart describes schematically the "Stammpflanzen" breeding system used by Baur to analyse the genetic composition of the races of *Antirrhinum majus*. "A" signifies "Stammpflanzen." Source: Baur, Mutationen 1918, p. 187.

While Baur repeated this alternate procedure of cross-breeding and inbreeding several hundred times,[49] mutations came through the backdoor. In 1910, Baur noticed the first mutant plant in his sowings. Already the circumstance of this observation should become decisive for the

48 Ibid., p. 91.
49 In January 1912, Baur reported 300 crossings that were analysed until the second and third generation (F2 and F3)—"a very time-consuming work." Baur, Vererbungsversuche II 1912, p. 202.

experimental domestication of later mutations. In 1908, Baur had crossed two plants that were special in the colour of their blossoms because he was interested in the heredity of those colours. The following summer, the progeny split up in a quite normal Mendelian ratio. Afterwards, Baur selected two plants out of the "normal" looking bed which would become "Stammpflanzen." After self fertilisation, he seeded the progeny. However, when the second generation (F2) grew up, Baur noticed plants with an unusual form of the blossom in the progeny of one of the new hopeful "Stammpflanzen." He was certain he had found a mutation and named the variety *A. majus* globosa.[50] This kind of incident occured a number of times in the following years.[51] Baur's interpretation was that a heterozygous and recessive mutation had occurred in the gametes of the parental plants. However, the mutation only became visible in a homozygous condition after he had selected and inbred one offspring carrying that mutation.

There was another incident that dramatised this game of visibility. One day Baur stood in front of his experimental field in Potsdam and admired the fresh green of the growing, not yet blooming plantations ordered into chessboard-like units. He was surprised when he noticed that one section differed in the overall colour with the *leaves* being somewhat lighter than normal.[52] The inscription revealed that the lighter plants were the inbred progeny of a cross-breeding in the *third* generation. Why had Baur not noticed the mutants already in the second generation like in the case of the other mutations? Baur thought he had been inattentive and, in any case, the effect of the mutation was as small as not hereditary changes that often occurred.[53] There was no chance to notice the mutation as long as there was only a small number of mutants. The mutation became only visible when one homozygous mutant was inbred and *all* plants of a generation were homozygous for the mutation.[54] The trained view of the experimenter was betrayed by the ever modifiable plants such that the original event, the mutation, only showed up by difference (e.g. as the pattern of the experimental field).

In Baur`s view this game of visibility fit well into his struggle against the pitfalls of "seeing" since he started with debunking the myth of variegated plants appearing as de Vriesian mutations. What was the true difference between mutants and modifications? There was *neither a visible* nor a clearly distinguishable borderline between heredity and nurture. Since the hereditary effects were often within the range of environmental influences, there was no reason to trust the eye. The recent experiences warned him that he himself had been the victim of his eyes.

Nevertheless, Baur's first experimental mutation system was based on his visual skills. Mutations arose while Baur bred thousands of snap dragons. Looking back Baur stated, "In the first years, I have not seen and investigated most of the mutants because my glance was not skilled ["geschärft"]."[55] Often there was a deficit of time to look more closely since Baur went for military service during World War I. He was reluctant when there was time to distinguish just the prominent newly bred variations of *Antirrhinum*.[56] Over the years, Baur's visual acuity became more and more attuned, so he would see (or "suspect") an anomalous individual earlier.[57] By

50 Baur, Einführung 1911, p. 201.
51 Baur, Einführung 1914, p. 292.
52 Baur, Einführung 1911, p. 189.
53 Baur, Bedeutung 1925, p. 112.
54 Baur, Untersuchungen 1924, p. 144.
55 Ibid., p. 142.
56 Baur, Mutationen 1918, p. 181; Baur, Bedeutung 1925, p. 111.

1918, Baur had grown 200,000 individuals during his original experiments and found some 20 mutants.[58] However, this was only the number Baur knew for certain. He suggested that there were many more mutations but he had not been able to analyse them because they behaved with too much variation.[59] However, this vague assumption was obviously encouraged by his conviction that many hereditary units produced only slight changes in the normal range of variability. In general, Baur`s regime of mutation detection was simply based upon the 'naked glance.' Mutants showed up as a disturbance of the homogeneity Baur intended to maintain by inbreeding his cross-breeding products.

Mutations as objects of research: dividing chance/technique and substance/nature

Mutations arising as a by-product of ongoing breeding experiments may remind one of the case of the fruit fly *Drosophila melanogaster,* transformed into a model organism for genetic research around the same time Baur found his first mutants. New *Drosophila* mutants emerged one after another among the new inhabitants of the Columbia University in New York during the experiments on the coupling of genes. Kohler has described this system as "a breeder reactor."[60] Thus in 1919, Thomas H. Morgan and his crew had found some 100 mutants in *Drosophila* so far.

1919 was not a big year in the history of genetics. Nevertheless, there were three important—albeit different—publications that entailed a summary of the knowledge about mutations. All three believed in the decisive role of mutations for the evolutionary process.[61] However, Baur put 'water into the wine': "What we have is enough to describe the formation of new races but we have not enough variations to describe the formation of new species."[62] Baur's primary problem was that most of the mutations found so far were recessive in genetic terms. According to a common interpretation a recessive mutation was just the loss of the normal function of a gene. This became now a problem because from an evolutionary perspective some of the mutations might have been good for agricultural purposes but, in general, the pool of valuable mutations was limited.[63] Baur realized this in 1919 and actually became depressed.

However, Baur was a go-getter by conviction and blamed the theory for finding no more mutants. His target became the presence-absence theory that was originally about the difference between recessive and dominant genes. With respect to this common idea, a recessive mutation meant a loss in the function of a hereditary unit. As early as 1911, Baur had been sceptical about

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57 Baur, Bedeutung 1925, p. 111.
58 Baur, Mutationen 1918, pp. 177 and 188.
59 Baur, Untersuchungen 1924, pp. 100 f. Baur estimated to have found over 40 (recessive, heterozygous) mutations. Baur, Einführung 1919, p. 287.
60 Kohler, Lords 1994, p. 47; for a recent approach see Dotan, Interrogation 2006.
61 I refer here to Morgan's "The Physical Basis of Heredity" (p. 269), a paper of Hermann Muller and Edgar Altenburg on "The Rate of Change of Hereditary Factors in Drosophila" (Muller, Studies 1962, pp. 217-220), and the third edition of Baur's handbook "Introduction into Heredity Research" (p. 346).
62 Baur, Einführung 1919, p. 345.
63 In 1911, Baur still agreed with the "presence-absence theory." He pointed out that his experimental results were in accordance to those of his friend Hermann Nilsson-Ehle at the Svalöf agricultural station. Baur, Einführung 1911, p. 197. However, Nilsson-Ehle was more consequent in concluding that the combination of genes provided the material for evolution not mutations. Baur, Untersuchungen 1924, 146 f.

