Hybrids, pure cultures, and pure lines: From nineteenth-century biology to twentieth-century genetics

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Abstract

Prompted by recent recognitions of the omnipresence of horizontal gene transfer among microbial species and the associated emphasis on exchange, rather than isolation, as the driving force of evolution, this essay will reflect on hybridization as one of the central concerns of nineteenth-century biology. I will argue that an emphasis on horizontal exchange was already endorsed by 'biology' when it came into being around 1800 and was brought to full fruition with the emergence of genetics in 1900. The true revolution in nineteenth-century life sciences, I maintain, consisted in a fundamental shift in ontology, which eroded the boundaries between individual and species, and allowed biologists to move up and down the scale of organic complexity. Life became a property extending both 'downwards', to the parts that organisms were composed of, as well as 'upwards', to the collective entities constituted by the relations of exchange and interaction that organisms engage in—order to reproduce. This mode of thinking was crystallized by Gregor Mendel and consolidated in the late nineteenth-century conjunction of biochemistry, microbiology and breeding in agro-industrial settings. This conjunction and its implications are especially exemplified by Wilhelm Johannsen's and Martinus Beijerinck's work on pure lines and cultures. An understanding of the subsequent constraints imposed by the evolutionary synthesis of the twentieth century on models of genetic systems may require us to rethink the history of biology and displace Darwin's theory of natural selection from that history's centre.
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1. Introduction

William Provine once argued that the evolutionary 'synthesis' of the 1930s and 1940s should rather be called an 'evolutionary constriction', because it consisted in 'a vast cut-down in variables considered important in the evolutionary process' (Provine, 1992, pp. 176–177). One of the most notable exclusions was hybridization, which many pre-synthesis evolutionists believed to be an important factor in evolution. Speciation was supposed to occur exclusively through the geographical separation of populations and subsequent independent development of these populations, resulting in their genetic isolation. Recent advances in understanding microbial phylogeny and evolution present a picture that extends far beyond this 'sterile conception of evolution' (Sapp, 2007, this section) and brings

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back an alternative view of evolution that emphasizes exchange, rather than isolation, as a driving force of evolution (see the tables in Sapp 2003, p. 205).

In this essay I want to take a look at hybridization as one of the central concerns of nineteenth-century biology. In particular, I will argue that the emphasis on horizontal exchange, that currently preoccupies present-day evolutionary microbiology and microbial phylogeny (e.g. Gogarten & Townshend, 2005), was 1) endorsed already by 'biology' when it came into being around 1800, and 2) brought to full fruition with the emergence of genetics in 1900. Attention to microscopic and sub-microscopic entities accompanied these two defining events in the history of biology, but was not sufficient to bring them about. Size, to put it differently, never mattered for biology (cf. O'Malley & Dupré 2007). What mattered instead was a fundamental shift in ontology that eroded the age old dichotomy of individual and species, and allowed biologists to move up and down the scale of organic complexity. Life became a property extending both 'downwards', to the parts ('organic molecules', cells, tissues, organs) that organisms were composed of, as well as 'upwards', to the collective entities (varieties, species, ecosystems like coral reefs) constituted by the relations of exchange and interaction that organisms engage in order to reproduce. The 'constriction' that was brought about by the modern synthesis thus appears to document a tactical move, rather than a conceptual revolution. It was meant to save classical natural history—the natural history of paradigmatic organisms like insects, birds and mammals (including humans), and its clear-cut distinction of individuals and species—from the consequences of this shift in ontology.

2. What biology is

It is a well established historical fact that the term 'biology' only came into use around 1800. Michel Foucault and François Jacob, in particular, have identified 'organization' as the key concept of the new science, which Jean-Baptiste Lamarck and Gottfried Reinhold Treviranus termed 'biology' in 1802 (Foucault, 1966, pp. 238–245; Jacob, 1993, Ch. 2). To gain a full understanding of this terminological innovation, however, it is important to recognize the inter-individual dimensions of the concept of 'organization'. On the face of it, organization seems to refer to the individual organic body and its peculiar structure. However, as both Foucault and Jacob emphasized, it was the 'hidden architecture' (Jacob, 1993, p. 82) of reproductive relations connecting parts of organized wholes, rather than their manifest structure, which became the focus of 'biology'. Organic functions like generation, growth, development, nutrition and sensation were increasingly perceived not as functions carried out by individual entities, but as functions resulting from the coordinated interaction of individ-

ual, but interdependent entities (Roger, 1993, pp. 567–582; Jacob, 1993, pp. 88–92; Lenoir, 1982, Ch. 1; McLaughlin, 1990, pp. 44–51). Georges Louis Leclerc Comte de Buffon (1707–1788) had already expressed this programmatically in 1749:

> The history [. . . of the species] ought to treat only relations, which the things of nature have among themselves and with us. The history of an animal ought to be not only the history of the individual, but that of the entire species. It ought to include their conception, the time of gestation, their birth, the number of young, the care shown by the parents, their sort of education, their instinct, the places where they live, their nourishment and their manner of procuring it, their customs, their instinctual cleverness, their hunting, and, finally, the services which they can render to us and all the uses which we can make of them. (Quoted from Lyon & Sloan, 1981, p. 111)

Along similar lines, Buffon's life-long rival and adversary, the Swedish botanist Carl Linnaeus, claimed that one had to follow 'the various routes through the vast provinces of the kingdom of plants', and observe the budding, the annual succession, the development, the habitats, the flowering, and the ecology of plants, 'to understand the nature of plants correctly' (Linnaeus, 1788, pp. 109–110).[1] The 'life of the species'—*das Leben der Gattung* as the German naturalist and teacher of Georges Cuvier, Carl Friedrich Kielmeyer, called it (Kielmeyer, 1993, p. 5)—or the vital processes connecting a multiplicity of beings became the subject of biology. Kielmeyer made it clear, in this context, that 'life' as he understood it extended both ways, both 'down' to the 'organs' and 'organic materials' making up individual bodies, and 'up' to 'that higher system of effects' that connected members of a species, and species in the 'natural system' (Lenoir, 1982, pp. 38–39). Generation, that age old, enigmatic concept, began to develop a Janus face in consequence. On the one hand generation came to designate the delicate moment in which a fragment of an organism broke away (or two fragments broke away to unite in a third) and started to develop and multiply on its own, thereby forming a new being. Early cell theory thrived on analogies between the world of 'infusoria' and the elementary components of more complex organisms, considering 'the small organism as an element of the large one' (Jacob, 1993, p. 116). Organisms came to be seen as integrated collectives, a 'plant or an animal represented a colony of . . . smaller individuals' (Sapp, 2003, p. 83). On the other hand, generation began to acquire a new, additional meaning, that of a collective of individual organisms sharing the same age, whether they formed a population born around the same time or whether they occupied the same developmental stage. This was a conceptual innovation of fundamental importance for nineteenth-century

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[1] All translations are my own unless otherwise stated.