that concept. It is not "imaginable that the complete variety of forms is due to the progressive loss of genetic units."[64] Some years later, he complained that the idea of a loss of function had slowly changed into a statement about the material essence of mutations. Most geneticists would now think that a mutation meant the *material* loss of the substance of a gene.[65] Baur annotated in a sudden philosophical inspiration that this story should be a cautioning example of how language controls our conceptions.[66] Of course, the main message of Baur was that the distinction between genetic material and the object of experiment, the genetic factor, was more important than ever. Thus following the isolation of World War I, Baur angrily reappeared on the scientific scene, directly doubting the value of the presence-absence theory.[67] Its "fatal role" had been to block the idea that mutations are rather diverse.[68]

To direct the attention from the quantity to the diversity of mutations was a crucial move in the transformation that Baur's experimental system would experience in the next years. The year of 1919 became the actual turning point of Baur's efforts, for now mutations became the key object of his research. Two years later, Baur presented a plan how to check on the mutations on the first congress of the German Society for Genetics. His confidence to domesticate the tramped and invisible mutations was formed by two choices:

1. He now interpreted his former findings of mutants not so much as a product of a lucky glance, but as the product of the conditions of the experiment; in other words by artificial chance. Most mutations were overseen by researchers, "myself included," and are only found "by chance" through ongoing experiments "*representing material that was selected by their striking appearance.*"[69] The findings had now changed into technical shortcomings of the experimental system that meant, practically speaking, that Baur had to eliminate chance.
2. Using the new term diversity ("Mannigfaltigkeit"), Baur introduced a new distinction into the realm of the so far known mutants. By that phenomenological term he redefined the problem of mutation research. Of course, there was the question of the frequency of mutations. "A completely different question is whether the diversity of mutations is sufficient to provide material that is rich enough for the selection process."[70] This new emphasis on the quality of mutations redirected the problem of the frequency of mutations that was even more virulent because of the shortcomings of the presence-absence theory. The mutations Baur had found became his 'white knight.' Baur's chief witness was the case of the mutant that had shown up only in the third generation as the pattern of the bet. Nobody had thought that these mutations could be different because they had not been noticed until then.[71] This idea became more plausible in the light of the "norm of reaction" that implicated that there were mutations that overlapped with the slightest non-hereditary modifications of the individual.

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64 Baur, Einführung 1911, p. 198.
65 Baur, Einführung 1914, p. 149.
66 Ibid., p. 150.
67 Baur, Mutationen 1918, p. 178.
68 Baur, Einführung 1919, p. 344.
69 Baur, Anzahl 1921, p. 241. Emphasis by AS. Baur, Untersuchungen 1924, p. 142.
70 Baur, Einführung 1919, p. 343.
71 Ibid., p. 344.

> It is possible, no, it is probable that small mutations, whose curves of modification overlap with those of the wild race, are usually overlooked.[72]

Baur had already considered that possibility in 1911. In 1921, it became an apodictic proposition that guided the upcoming practical transmutation of the experimental system. Eliminating chance meant to enter into a competition to find more of the "little mutants" and above all the "'barely noticeable' ["eben noch gerade"], slightest mutants."[73]

> It is not possible to notice most mutations as such, neither most of the mutations in the controlled breeding cultures of our best studied experimental animals and plants! In order to find all mutations that have been arisen one has to introduce special experimental condition never realised until now.[74]

The mutations had been lucky moments in Baur's experimental system that could now be described as statistical events. Now they became a matter of technical chance. The production depended on the correct arrangement of the experiment. The path Baur would choose was already predetermined by his conceptual idiosyncrasy that originated in experiments 15 years prior; namely his obsession with the evolutionary process and the recent experimental experience made on the soil of Potsdam.[75] Thus, the key target of Baur's experimental calculus became the recessive mutations that usually first appeared in a heterozygous form and in almost unchanged plants.

Also, these mutations began to naturalize—but not in the sense that Baur now introduced a material correlate. Instead he introduced a classification into the former continuous realm of small to big mutations. The big divide became the distinction of normal mutations and pathological mutations suggesting that these both classes correlated with the scale of effects.[76] Actually, only around that time Baur associated eugenic sentiments with the epistemic problem of mutations. The impact of eugenic normalisation legitimized Baur to introduce a dual classification equating big mutations with pathologic mutants and small mutations with the useful diversity representing the material of evolution.[77] Baur's message when speaking to the geneticist society was that "people in general would think today that most mutants are deformities. Therefore they are not candidates for evolution […] However, the many small mutations, which are quite good for evolution are normally overlooked."[78] It was in this social-technical constellation that Baur developed a naturalising speech about small and large mutations, suggesting that they represented a sort of natural type of their own right, although they still belonged to the same recessive type of Mendelian inheritance.

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72 Baur, Einführung 1911, p. 266.
73 Baur, Bedeutung 1925, p. 114.
74 Baur, Einführung 1922, p. 32.
75 Not mentioned here are further reasons why just recessive and heterozygous mutations became central in Baur's experiments, see footnote 99.
76 Canguilhem has described this pattern of modern normalisation when he showed how distinctions were reintroduced in Broussais' quantitative order of continuous scales. Canguilhem, Normal 1991, p. 56.
77 The role of mutations for the eugenic mobilisation of geneticists has not until now been well investigated. It seems that the mobilisation came together with the rise of the mutational dispositive in the 1920s. The examples of Muller and Baur at the very least confirm this guess.
78 Baur, Anzahl 1921.

Baur's inbreeding system: a new breeding system for the domestication of mutations

Beginning in 1922, in order to overcome all the hindrances that made the detection of small mutations a matter of chance, Baur introduced a new breeding system. It was however not completely new, but a transformation of his "Stammpflanzen" system.

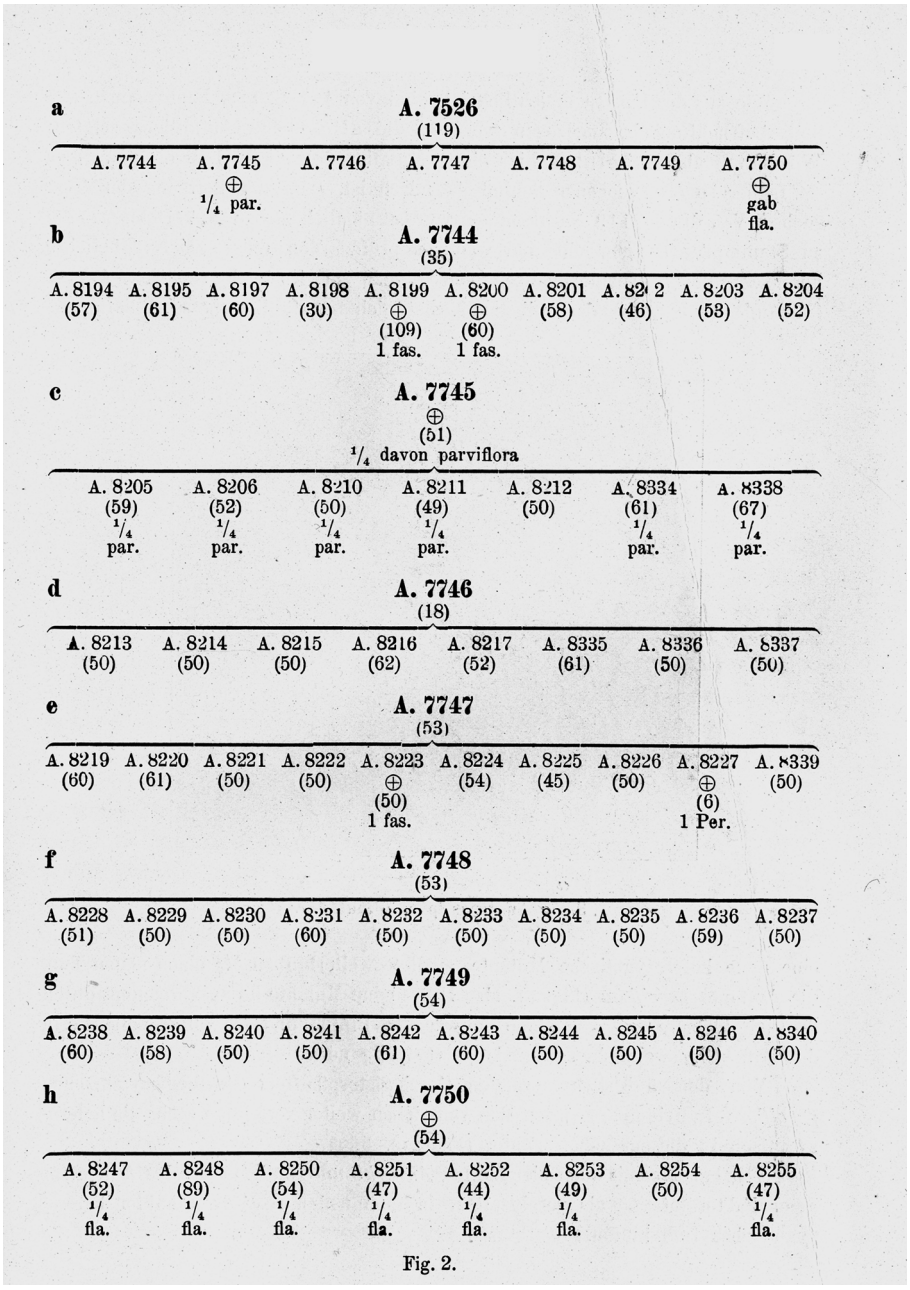

Figure 3: This genealogic chart depicts Baur's strategy to detect recessive, inconspicuous mutations. It was based purely on inbreeding and showed hierarchically the accumulated progeny of one individual (A.7526). Source: Baur, Untersuchungen II 1926, p. 253.

The genealogic chart in figure 3 shows the descent of the plant A.7526. This kind of pedigree differed at some decisive points from the schema that represented Baur's "Stammpflanzen" breeding system. First of all, the experiment did not start with the crossing of two individuals, but rather with the self-fertilisation of plant A.7526. Baur now profited from the resources he had established by then with over 4.000 "Stammpflanthat were supposed to be pure lines.[79] But the reference system of the "Stammpflanzen" was now outstripped. The experiment system focussed on the very progeny of one plant.

Although now the experiment was limited to one ancestral lineage, it was still open-ended. Each breeding extended the statistic basis of the calculation. And the numbers grew rapidly because Baur did not just select one or two individuals from the offspring (F1). He now claimed that this limitation had been the critical chance moment as it was unlikely that he caught the single plant carrying a recessive mutation out of 1.000 offspring.[80] Baur now chose several individuals in order to inbreed them.[81] He used his experienced glance to select just those individuals who seemed to be promising candidates for mutants.[82] Afterwards, he inspected the second generation to see whether a mutation arose. In the example (see figure 3) Baur selected seven plants (A.7744 to A.7750). The progeny of these plants is shown in lines b to h.

However, at that point the experiment was still not complete. Baur repeated the same procedure now with 53 plants of the second generation (A.8194 to A.8255). The principle of his inbreeding scheme now becomes clear: the chart shows only the plants of one generation that were selected for further inbreeding. The family tree expanded rapidly. The small numbers in brackets showed the individuals grown in the third generation (F3) which grew to 3,366 plants. [83] Each plant functioned not only as a test of the mutational status of the grand-mother generation, but also as the starting point for the investigation in the next generations. The calculus of Baur was that he could accumulate the number of inbred plants and of mutants deliberately over generations and calculate the rate of mutation. The transformation of the old system narrowed the scope of the experiment in terms of a clear-cut hierarchical descent schema forming a eugenically-based model inbreeding family tree. However, at the same time the experiment was widened with respect to its statistical basis.

Baur was rather content. Mutants proliferated and in 1924, Baur published a comprehensive overview of his experiments with *Antirrhinum* and all mutations found. He reported that he had found 5% mutation rate in one inbred family.[84] This was a true success since, in 1918, he had calculated a rate of recessive mutations of only 0.2% and the scale now seemed to be open. The experiment illustrated in figure 3 was introduced by Baur one year later. He reported five mutants and calculated a rate of mutation of 6-7%.[85] When Baur presented these results to the surprised

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79 See the examples in Baur, Mutationen 1918.
80 Baur, Untersuchungen 1924, p. 143.
81 Baur, Untersuchungen II 1926, p. 253. Baur announced that one should select at least 30 or 100 siblings. Baur, Einführung 1930, p. 316; Baur, Einführung 1922, p. 372. However, the number was not essential because the experiment did not depend on the number selected in one generation but the accumulated number across all generations.
82 Baur, Mutationen 1918, p. 184.
83 Altogether, Baur checked 4.000 individuals including the third generation. Baur, Untersuchungen II 1926, pp. 255 f.
84 Baur, Untersuchungen 1924, p. 144.