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biology, since it prepared the framework in which it became possible to see variation and inheritance as interconnected problems of hereditary transmission (Parnes, 2007). 'Evolutionary history' (*Entwicklungsgeschichte*), most notably in the work of Karl Ernst von Baer, became a term that systematically articulated the development of individuals alongside the generational succession of beings. Both the cell lineages making up individual bodies, and the genealogical lineages making up species, formed a single tree of life (Lenoir, 1982, pp. 72–95). This was a tree, to be sure, bifurcating *and* anastomosing, but a coral reef rather than an oak tree of life (Müller-Wille, 2007).

3. Hybrids and life's maelstrom

A research tradition in the nineteenth century which made consistent and conscious use of this perspective on evolution was the research tradition of 'hybridism'. It included such figures as Karl Friedrich Gärtner, Charles Naudin, William Herbert, Charles Darwin, Carl Nägeli, and, somewhat erratically, Gregor Mendel. This tradition has been systematically underrated in the aftermath of the modern synthesis. Since the mid eighteenth century, hybridization was identified as a source of variation, alongside migration and subsequent climatic degeneration, which were factors that could explain the puzzling distributional patterns biogeographers and palaeontologists came up with (Larson, 1994, Ch. 3). By the mid nineteenth century hybridization had come to be seen as a process subject to 'evolutionary laws' (*Entwickelungsgesetze*) that could be uncovered by experimental and mathematical means (Gliboff 1999). Hybrids had once been paradigmatic for the irregularities occasionally produced by nature (Zirkle 1935).[2] With the advent of the modern period they became constitutive of the natural order.

In hindsight, and with the adoption of Ernst Mayr's so-called biological species concept, the research tradition of hybridism appears to be hopelessly confused. In so far as hybridists were interested in the origin of species, their observations and experiments could amount to nothing. The 'species' they worked with were either 'good' species, in which case they failed to produce fertile offspring and thus contributed nothing to the evolution of organic forms, or they were mere varieties whose combination, while resulting in fertile offspring, would not by themselves transcend the variation that was present anyway within the species to which they belonged. Hybridization, therefore, could well be a source for intraspecific variation but could not by itself account for the origin of new species. For that, other processes, notably mutation and geographic isolation, had to be taken into account. It is in this sense, for example, that Ernst Mayr maintained that Gregor Mendel 'had little idea what a species was' (Mayr, 1982, pp. 712–

713). The agenda of hybridizers went far beyond a mere preoccupation with the origin of new species, however. Gärtner, one of the most influential early hybridizers, formulated this agenda as one of 'determining' species. 'The question of what distinguishes species from varieties', Gärtner explained,

> is . . . a purely biological one: a secure foundation for determining species cannot be found solely in abstraction, neither in the characters, nor in the intermediate forms, but has to be sought in reflection, that is in the individual history [*individuellen Geschichte*] of each species, its whole development [*Entwickelung*], and not in a particular aspect only. (Gärtner, 1849, p. 151)

What Gärtner had in mind with the philosophical term 'reflection' becomes clearer when one looks at the definition he gave of species:

> The essence of the species . . . consists in the determined relationship its sexual forces possess with respect to other species. This relationship, in addition to the specific form, is a proper, particular, and constant one in each species. In this respect, form and essence are one. (Ibid., p. 163; translation partly based on Olby, 1985, p. 33)

What distinguishes species are not the characters that this or that particular organic form might possess—'external affinities' as Gärtner called them—but the constant effects that were produced when one organism, or rather part of an organism, acted on another to produce a third. Hybridization was a means to uncover the 'internal' or 'elective' affinities among organisms (Olby, 1985, Ch. 2).

Two remarks are pertinent here. The first pertains to the chemical analogies Gärtner employed. 'Elective affinity' was a chemical term at the time, referring to the ability of certain substances to displace others from a chemical compound. Gärtner was careful, however, not to equate life with chemistry. The analogy referred to the possibility of analysing life in a similar manner to the way chemists analysed 'dead nature' rather than to the subject matter of that analysis. With respect to organisms one had to assume that it was

> the two material substrates of the sexes in plants and their mutual attraction which cause the ability to produce hybrids. In what, however, the particular quality of one or the other factor consists, can neither be answered by microscopic nor chemical examinations, as we are dealing with a purely vital activity. (Gärtner, 1849, p. 186)

Life, therefore, could not be analysed adequately simply by subjecting organisms to external observation and chemical operations. Life had to be analysed by manipulating life by life itself, by having living entities act on one another, just

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[2] Bazopoulou-Kykanidou (2001) shows that this view still dominates public discourses about biotechnology.

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like the chemist determined chemical substances by letting such substances react with one another.

The second point pertains to the ease with which Gärtner switches from talking about organisms to talking about the submicroscopic entities ('factors') that mediate their reproduction. It was Gregor Mendel, in his famous experiments with peas, who made full use of this metaphorical potential, by systematically drawing analogies between whole organisms, individual traits and 'elements' contained in reproductive cells. As is well known, Mendel used pea varieties in his experiments that differed from one another only with respect to a single character pair, and he assumed that the gametes that these varieties produced were equally distinguished by a single difference only. By bringing such gametes together through hybridization, Mendel was thus able to manipulate his experimental plants at precisely defined, albeit invisible, points of overall organization, all the way from the organismic down to the cellular level. It follows from this that Mendel's theoretical approach was biological through and through. Although he followed a reductive strategy in explanation, the cytological 'elements' he identified as being involved in the determination of plant form were neither chemical substances, nor organic forces, but structural (though not necessarily particulate) elements of reproductive cells. What Mendel achieved by his experimental analysis was a kind of anatomy of inheritance (Müller-Wille & Orel, 2007).

While the way in which Mendel presented his results may have seemed idiosyncratic to his contemporaries, the general reasoning that underwrote his experiments was not. By the mid nineteenth century organic reproduction had generally come to be seen as a system of circulating elementary entities—Keime and Anlagen as Immanuel Kant had called them—which freely separated themselves from individuals, and combined to form new individuals. Darwin expressed this 'microbiological' perspective on macroscopic life in a passage of his *Variation of plants and animals under domestication* (1868) that merits full quotation.