German geneticists in 1925, he pointed out that he had expected a mutation rate of 10%—an immense proportion.[86] There was an immediate resonance amongst the German geneticists who were already speaking of the revival of the selection theory. Asked by a newspaper, Max Hartmann pointed out that the experimental "Vererbungsforschung" was on its way to forming the basis for the return of the "doctrine of the natural selection": "*Small mutations that are very frequent* can have an especially significant value for selection—supported by environment and bastardisation."[87] Referring to "small mutations," Hartmann recalled Baur's results.

The conditions of a new type of mutation: the constellation of experiment, evolution and eugenics

The transformation of the frequency problem of mutations into the frequent variety of mutations paid off. Baur had successfully merged the methodological pitfalls of genetic research, the needs of the evolutionary process and the evaluation of mutations. The breeders—and Baur included himself—had not realised that this realm of small mutants existed because they were both only able to use their eyes and had been only interested in striking mutants.[88]

Although Baur had learned to consider this situation as an artefact of the normal breeding dispositiv, now—when the mutations proliferated—there was no hindrance to re-naturalise the whole setting of the experiment. This was now an easy step after Baur had started to introduce the evaluation of the mutants in evolutionary and eugenic terms. Thus, by linking the agricultural dispositive, evolutionary mechanisms and eugenic normalization, it became obvious that the striking mutants were an artefact of the selection of the breeder as they normally would have been extinguished by natural selection.[89]

Nature and evolution left no doubt about the abnormal character of the commonly found mutants and their artificial existence. Most would actually admit that most of the "conspicuous" mutants are "almost without exception deformations" or "distinct pelories."[90] By contrast, the small mutations were in reality not only more frequent, but also they "do not belong to the field of the pathological, but are absolutely viable types."[91]

> The small mutations […] are of very different kind, they determine small differences in the colour of leaves, the colour of blossoms, the relative length of anthera, the manner of hair patterns, the size of seeds, etc. In short they form an enormous variety ["Mannigfaltigkeit"]![92]

Thus, small mutations affect

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85 There were 70 plants (in the chart: A.7526 to A.8255) whose progeny had been screened for mutations. Baur, Untersuchungen II 1926, pp. 255 f.
86 Baur, Bedeutung 1925, p. 112.
87 Max Hartmann: Die Lehre von der natürlichen Zuchtwahl überholt?, in: Berliner Tageblatt, Nr. 496, 1. Beiblatt, 1926.
88 Baur, Einführung 1930, p. 398.
89 Baur, Untersuchungen 1924, p. 147.
90 Baur, Anzahl 1921, p. 241; Baur, Bedeutung 1925, p. 111.
91 Baur, 1925 Bedeutung, p. 111.
92 Baur, Bedeutung 1925, p. 113.

> all possible morphological and physiological attributes of an organism. They do not determine changes that are monstrosities or pathologies but changes that are within the norm, that do not decrease viability, but can increase it.[93]

The effects of small mutations were small in scale but potent. As such, they were similar to those traits that constituted the species. Small mutations

> are normally within the frame of physiology. *In the case that factor mutations will in general likely provide the material for natural selection, and thus for evolution, small mutations will be the candidates.*[94]

Baur's mutual mobilisation of techniques, concepts and beliefs finally resulted in the deification of both small mutations and large ones. Against the common thinking, Baur pointed out that striking mutations were not usual but rather the "extreme cases."[95] Instead, the small and "smallest mutations" (Baur) turned out to be the normal, that is, natural cases. To make this difference clear, Baur introduced the proper name "Kleinmutationen."[96]

> Most of all mutations are—as far as I can see—mutations of this *mode*.[97]

Recalling the statements of Kühn and Timoféeff-Ressovsky in the beginning of the 1930s, small mutations and large ones became types with an epistemic status somewhere between their use as tool and true natural kinds.

The new system that bore Baur's wave of mutations was full of traces that reflected the material work of Baur as a biologist and his convictions as an evolutionist. He always believed in selection theory and was deeply impressed by de Vries' project of an experimental approach towards the "synthesis of species." Beginning in 1907, the concept of the norm of reaction gave rise to the idea of "small changes." Around 1910, Baur mentioned small hereditary changes as a subject of evolutionary change and the material for agricultural domestication. Additionally, Baur's first breeding system pre-formed the development of his mutation research. Practically speaking, the "Stammpflanzen" system became the starting point of the inbreeding system. The pure lines stored so far provided the material for the experiments started since 1922. Additionally, the choice of his experimental object mattered because the mutations detection system was only realisable with an autogamous plant such as *Antirrhinum* and not with model organisms like *Drosophila*.[98] Another condition and line of research should be mentioned here. The experimental system for the detection of mutations entailed a crucial decision about the moment when mutations occur in the development of an organism. Baur performed extended experiments on that problem that finally emphasised the relevance of recessive mutations and of artificial chance.[99]

It is noteworthy that this constellation was strong enough to rule out conceptual claims such as the "presence-absence theory," the combinatory concept of selection theory and, last but not

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93 Baur, Untersuchungen 1924, p. 143.
94 Baur, Einführung 1930, p. 398.
95 Baur, Bedeutung 1925, p. 111.
96 Baur, Untersuchungen 1924, p. 146.
97 Baur, Bedeutung 1925, p. 112. Emphasis by AS.
98 Baur, Bedeutung 1925, pp. 113 and 115; Baur, Einführung 1930, p. 316.

least, the concept of pure lines. In 1924, Baur explained that the path breaking concept of pure lines had been revealed as a hindrance for the new view of mutations because it favoured perceiving modifications where actually small mutations were at work. The comment of Baur is worth citing at length:

> We have—impressed by the basic studies of Johannsen on the constancy of pure lines—overestimated constancy. I do not want to criticize Johansson, neither his method nor his conclusions. […] But also in this case the successors of Johannsen were rather orthodox ["päpstlicher als der Papst"]. Johannsen himself did not speculate on the occurrence of mutations. But in general, the idea became widely appreciated that mutations and factor mutations were something uncommon and rare and that there are only monstrosities coming out of them. In effect, we have a completely false estimation of the frequency and the variability of factor mutations, probably because of a total "ignorabimus" in the question of evolution or because of trials to explain evolution by natural selection of combinations (see Lotsy and Heribert Nilsson).[100]

Outlook: Baur's story in the context of biomedical research from the 1920s on

The history presented shows how a specialised experimental system for the domestication of mutations evolved out of the practical and situated heritage of the botanical and agricultural research of Erwin Baur. Considering the conceptual and practical constellation, it becomes clear why no other geneticists chose the path that Baur did. Baur was not the only one who was puzzled about small mutants, which appear to be part of the longer plan of Neo-Darwinian geneticists. For example, Thomas Hunt Morgan made up his mind about small mutations, but those mutations fell behind because he was too busy counting the larger ones.[101] Also, Hermann Muller prominently mentioned Baur's "elusive class of 'invisible' mutations" in his article on the artificial inducement of mutations in 1927.[102] Muller himself reported cases of mutants that decreased viability or produced other "invisible" and "inconspicuous" effects. Baur's experiments on Antirrhinum in particular had proven the existence of mutants "that approached or overlapped the normal type to such an extent that ordinarily they would have escaped observation."[103] However, those mutations that were especially important for the question of natural selection "were not subjected to study" as Muller put it.[104] In other words, the trajectory of Muller's

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[99] Baur recognised this as a key question of mutation research since roughly 1918. Baur was finally convinced that most mutations happened just at the moment when a sexual cell formed in the plant. Thus, normally only one egg was mutated and, consequently, *only one* plant of the offspring carried a mutation. Baur, Untersuchung II 1926, p. 255. This model of the generation of mutations supported Baur's view of chance because he was unlikely to select just the single plant carrying a heterozygous mutation.

[100] Baur, Untersuchungen 1924.

[101] Kohler, Lords 1994, pp. 39 ff. For Morgan's mutation experiments in particular see Dotan, Interrogation 2006.

[102] Muller, Studies 1962 [Artificial Transmutation of the Gene, in: Science 1927], p. 246.

[103] Ibid., p. 247.

[104] Ibid., p. 246.

experimental work established another specialized experimental system for detecting mutations. His system had its own special protagonists: lethal mutations.[105]

In general, Baur shared a growing interest in mutations among geneticists. His inbreeding system was just one approach that evolved in order to proliferate mutations. Other approaches would be part of a more comprehensive history. This history would show that different interests were connected to variant trials to domesticate mutations. It would embrace both the artificial induction of mutations and the detection of "natural" ones. Not all of these activities were tied to evolution or used the same model organism, but there was a field of activities grouped around mutants forming. Thus, the German geneticists Kühn and Timoféeff-Ressovsky considered "Kleinmutationen" as a research tool and envisioned special breeding stations for experimental animals that should serve biomedical research by screening animals for hidden mutants.[106] Mutants became a type of "leading technology" in a variety of fields including medicine, agriculture, eugenics and biomedical research. The domestication of mutations became an aim that served different interests and resulted in a growing experimental culture of mutation that embraced different experimental objects, manipulative agents, breeding techniques and interests.

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[105] Muller, Studies 1962 [The Problem of Genic Modification, lecture in Berlin 1928], p. 253.
[106] Schwerin, Experimentalisierung 2004, pp. 175 f.

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Heredity and the Century of the Gene

Raphael Falk

Concluding remarks

This has been the 4th of the series of workshops on *A Cultural History of Heredity*, and it was entitled "heredity and the century of the gene." Let me start by challenging the headline of the workshop and claim that it gives a twisted view of the cultural history of heredity. As has been pointed out repeatedly by different speakers during the last days, to the extent that the gene took a central position in the history of genetics, this changed dramatically in the 1960s. It is true that, as noted by Hans-Jörg Rheinberger, "a gene is a gene, is a gene." This gene, however, became increasingly a bewildering concept and it has served more and more just as a *generic* term, like 'table' or 'chair', rather than as a specific structural entity. In spite of an attempt like that of Lenny Moss to rescue the gene concept by introducing two distinctive modes, of a gene-P and a gene-D, and Evelyn Fox Keller's suggestion of a shift from a "discourse of gene *action*" to that of "gene *activation*" —although, as we learned from her talk last night, she has been accused to lead a jihad against the gene—I suggest that the shift was elsewhere in the cultural level of the history of heredity, namely in the role of reductionist conceptions in genetic research. In two workshops on "Representing genes," organized a couple of years ago by Karola Stotz and Paul Griffiths in Pittsburgh, we ended up with more than a dozen different phenomena in our attempts to define "a gene." In the recent book of Bob Weinberg, *The Biology of Cancer*, the term "gene" as such does not appear at all in the glossary; there are only items like "gene amplification," "gene family," "gene pool" etc.

It is not in vain that the previous workshops of this series on the Cultural History of Heredity started with the 17th and 18th centuries. Indeed, if we insist on parsing the centuries of the cultural history of research on heredity, I suggest that we start with Linnaeus. The century from 1750 to1860 being the Century of Rationality (for the lack of a better name), with Darwin at its peak; the century from 1860 to1960—starting with Mendel and ending with Crick—as the Century of Reductionism; and starting in the 1960s, the so-far half Century of Integration, of the genome, the proteome, and the return of evo-devo.

The publication of Linnaeus' Systema naturae in 1735 and the fixation of the systems of nature on the one hand, and the publication of the first three volumes of Buffon's *Histoire naturelle* in 1749, on the flexibility of nature, introduced the century of claims for rational research of biological synthesis of change. It was characterized by two major research modes: The one, leading from Linnaeus through Koelreuter and Gärtner to Mendel, put the emphasis on *hybridization* as a mode of research. The other, leading from Buffon, through Lamarck and Geoffroy Saint Hilaire to Darwin, puts the emphasis on *morphogenesis*, comparative anatomy and embryology as modes of research. Whereas Lamarck's publication of *Philosophie zoologique* in 1802 may be noticed as the significant mid-century event, Darwin's *Origin* of 1859 and Mendel's *Versuche* of 1864 introduce a new century.