The fertilized germ of one of the higher animals, subjected as it is to so vast a series of changes from the germinal cell to old age—incessantly agitated by what Quatrefages well calls *tourbillon vital* [the maelstrom of life]—is perhaps the most wonderful object in nature. It is probable that hardly a change of any kind affects either parent, without some mark being left on the germ. But on the doctrine of reversion, as given in this chapter the germ becomes a far more marvelous object, for, besides the visible changes which it undergoes, we must believe that it is crowded with invisible characters, proper to both sexes, to both the right and left side of the body, and to a long line of male and female ancestors separated by hundreds or even thousands of generations from the present time: and these characters, like those written on paper with invisible ink, lie ready to be evolved whenever the organization is disturbed by

certain known or unknown conditions. (Darwin, 1988, pp. 30–31)

Jonathan Hodge has emphasized Darwin's lifelong interest in colonial organisms—an interest which allowed him to draw analogies between entities above the level of the individual organism, such as species and populations, to entities below that level, such as buds, cells and gemmules (Hodge 1985). The same perspective transpires from the passage just quoted. The metaphor of the 'maelstrom of life' makes this particularly clear. It is borrowed from Armand de Quatrefages's *L'espèce humaine*, a book preoccupied with the defence of human monogenism on the basis of the fact that humans of different races freely interbreed. Despite this subject, and despite the book's title, it was not the serendipity of human life that the metaphor of *tourbillon vital* referred to, but rather the 'curious movement . . . in that quasi-carnal substance that covers the calcareous or siliceous skeleton of certain marine organisms' (Quatrefages, 1879, p. 3). Both Darwin and Quatrefages 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.

4. Manipulating life

Robert Olby has demonstrated that Gregor Mendel did not share the twentieth-century notion of genes as paired, particulate, constituent elements of cells (Olby 1979). But neither did the early Mendelians (see, e.g., Meijer 1985). What united early Mendelians, including Mendel himself, was not so much a common model of hereditary transmission, but rather a peculiar style of reasoning. I believe that this style of reasoning can be characterized by two dispositions that make themselves already obvious in Mendel.

(1) A disposition for *reduction*. Mendel, as pointed out above already, worked with pea varieties differing in single character pairs. Yet he referred to these varieties as 'species' (*Arten*), because they bred true, that is, they reproduced their differences constantly under controlled, external conditions. Mendel could thus treat his model organisms as if they were characterized by a very small set of properties only, and he systematically neglected the wealth of properties they possessed in other respects. This connects with a second reductionist move made by Mendel. From the differences in the macroscopic structure of his model organisms, he concluded that their reproductive cells also differed with respect to one 'element' or 'factor' only. He was thus able to present his experiments as instantiating direct manipulations of gametes and zygotes (or *Befruchtungszellen* and *Grundzellen*, as

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he called them). Mendel used his model organisms, therefore, as precision tools for manipulating the unit of life, the cell (Müller-Wille & Orel 2007).

(2) A disposition for *construction*. Through hybridzation, Mendel constructed pedigrees which he regarded not as *objects* of his research but as *tools* to uncover the genetic constitution. He understood the genetic constitution as an organic structure of the parental generation or, more precisely, of the zygotes formed by the parental generation. As the philosopher of biology Jean Gayon put this: '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). Mendel's constructive attitude becomes particularly apparent in his backcrossing experiments. What he proved in these experiments was that a hybrid form, united with one of its parental species, would reproduce the parental, non-hybrid form instantaneously in a determinate fraction of its offspring, because a certain fraction of the hybrid's reproductive cells was of the same kind as the reproductive cells produced by the parental species. In a certain sense, then, it was possible to 'build up' organisms from elementary building blocks, without having to rely on organic forces which could only unfold their effects over historical time spans (as Gärtner, like most nineteenth-century evolutionists, still believed).

Wilhelm Johannsen, the Danish botanist, who in 1903 showed experimentally that selection had no effect in what he called 'pure lines' of organisms, and who in 1909 coined the terms 'gene', 'genotype', and 'phenotype' on this basis (Roll-Hansen, 1989), clearly shared these two dispositions. The first thing to note about his early career in this respect is that he did not start off as a student in botany or zoology, but as an apprentice in pharmacy. By training, Johannsen was a chemist, and chemistry, not physics, was for him, and for many other scientists of his generation, the queen of sciences (Bensaude-Vincent, 2002).

This perspective had far-reaching effects. For Johannsen ancestral inheritance was a 'mystical expression for a fiction' (Johannsen 1911, p. 138), and his contempt for biologists endorsing such views—especially Ernst Haeckel—was profound (Johannsen, 1914). Johannsen stressed that the genotype had to be treated as independent of any life history and thus as an 'ahistoric' entity amenable to analysis just like the objects of chemistry. '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' he stated in 1911, and added: 'I suggest that it is useful to emphasize [a] "radical" ahistoric genotype conception in its strict antagonism to the transmission- or phenotype view' (Johannsen, 1911, p. 139). 'Ancestry by

itself is irrelevant; dispositions are decisive', was how Johannsen put it provocatively in his 1905 textbook *Arvelighedens elementer* (Johannsen, 1905, p. 216).

However, just like Gärtner more than half a century earlier, Johannsen drew this analogy with chemistry not with respect to its subject matter, but with respect to the analytical method it employed. Over his entire career Johannsen astutely resisted the temptation to identify 'genes' or 'genotypes' with any part or particle of the organism, even when the Morgan school was reaching its triumphs by successfully mapping genes to chromosomes. For him, the genotype was not localized in the body of the organism, just as hydrogen and oxygen were not localized in a body of water. Just as elements were chemically defined by the reactions they underwent when forming compounds, genotypes were defined by the 'reactions' they underwent when joined in a zygote. The 'personal qualities' of individual organisms, or the phenotype, resulted from these reactions, but did not determine the genotype.

> 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. (Johannsen, 1911, p. 130; original emphasis)

Despite its reductionism, this was an entirely biological view, as the fundamental elements it referred to were biological entities, not chemical or physical ones.

This is where the next step in Johannsen's career becomes relevant, as it added an even stronger biological element. In 1881 Johannsen was appointed research assistant at the Carlsberg Laboratory, a private research laboratory in Copenhagen associated with, but largely independent of, the famous Carlsberg brewery. Here, he worked in the chemistry section, applying analytic methods to determine organic nitrogen developed by the head of the chemistry section, Johan Kjeldal, to study metabolic processes connected with ripening and germination in plants, especially barley. In 1887 Johannsen left the Carlsberg Laboratory to take up a lectureship at the Royal Veterinary and Agricultural College in Copenhagen, a position he held until he was appointed professor of botany at Copenhagen University in 1905. He continued his collaboration with the Carlsberg Laboratory, now turning to experiments in breeding high quality strains of barley (Nilsson-Ehle, 1927; Roll-Hansen, 2005). Both projects were intimately connected, because the nitrogen content of barley was an important variable in the brewing process, and the quality of barley, in consequence, could be assessed simply by measuring its protein content. The variation of plant form, therefore, was reduced to variation of a single, measurable chemical variable (Johannsen, 1899).