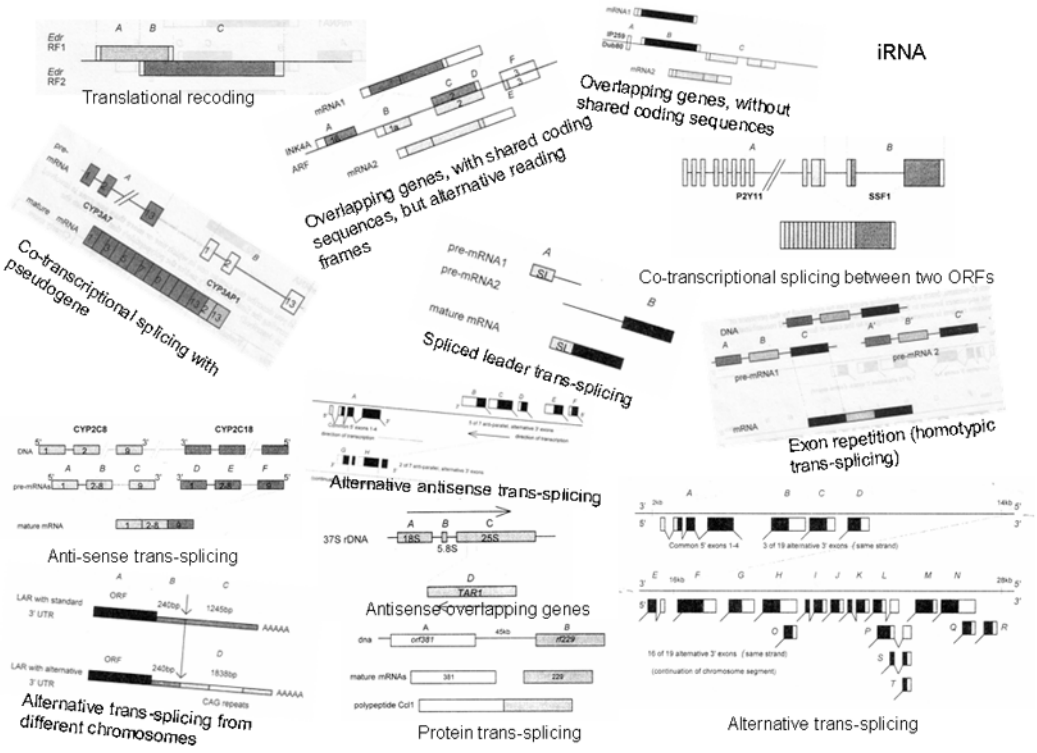

Figure 1. Which one is *the gene* ? Forms proposed by Paul Griffiths and Karola Stotz at a conference in Pittsburgh, 2003.

The second century, which started with the 1860s soon confronted the dialectical conflicts of methodological reduction and conceptual reduction of biological diversity. The *Century of Reductionism* of hereditary research reached its peak with Crick's paper "On protein synthesis" at the Society of Experimental Biology in which he formulated the *Central Dogma of Inheritance,* and with the statement, attributed to Jacques Monod: "Anything found to be true of *E. coli* must also be true of elephants." Morgan's "Chromosomes and heredity" may be considered as the significant mid-century event.

The controversies initiated with the publication of Richard Dawkins' *The Selfish Gene* and Edward O. Wilson's *Sociobiology* were the more spectacular indicators of the demise of the *Century of Reductionism*. Britten and Kohne's discovery that what is true of prokaryotes is *not* true of eukaryotes was one of the earliest experimental findings that heralded the end of the Century of Reductionism. Roberts and Sharp's discovery that genes in eukaryotes are not contiguous strings but contain introns, and that the splicing of messenger RNA to delete introns can occur in different ways, yielding different proteins from the same DNA sequence, opened a new era. Gould and Lewontin's paper on "The spandrels of San Marco and the Panglossian paradigm," challenging the New Synthesis's reduction of evolution to changes in gene frequencies, may be considered as one of the first signals on the conceptual level of the emergence of the third century, the *Century of Integration*.

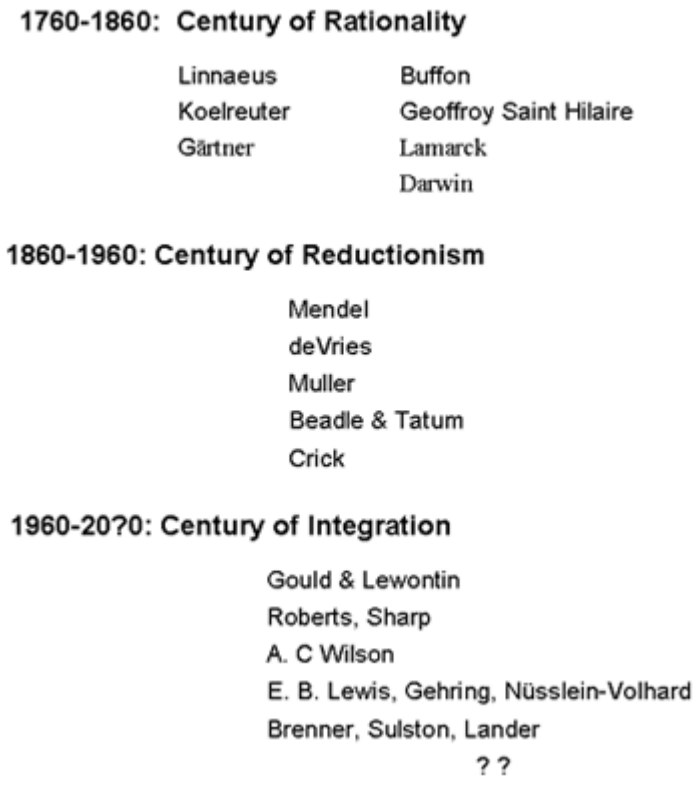

Figure 2. Heredity over the centuries. Source: Raphael Falk.

It was no accident that of the eighteen odd talks in the workshop's program, all but one dealt with the period preceding 1960, that is, with the century of reductionism. Only one, the programmatic talk of Jean Gayon "Widening heredity: From soft to hard inheritance and back" promised to deal with abridging the centuries of reductionism and integration (unfortunately Jean could not present his talk); also Christina Brandt attempted to reach out to integration with the modern notion of clones. Notwithstanding Jon Hodges' comment on the origin of the term "soft inheritance," as Gayon pointed out in his abstract, "The emergence of the concept of 'hard inheritance' was *crucial* to the constitution of an experimental science of heredity" in the 1910s: These were the years of bitter but constructive dialectic confrontation between "experimental" and "conceptual" reductionism in hereditary research. It is too bad that Jean could not elaborate more on this subject. As Jean Gayon wrote in his abstract, the late "relaxing of conceptual and empirical constraints imposed by 'hard' inheritance," was another consequence of the change of the culture of hereditary research, from that of reductionism to integrationism.

For Johannsen pure lines were significant as *instruments* to discern phenotypic from genotypic phenomena. As Judy Schloegel has shown, for Jennings the pure line, and even more so the clone, provided empirical means for the establishment of the *conceptual* reduction of the phenotype to an ultimate genotype. Victor Jollos' *Dauermodifikationen* of "soft" or epigenetic inheritance posed, however, a threat to deterministic reductionist genetics, which could not be tolerated in the

century of reductionism, and was denoted as neo-Lamarckism. I wonder to what extent Jollos's difficulties in emigrating from Germany and his short, unhappy period in the US were not another aspect of Veronika Lipphardt's claim that many Jewish-German scientists, who had been immanently neo-Lamarckians because of the aggressive Darwinian claims of German racial scientists, had difficulties when forced to immigrate to the Anglo-American world in which neo-Darwinism prevailed.

It needed conceptual integration (without abandoning reductionism as a heuristic) to re-introduce the top-down perspective as a respected aspect of genetic research, and to investigate group selection, developmental constraints, or the role of epigenetic mechanisms. When I congratulated Marion Lamb on her and Eva Jablonka's first book *Epigenetic Inheritance and Evolution*, suggesting how fortunate they were to publish the right book at the right moment, Marion corrected me, pointing out that it was the other way round: It was their book that helped create the right moment.

By the way, the inventor of the term "gene," Johannsen himself, never liked the term. He consistently rejected the reductionist "unit character," and to the end of his career he continued to talk of genotypical (and phenotypical) variation, and remained reserved towards the meaning of the concept of the gene. As suggested by Staffan Müller-Wille, a scientific basis meant for him a thoroughly instrumental basis. *Conceptually* Johannsen was an organicist, though *instrumentally* he was a reductionist, or as Staffan put it in his talk: "The assumption that the organism is an ensemble of individually reproducing parts drove Johannsen mad."

I am sorry that I cannot dwell on many of the interesting papers of the Workshop in these brief comments.

Greg Radick redirected our attention from the Bateson-Pearson polemic to its more profound foundations, which is actually the Bateson-Weldon polemic. Whereas Bateson—as well as de Vries—abandoned the traditional morphogenic approach to the study of variation of species, to join the competing hybridists' tradition, Weldon adhered to the old tradition of the morphogenicists. Radick highlighted Weldon's criticism of the Mendelians' inbuilt methodological bias of discontinuous classification into a finite number of categories. This may indeed be a serious problem, as shown years later by Raymond Pearl who asked fifteen trained geneticists to classify 532 F_2 corn kernels from a cross of yellow starchy and white sweet varieties. However, one has to keep in mind that Mendel was very much aware of the possible biases of his empirical methodology and devoted two years selecting the proper strains and traits before testing his hypothesis. Indeed, large scale repeats of Mendel's experiments over the years proved upholding his classification.

It may also be kept in mind that already in1902 Udny Yule showed that much of the Pearson/Weldon—Bateson polemics concerned the formulation of the problems: *Mathematically* the Law of Ancestral Heredity could be reduced to that of Mendelian inheritance. Mendelism, Yule pointed out, was focusing on *hybridization*—the study of specific difference-characteristics between *individuals*; The Law of Ancestral Heredity, on the other hand, was concerned with *heredity*. Heredity represents the *population*-aspect of inheritance; it regards the correlation of variance in one generation of the population with that of another. Accordingly, Yule opened his

1903 paper: "The statistical theory of heredity, as developed in the work of Galton and Pearson, concerns itself with aggregates or groups of the population and not with single individuals."

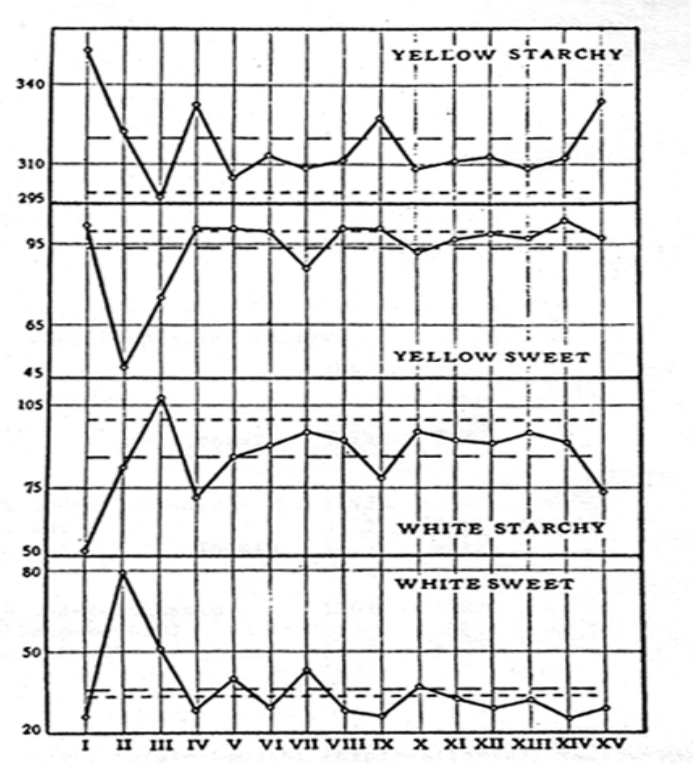

Figure 3. In 1911 Raymond Pearl crossed yellow-starchy with white-sweet homozygous varieties of maize. Fifteen trained scientists (abscissa) counted the same set of 532 F2 kernels (ordinate). The horizontal dotted line gives the Mendelian expectation, and the horizontal dashed line the average of the counts of the fifteen observers. Source: R. S. Root-Bernstein (1983). "Mendel and methodology." History of Science 21: 275-295.

Investigator	Yellow seeds		Green seeds		Total
	No.	%	No.	%	
Mendel, 1865	6,022	(75.05)	2,001	(24.95)	8,023
Correns, 1900	1,394	(75.47)	453	(24.53)	1,847
Tschermak, 1900	3,580	(75.05)	1,190	(24.95)	4,770
Hurst, 1904	1,310	(74.64)	445	(25.36)	1,755
Bateson, 1905	11,902	(75.30)	3,903	(24.70)	15,806
Lock, 1905	1,438	(73.67)	514	(26.33)	1,952
Darbishire, 1909	109,060	(75.09)	36,186	(24.91)	145,246
Totals	134,707	(75.09)	44,692	(24.91)	179,399

Figure 4. Summary of F2 results of seed color in pea crosses, counts of seven studies. Source: E. W. Sinnott & L. C. Dunn (1932). Principles of Genetics. (2nd ed.) New York: McGraw-Hill. p. 48.