It is well known that many of the early Mendelians worked in contexts of 'applied' biology, most notably agricultural breeding (Paul & Kimmelmann, 1988; Palladino, 1990). In 1896, Johannsen published a small booklet on heredity and variation, in which he claimed that 'the sci-

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ence of heredity is necessary for transformism, but not vice versa' (Johannsen, 1896, p. 12), and suggested that a study of techniques like pedigree breeding could help to elucidate inheritance. Johannsen's relationship with breeding remained uneasy, however. He was clearly aware that the distinction of genotype and phenotype was not only difficult to draw in practice, but that relying exclusively on the genotype in practical contexts like breeding would not be a successful strategy at all. Bigger beans *do* produce bigger plants because they provide more nutriment to the embryo (Johannsen, 1905, p. 177), so Johannsen knew about those factors we would nowadays call 'epigenetic'. The pure line was not characterized by a certain phenotypic property, but by the way in which its offspring developed— and that behaviour was not simply observed, but was a behaviour organisms were made to accord with. The amount and difficulty of the work that went into their construction can hardly be overestimated, and it was correspondingly difficult to grasp the concept of the genotype on that basis.

Basically, pure lines were produced by isolating one individual, and then 'purifying' its offspring by selecting out all deviant individuals from each generation of offspring. As hybridization by cross-fertilization produced renewed variability, the easiest way to produce pure lines was with mandatory self-fertilizers, such as cereals or beans. In self-fertilizing plants there is 'no doubt about the father', as Johannsen once put it, and the vagaries of ancestry were thus reduced to a minimum (quoted in Roll-Hansen, 2005, p. 47). When Johannsen prepared his 'pure line experiments' for publication in 1903, he wrote a letter to the famous plant breeding station at Svalöf (Sweden). What he wanted to know was whether selection for certain phenotypes in the so called 'pedigree lines' produced in Svalöf still yielded any effects. One of the plant scientists working at Svalöf, Hermann Nilsson-Ehle, assured him that this was not the case, and Johannsen included a long discussion of the work carried out at Svalöf in the final version of his paper (Johannsen, 1903, pp. 6–8; see Roll-Hansen, 1978, on the relationship of Johannsen to Svalöf).

The hard work that went into their production is clear from the answer given by Nilsson-Ehle (Fig. 1), which, with its many deletions and new starts, expresses both the difficulty of producing pure lines and of grasping what they actually represented. The particular cause of Nilsson-Ehle's difficulties was the fact that the practical production of pedigrees involved continuous selection in order to clear the strains of variants caused by mutations or accidental cross-fertilizations. The production of pedigrees needed bureaucratic record keeping (Fig. 2) and hierarchically organized labour, almost on an industrial scale, with scientific 'managers' at the top, and a basis of unskilled labour (Fig. 3). It also involved a plurality of localities, regionally, nationally and internationally, among which the isolated pedigrees were circulated to test them against a variety of background conditions (Müller-Wille, 2005). Left to themselves pedigrees would quickly degenerate. So, if selection

produced no effects in pedigree lines, was this not simply due to the fact that breeders selected them to remain constant?

With these complexities of plant breeding in mind, it is highly revealing to note that Johannsen did not refer to plant breeding but to the pure cultures of bacteriology as the models for his pure line approach. In the 1913 edition of his textbook *Elemente der exakten Erblichkeitslehre*, Johannsen stated:

> It is remarkable in the recent history of biology that while with respect to micro-organisms enormously important results were achieved by 'pure culture' (i.e. by culturing with a single cell as starting point), inheritance in higher organisms continued to be studied in a much cruder, summary and statistical way. But the methods of Koch and Hansen have the same significance for the exact study of microorganisms, as for the study of inheritance ... Without pure cultures no clear insights, but confusion and error! (Johannsen, 1913, pp. 196–197)

Again, Johannsen's years at the Carlsberg Laboratory must be seen as formative in this respect. When he entered the Carlsberg Laboratory in 1881, it was Emil Christian Hansen (mentioned above) who headed its bacteriology section. Hansen adopted the pure culture methods developed by Louis Pasteur and Robert Koch in 1883 to prevent beer from turning sour occasionally. By isolating single yeast cells by repeated dilution, microscopic examination and cultivation under sterile conditions, he was able to produce yeast consisting of beneficial strains of brewer's yeast only. The strains were produced and marketed successfully as 'Carslberg bottom-yeast No. 1' in the same year (Teich 1983). As the only illustration of an organism in Hansen's *Practical studies of fermentation* from 1896 shows (Fig. 4), yeast remained to him what one may call a 'minimal organism', an 'organism without organs' as Ernst Haeckel once referred to protists (see Sapp, 2007, this section). The different strains of yeast were only distinguished by the different qualities of the beer they produced. Their production, to be sure, also involved industrial forms of labour, but it was much more akin to chemistry than to agriculture (Fig. 5).

Another figure merits mention in this context. Martinus Willem Beijerinck is known today as the founder of the Delft School of Microbiology, and for his work on the Tobacco Mosaic Virus. In 1884, he was invited by the industrialist L. C. van Marken to establish a bacteriological laboratory at the Dutch Yeast and Alcohol Works. In order to prepare for this task, Beijerinck visited the Carlsberg Laboratory in Copenhagen. Back at the laboratory of the Dutch Yeast and Alcohol Works, Beijerinck enjoyed considerable freedom in his research, engaging in such varied projects as producing yeast cultures free of pathogenic bacteria, cross-fertilizing wheat to gain stable varieties (carried out at the Agricultural High School of Wageningen, where he had been a teacher before), isolating the nitrogen-fixating *Bacillus radicicola* from leguminose