Finally, allow me to relate briefly to the two papers to the "left" and to the "right" of Muller's research program of the nature of the *gene*: Luis Campos's paper on Blakeslee's "chromosomal mutations" in *Datura*, and Alexander Schwerin's discussion of Erwin Baur's "Kleinmutationen" in *Antirrhinum*. Muller was, of course, aware of both chromosomal aberrations and minute mutations and on their role in evolution. However, in his programmatic paper of 1922, Muller emphasized that "it is not inheritance *and* variation which bring about evolution, but the inheritance *of* variation, and this in turn is due to the general principle of gene construction which causes persistence of autocatalysis despite the alteration in the structure of the gene itself." His research program was not to review the *kinds* of mutations and their relative contribution to population structure and evolution, but to disclose the *nature of the gene*. Muller was explicitly after the property that makes genes unique, namely mutations, which maintain autocatalysis in spite of change of function, and to do this he needed a *quantitative* analysis of mutagenesis. Blakeslee appropriately opposed the Drosophilists' relentless reductionism, treating organisms "like a child's house of blocks," but it is necessary to discern the difference between Muller's conceptual reductionism and his reductionist heuristics. The collective concept of "mutation" employed by de Vries and his followers only confused matters. Many devices and materials were tried out and proved to be mutagenic in those years. However, it was the establishment of the *ClB*-method that provided the heuristics for the quantitative determination of the efficiency of a mutation inducing agent, which made Muller's 1927 contribution to genetics so unique and justifiably entitled him to the priority he was seeking. And I think it still is a central contribution to the century of hereditary reductionism, in which the gene concept played a central role.

Let me finish my comments by thanking—I hope in the name of all of us—the organizers of this Workshop both at the Centre for Genomics in Exeter, and at the Max-Planck Institute in Berlin, for a pleasant and fruitful conference. Thank you!

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Workshop

Heredity in the Century of the Gene

(A Cultural History of Heredity IV)

December 11-14, 2006

ESRC Research Centre for Genomics in Society, University of Exeter, UK

in collaboration with the

Max-Planck-Institute for the History of Science, Berlin, Germany

Organizers:

Staffan Müller-Wille (Exeter), Hans-Jörg Rheinberger (Berlin), John Dupré (Exeter)

Venue:

Reed Hall

Monday, Dec 11

14:00 *Registration*

14:30 *Welcome*

John Dupré, Staffan Müller-Wille, Hans-Jörg Rheinberger

15:30 *Coffee break*

16:00 *Session I: The Mendelian Break*

Staffan Müller-Wille, University of Exeter

Leaving inheritance behind: Wilhelm Johannsen and the politics of Mendelism

Greg Radick, University of Leeds

The Professor and the Pea: Weldon's Critique of Mendelism

Barry Barnes, University of Exeter

comments

17:50 *Drinks and standing buffet*

Tuesday, Dec 12

09:00 *Session II: Contexts of Heredity*

Ilana Löwy and Jean Paul Gaudillière, Centre de recherche médicine, sciences, santé et societé, Villjuif

Transmission of human pathologies 1900-1940: the elusive "mendelization" of the clinic

Bert Theunissen, University of Utrecht

Breeding Dutch dairy cows (1900-1950): Heredity without Mendelism

Soraya de Chadarevian, University of California, Los Angeles

comments

10:50 *Coffee break*

11:20 Daniel Kevles, Yale University, New Haven, Ct.

Innovation and Ownership in New Fruits: The Horticultural Industry and Intellectual Property in the United States, 1880-1930

Maria Kronfeldner, Max-Planck-Institute for the History of Science, Berlin

Coalition and Opposition: Heredity, Culture, and the Boundaries of Anthropology in the Work of Alfred L. Kroeber

Edna Suarez, Max-Planck-Institute for the History of Science, Berlin

comments

13:10 *Lunch*

14:30 *Social event and dinner*

Wednesday, Dec 13

09:00 *Session III: Breeding and Inheritance*

Christophe Bonneuil, Centre Alexandre Koyré, Paris

What genes could not do: French plant breeders' reception of Mendelism (1900-1930)

Ana Barahona, Universidad Nacional Autonoma México, Mexico City

Mendelism and agriculture in the first decades of the 20th century in Mexico

Jonathan Harwood, University of Manchester

comments

10:50 *Coffee Break*

11:20 *Session V: Heredity and the Creation of Model Organisms*

Judy Jones Schloegel, independent scholar, Clarendon Hills/Ill.

Herbert Spencer Jennings, Heredity, and Protozoa as Model Organisms, 1908-1918

Christina Brandt, Max-Planck-Institute for the History of Science, Berlin

Clones, pure lines and heredity. The work of Victor Jollos

Hans-Jörg Rheinberger, Max-Planck-Institute for the History of Science, Berlin

comments

13:10 *Lunch break*

14:30 *Session IV: Genealogy and its Uses*

Bernd Gausemeier, Max-Planck-Institute for the History of Science, Berlin

Human Heredity and Mendelism: the Case of Psychiatry

Philip Wilson, Penn State University College of Medicine, Hershey (Pennsylvania)

Pedigree charts as tools to visualize inherited disease in progressive era America

15:50 *Coffee break*

16:20 Veronika Lipphardt, Humboldt University, Berlin

Jews as an object of Mendelian research (1900-1935)

Carlos López Beltrán, Universidad Nacional Autonoma México, Mexico City

comments

17:30 *Break*

19:30 *Public evening lecture* (Venue: Queens Lecture Theatre 1)

Evelyn Fox Keller, Massachusetts Institute of Technology, Cambridge, MA

What's in a Word? Genes, Heredity, and Heritability

Thursday, Dec 14:

09:00 *Session VI: Managing Variation*

Marsha Richmond, Wayne State University, Detroit

William Bateson's Pre- and Post-Mendelian Research Program in `Heredity and Development'

Luis Campos, Harvard University, Cambridge/Mass.

Genetics Without Genes: Blakeslee, Datura, and 'Chromosomal Mutations'

10:20 *Coffee break*

10:50 Alexander von Schwerin, Technical University Braunschweig

Seeing, breeding and the organisation of variation – model organisms in the genetics of the twenties

Jonathan Hodge, University of Leeds

comments

12:00 *Lunch break*

12:45 Lenny Moss, University of Exeter

comments

Raphael Falk, Hebrew University, Jerusalem

comments

Final discussion

14:15 *End of workshop*