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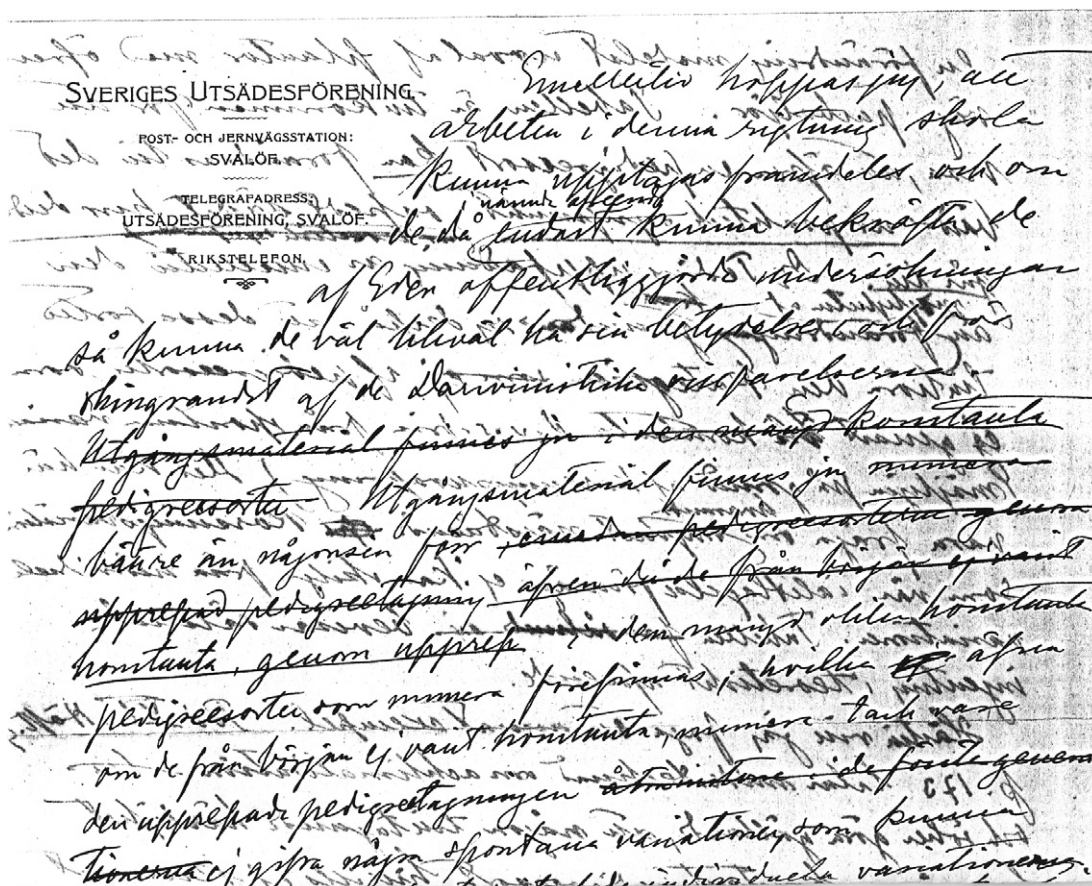
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Fig. 1. Letter from Herman Nilsson-Ehle to Wilhelm Johannsen, 27 January 1903 (Universitetsbiblioteket, Lunds Universitet, Saml. Nilsson-Ehle, hermann, kaps. 23; used with the permission of Lund University Library). The text reads in English translation: 'In the meanwhile I hope that work in this direction can be taken up in the future, and even if it only can reinforce your published investigations, this work will nonetheless be of significance (and dissipation of Darwinian delusions). Material to start with after all now exists better than anytime before, in the great number of different constant pedigree-sorts which now exist, which, even if they had not been constant to begin with, now, thanks to repeated pedigree-taking, do not give any spontaneous variations that could disturb the study of individual variation'.

root nodules, and establishing pure cultures of unicellular green algae, zoochlorella and gonidia of lichens (Iterson et. al., 1983; Bos & Theunissen 1995). What inscribes Beijerinck into the history of genetics, however, is the fact that it was he who 'rediscovered' Mendel in 1899. It was Beijerinck who pointed de Vries—a close friend of his, who had also engaged in agricultural research in his early career—to the importance of Mendel's paper, of which he possessed an offprint (Jahn, 1958). When de Vries published his seminal paper 'Sur la loi de disjonction des hybrides' in 1900, Beijerinck reacted immediately with a paper maintaining the existence of heritable variation in microbes, and advertising microbes as 'an extremely useful material for the investigation of the laws of heredity and variation'. Microbes, he maintained, were easily produced in large numbers from single individuals. And once pure culture technologies were mastered, biochemical characters of microbes provided accurate methods of distinction, as they could be measured precisely with devices such as the saccharometer (Beijerinck, 1921–1940, Vol. 4, p. 37).

What the case of Johannsen demonstrates is that the conjunctions of biochemistry, microbiology and breeding in the industrial mass production of beer provided one of the contexts that predisposed research to what I have described at the beginning of this section as the Mendelian mindset. The apparent lack of structural complexity, often reducing microbial life to a single character, which was often only assessable through chemical operations or *in vivo* experiments, as well as the fact that microbial life forms could only be made visible through elaborate genealogical constructs—pure cultures or 'clones', as they were later called—inclined microbiologists to a kind of proto-genetic thinking. Species were replaced, or rather marked and traced, by specificities, that is, by the reliably predictable effects that organic units produced in their interaction with other organic units and their environments (Gradmann, 2001).

In the case of Johannsen this became especially clear in a peculiar one-sidedness that marked his later career. Although he acknowledged the importance of hybridization experiments for genetics, he himself never embarked on crossing experiments. Throughout his career, Johannsen himself remained content with having reduced his beans to genotypes, just like bacteriologists in general remained con-

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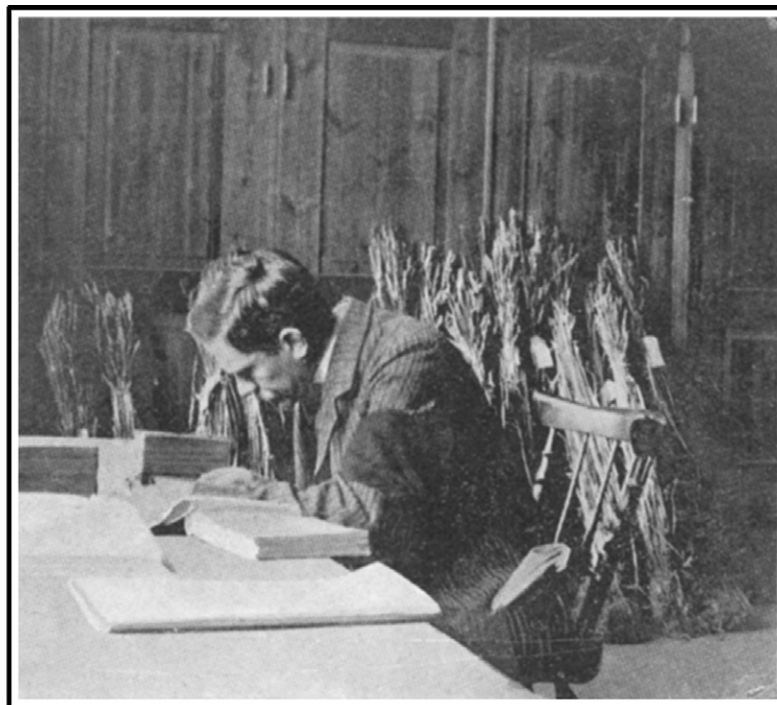

Photo by L. H.ˉN.

FIG. XXVII.—Nilsson-Ehle examining segregation in the *Club* × *Pudel* wheat crossing on the basis of color of grain.   *Club* is said to have 2 units for red color.

Fig. 2. Hermann Nilsson-Ehle working at his desk at the Svalöf Plant Breeding Station, ca. 1912 (from Newman, 1912, p. 111).

Handhackning av förökning av ärtor 1907.

Fig. 3. Women working on a field for multiplying peas at the Svalöf Plant Breeding Station, 1907 (from Enge, 1986, p. 39; used with the permission of Svalöf Weibull B).

tent with producing identifiable and reproducible strains for another thirty years, despite Beijerinck's early call to use microbes as model organisms of genetics (Singleton, 2000). As Frederick Churchill commented, Johannsen embarked on a 'vertical' analysis of the genotype, while it was the Morgan school that realized the potential for a 'horizontal' analysis in mapping the genes of *Drosophila* (Churchill, 1974). When microorganisms, notably *E. coli* and its phages, finally became the subject of classical genetics in the 1940s and 1950s, they characteristically did so as systems involving multiple viral transductions and the bacterial transformation of genetic material, which allowed the simulation of the exchange of genetic material in diploid organisms (Holmes, 2006).

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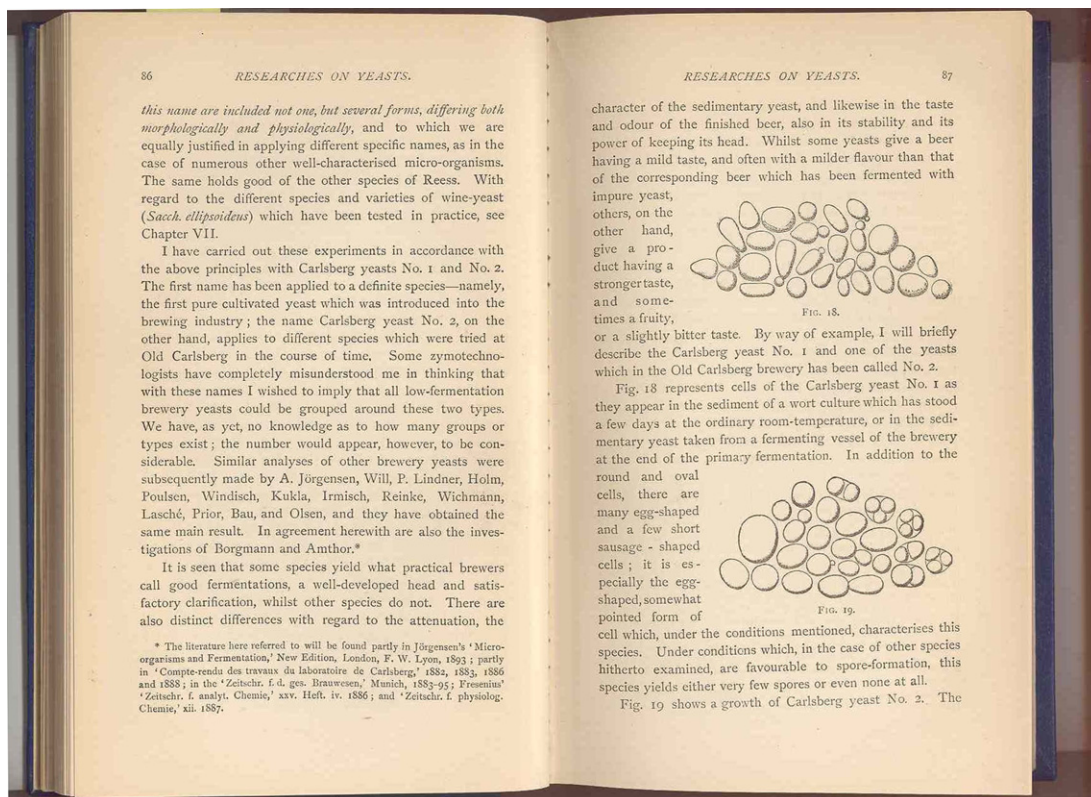

Fig. 4. Cells of Carslberg bottom-yeast No. 1 (from Hansen, 1896, p. 87).
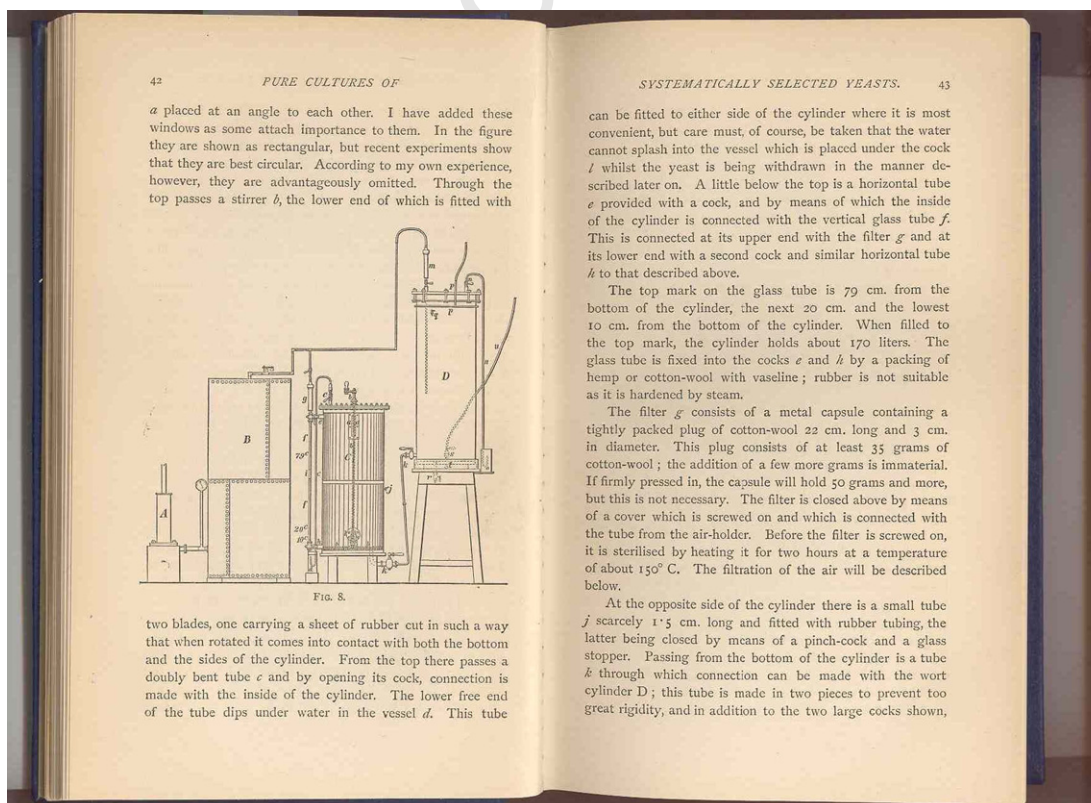
Fig. 5. Apparatus for the production of Carslberg bottom-yeast No. 1 (from Hansen, 1896, p. 42).

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5. Conclusion

The agro-industrial contexts that furthered the emergence of genetics around 1900 through ~~the~~ conjunctions of biochemistry, microbiology and the breeding of higher organisms ~~they provided~~ were clearly sites dominated by an interest in reducing life to something that ~~can~~ be circulated and recombined with predictable efficiency (Mendelsohn, 2005). This, however, should not distract attention from the fact that the industrial world was an exceedingly complex world, dominated as much, if not even more, by exchange and cooperation as by isolation and competition. Breaking organisms down to genes and communities of microorganisms into 'species' were activities often performed to gain control over complex problems that seemed out of reach of any kind of analysis: breeding for physiological characters like winter hardiness or resistance to pathogens; assimilation of gaseous nitrogen by microbes inhabiting the root nodules of leguminous plants; producing vaccines immunizing against contagious diseases. Sergeij Vinogradsky, whose work as well was carried out in contexts informed by agro-industrial concerns, always 'supported a staunch monomorphism' and the pure culture methods associated with it, even though he was acutely aware of the ecological complexity of microbial communities (Ackert, 2006, p. 380). The language of engineering that permeates present day microbiology when it comes to describe the complex systems that make up the microbial world provides us with a constant reminder of this relationship (see Shapiro, 2007, this section). What I have tried to argue, then, in this essay is that genetic systems, whether hosted by microbes or macrobes, are systems of exchange that systematically cut across notions of a one-to-one relationship between individuals and species. Individuals of different kinds merge in hybridization to form individuals of a new, third kind, and the borders of kinds become permeable as a consequence. Problematizing species in these two senses has a long history that goes back to the origins of modern biology in the early nineteenth century. The evolutionary synthesis of the twentieth century, as I see it, was an attempt to focus on one particular model of genetic systems only—speciation by isolation—and to reinstate a clear one-to-one relation between individual and species. This relationship was vital for the long-standing practices of classical natural history and was, in a sense, an attempt to save natural history from the consequences of biology. If molecular microbiology forces us today, as Jan Sapp argues in this section, to rethink biology, it will also force us to rethink the history of biology. The true revolution of the nineteenth century did not occur with Darwin's theory of natural selection, but with cell theory. Darwin, of course, had a share in this revolution as well with his theory of pangenesis, but it is one that needs to be rediscovered.

6. Uncited references

Mayr (1986), Vries (1900).

References

Ackert, L. (2006). The role of microbes in agriculture: Sergei Vinogradskii's discovery and investigation of chemosynthesis, 1880–1910. *Journal of the History of Biology*, 39, 373–406.

Bazopoulou-Kyrkanidou, E. (2001). Chimeric creatures in Greek mythology and reflections in science. *American Journal of Medical Genetics*, 100, 66–80.

Beijerinck, M. W. (1921–1940). *Verzamelde geschriften van M.W. Beijerinck ter gelegenheid van zijn 70sten verjaardag* (6 vols). Delft: Nijhoff.

Bensaude-Vincent, B. (2002). Changing images of chemistry. In I. H. Stamhuis, T. Koetsier, & C. D. Pater (Eds.), *The changing image of science* (pp. 29–41). Dordrecht: Kluwer Academic.

Bos, P., & Theunissen, B. (1995). *Beijerinck and the Delft School of Microbiology*. Delft: Delft University Press.

Churchill, F. (1974). William Johannsen and the genotype concept. *Journal of the History of Biology*, 7, 5–30.

Darwin, C. (1988). *The variation of plants and animals under domestication, Vol. 2*. The Works of Charles Darwin, Vol. 20 (P. H. Barrett, & R. B. Freeman, Eds.). New York: New York University Press. (First published 1868)

Enge, G. (1986). Allmänna Svenska Utsädesaktiebolaget. *Sveriges Utsädesföreningens Tidskrift*, 96, 27–49.

Foucault, M. (1966). *Les mots et les choses: Une archéologie des sciences humaines*. Paris: Gallimard.

Gärtner, C. F. (1849). *Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich*. Stuttgart: Auf Kosten des Verfassers.

Gayon, J. (2000). From measurement to organization: A philosophical scheme for the history of the concept of heredity. In P. Beurton, R. Falk, & H.-J. Rheinberger (Eds.), *The concept of the gene in development and evolution: Historical and epistemological perspectives* (pp. 69–90). Cambridge: Cambridge University Press.

Gliboff, S. (1999). Gregor Mendel and the laws of evolution. *History of Science*, 37, 217–235.

Gogarten, P., & Townsend, J. P. (2005). Horizontal gene transfer, genome innovation and evolution. *Nature Review Microbiology*, 3, 679–687.

Gradmann, C. (2001). Isolation, contamination, and pure culture: Monomorphism and polymorphism of pathogenic micro-organisms as research problem 1860–1880. *Perspectives on Science*, 9, 147–172.

Hodge, M. J. S. (1985). Darwin as a lifelong generation theorist. In D. Kohn (Ed.), *The Darwinian heritage* (pp. 204–244). Princeton: Princeton University Press.

Holmes, F. L. (2006). *Reconceiving the gene: Seymour Benzer's adventures in phage genetics*. New Haven: Yale University Press.

Iterson, G. van, Dooren De Jong, L. E. den, & Kluyver, A. J. (1983). *Martinus Wilhelm Beijrinck: His life and his work*. Madison, WI: Science Tech.

Jacob, F. (1993). *The logic of life: A history of heredity*. Princeton, NJ: Princeton University Press.

Jahn, I. (1958). Zur Geschichte der Wiederentdeckung der Mendelschen Gesetze. *Wissenschaftliche Zeitschrift der Friedrich-Schiller Universität Jena, Mathematisch-naturwissenschaftliche Reihe*, 7, 215–227.

Johannsen, W. (1896). *Om arvelighed och variabilitet*. København: Det Schubotheske Forlag.

Johannsen, W. (1899). Fortsatte Studier over Kornsorterne I. Om Variabiliteten med særligt Hensyn til Forholdet mellem Kornvægt og Kvæfstof-Procent i Byg. *Meddelelser fra Carlsberg Laboratoriet*, 4, 228–313.

Johannsen, W. (1903). *Über Erblichkeit in Populationen und in reinen Linien*. Jena: G. Fischer.

Johannsen, W. (1905). *Arvelighedslærens elementer: Forelæsninger holdte ved Københavns Universitet*. Copenhagen: Gyldendalske Bokhandel.

Johannsen, W. (1911). The genotype conception of heredity. *American Naturalist*, 45, 129–159.

Johannsen, W. (1914). *Falske analogier med henblik paa lighed, slægtskab, arv, tradition og udvikling*. Copenhagen: Universitetsboktrykkeriet.

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No. of Pages 11, Model 5+

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Kielmeyer, C. F. (1993). *Ueber die Verhältnisse der organischen Kräfte unter einander in der Reihe der verschiedenen Organisationen* (reprint ed.). Marburg: Basilisken-Presse. (Originally published 1793)

Larson, J. F. (1994). *Interpreting nature: The science of living form from Linnaeus to Kant*. Baltimore: Johns Hopkins University Press.

Lenoir, T. (1982). *The strategy of life: Teleology and mechanics in nineteenth-century Germany*. Chicago: University of Chicago Press.

Linnaeus, C. (1788). Transmutatio frumentorum. In *Caroli Linnaei Ammoenitates academicae, seu Dissertationes variae Physicae, Medicae, Botanicae antehac seorsim editae, Vol. 5* (pp. 106–119). Erlangen: Jo. Jacobus Palm. (Originally published 1757)

Lyon, J., & Sloan, P. R. (1981). *From natural history to the history of nature: Readings from Buffon and his critics*. Notre Dame: University of Notre Dame Press.

Mayr, E. (1986). Joseph Gottlieb Koelreuter's contributions to biology. *Osiris, 2nd series, 2*, 135–176.

McLaughlin, P. (1990). *Kant's critique of teleology in biological explanation: Antinomy and teleology*. Lewiston: Edwin Mellen Press.

Meijer, O. G. (1985). Hugo de Vries no Mendelian? *Annals of Science 42*, 189–232.

Mendelsohn, A. (2005). Message in a bottle: The business of vaccines and the nature of heredity after 1880. In *Conference: A cultural history of heredity III: Nineteenth and early twentieth centuries* (pp. 85–100). Berlin: Max-Planck-Institute for the History of Science.

Müller-Wille, S. (2005). Early Mendelism and the subversion of taxonomy: Epistemological obstacles as institutions. *Studies in History and Philosophy of Biological and Biomedical Sciences, 36*, 465–487.

Müller-Wille, S. (2007). Figures of inheritance, 1650–1850. In S. Müller-Wille, & H.-J. Rheinberger (Eds.), *Heredity produced: At the crossroad of biology, politics, and culture, 1600-1850* (pp. 177–204). Cambridge, MA: MIT Press.

Müller-Wille, S., & Orel, V. (2007). From Linnaean species to Mendelian factors: Elements of hybridism, 1751–1870. *Annals of Science, 64*, 171–215.

Nilsson-Ehle, N. H. (1927). W. Johannsen. *Nordisk Jordbrugsforskning*, 361–364.

Olby, R. C. (1979). Mendel no Mendelian? *History of Science, 17*, 53–72.

Olby, R. C. (1985). *Origins of Mendelism* (2nd ed.). Chicago: University of Chicago Press.

O'Malley, M. A., & Dupré, J. (2007). Size doesn't matter: Towards a more inclusive philosophy of biology. *Biology and Philosophy, 22*(2), 155–191.

Palladino, P. (1990). The political economy of applied research: Plant breeding in Great Britain, 1910–1940. *Minerva, 28*, 446–468.

Parnes, O. (2007). On the shoulders of generations: The new epistemology of heredity in the nineteenth century. In S. Müller-Wille, & H.-J. Rheinberger (Eds.), *Heredity produced: At the crossroad of biology, politics, and culture, 1600–1850*.

Paul, D. B., & Kimmelmann, B. A. (1988). Mendel in America: Theory and practice 1900–1919. In K. Benson, J. Maienschein, & R. Rainger (Eds.), *The American development of biology* (pp. 281–310). Philadelphia: University of Pennsylvania Press.

Provine, W. B. (1992). *Progress in evolution and meaning in life*. In C. K. Waters, & A. van Helden (Eds.), *Julian Huxley, biologist and statesman of science* (pp. 165–180). Houston: Rice University Press.

Quatrefages, A. de. (1879). *L'espèce humaine*. Paris: Germer Baillière.

Roger, J. (1993). *Les sciences de la vie dans la pensée française du XVIIIe siècle*. Paris: Albin Michel.

Roll-Hansen, N. (1978). The genotype theory of Wilhelm Johannsen and its relation to plant breeding and the study of evolution. *Centaurus, 22*, 201–235.

Roll-Hansen, N. (1989). The crucial experiment of Wilhelm Johannsen. *Biology and Philosophy, 4*, 303–329.

Roll-Hansen, N. (2005). Sources of Johannsen's genotype theory. In *Conference: A cultural history of heredity III: Nineteenth and early twentieth centuries* (pp. 43–52). Berlin: Max-Planck-Institute for the History of Science.

Sapp, J. (2003). *Genesis: The evolution of biology*. Oxford: Oxford University Press.

Singleton, R. (2000). From bacteriology to biochemistry: Albert Jan Kluyver and Chester Werkman at Iowa State. *Journal for the History of Biology, 33*, 141–180.

Teich, M. (1983). Fermentation theory and practice: The beginnings of pure yeast cultivation and English brewing, 1883–1913. *History of Technology, 8*, 117–133.

Vries, H. de. (1900). Sur la loi de disjonction des hybrides. *Comptes Rendus de l'Académie des Sciences [Paris], 130*, 845–847.

Zirkle, C. (1935). *The beginnings of plant hybridization*. Philadelphia: University of Pennsylvania Press.