France in the era of Mendelism (1900-1930)

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Abstract

This paper describes and explains the reception of Mendelism among French biologists at the beginning of 20th Century.

Three dimensions of description must be taken into account : scholarly diffusion ; transmission of the new science through teaching and textbooks ; effective research. These three axes of description do not provide the same picture : Mendelian research was widely reported among specialists ; no significant teaching of Mendelism took place in the years 1900-1930 ; by 1930 only one biologist, Lucien Cuénot, had done significant genetic research, but he abandoned his Mendelian research in 1914.

The resistance to Mendelism can be attributed to four categories of factors, none of which is sufficient. The first category includes a series of intellectual factors : a massively positivist conception of science , an approach to heredity that privileged a "physiological" theory, and a poor development of cytology. The second set of factors stems from the failure of French academic biologists to establish strong interaction with plant and animal breeding. The third factor is the relatively weak influence of the eugenic ideology in France. Finally, the particular organization of French universities, together with the death of numerous young scientists during the First World War, amplified the effects of the previous factors.

Résumé

La résistance des biologistes français au Mendélisme au début du vingtième siècle est décrite et expliquée.

Trois dimensions de description sont prises en compte : diffusion savante, transmission du nouveau corpus dans l'enseignement, recherche effective. Ces trois dimensions ne coïncident pas : la nouvelle science de l'hérédité fut largement diffusée parmi les spécialistes ; elle ne fut pas enseignée dans la période 1900-1930 ; seul un biologiste, Lucien Cuénot, contribua de manière significative par ses découvertes à la nouvelle science, mais seulement avant 1914.

La résistance au mendélisme s'explique par plusieurs catégories de causes, dont aucune n'est suffisante. Viennent en premier lieu des facteurs intellectuels : conception massivement positiviste de la science, exigence d'une théorie "physiologique" de l'hérédité, développement limité de la cytologie. Seconde cause : la faible interaction entre la recherche biologique théorique et la recherche agronomique, zootechnique et horticole. Le développement (comparativement) faible de l'idéologie eugéniste en France a aussi joué. Enfin l'organisation centralisée des Universités françaises a amplifié l'effet des facteurs précédents, ainsi que l'hécatombe de 1914-1918.

Keywords
History of science, Genetics, Mendelism, France.

Mots-clefs
Histoire des sciences, génétique, Mendélisme, France.

Introduction

In comparison with other major scientific countries, French biologists participated only modestly in the early development of genetics. Not only their contribution to the impressive list of discoveries that followed the rediscovery of Mendel's laws was limited, but also they resisted to a significant incorporation of Mendelian genetics into the research and teaching system. Because this resistance to Mendelism is a complex phenomenon, reflecting complex causes of many sorts, it is of considerable historical interest. Thus, for example, it is not enough to mention such intellectual factors as the supposedly exceptional Lamarckism of French biologists. Beside the fact that Lamarckism was probably not a distinctive feature of French biology around 1900, it was certainly not the only cause of the reluctance of French biologists to adopt Mendelism. Furthermore, even if Lamarckism did play an important role, the historian must explain why this intellectual preference lasted so long and remained so effective. In fact, “Lamarckism” is a symbolic label that covers an aggregate of factors of resistance to genetics.

The primary purpose of this paper is to provide a description of the reception of Mendelism and of genetics by French biologists in the years 1900 through 1930. A proper assessment of the extent and modes of this resistance is required before proposing any causal hypothesis to account for the phenomenon. Most of our communication will be devoted to this description, but we will close by proposing a classification of the various causes that collectively account for the resistance.

This synthetic paper is the result of a long and fruitful collaboration between the two authors (and also Doris Zallen, Virginia Tech, USA) on the subject of the history of genetics in France [1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15].

2. Reception of Mendelism : description

How did the French scientific community did receive Mendelism ? Denis Buican [16] has stressed the polemics between a majority of French biologists and the Mendelians, and the incomprehension that most often accompanied these polemics. This is certainly an important aspect of the story, but it is not the only one. Our description is based on the positive indications of the penetration of Mendelism in France.

From its very beginnings, Mendelian genetics was characterized by an operational approach to heredity. In this respect, it presented a sharp contrast with previous approaches to heredity, which were highly speculative. The penetration of this Mendelian style of scientific work in the French scientific community can be evaluated by answering three different questions.

- What could French biologists reasonably know about the Mendelian approach to heredity through the ordinary channels of specialized communication (scientific meetings and periodicals) ?

- What kind of teaching did the new discipline receive ? This question is different from the previous one : for a given scientific community, it is one thing to be correctly informed (or to have access to reliable sources of information) about a new body of knowledge, it is another thing to consider that this knowledge is so important that it must be transmitted to the next generation. The latter attitude has specific practical consequences, such as the organization of new curricula, the publication of textbooks and treatises, the creation of new chairs.

- How did Mendelism affect the research programs of French biologists ?

Each of these questions can be given a precise answer.

2.1. Scholarly diffusion of Mendelism

Let us consider the diffusion of Mendelism among professional biologists. We have exhaustively examined six periodicals in the period 1900-1930 : *L'Année Biologique,* the *Comptes rendus hebdomadaires des séances de l'Académie des Sciences,* the *Comptes rendus des séances de la Société de biologie et de ses filiales,* the *Archives de Zoologie expérimentale,* the *Bulletin scientifique* [later *biologique*] *de la France et de la Belgique,* and the *Revue scientifique*. There is no doubt that Mendelian data and Mendelian hypotheses were rapidly, precisely and widely reported in these journals, which were major channels of communication for French biologists. Here are some indications.

The history of the publication of Hugo de Vries' 1900 article in the *Comptes rendus hebdomadaires des séances de l'Académie des sciences* [17] need not to be repeated here (see F. Gros and C. Lenay in this volume). This article was an abstract of a bigger article that was published shortly after in *Berichte der Deutschen Botanischen Gesellschaft* [Reports of the German Botanical Society] [18]. The same year, the *Revue générale de botanique* published a French version of this article, which was in fact more fully developed than the German paper [19].

From 1900 to 1914, *L'Année biologique*, a journal entirely devoted to reviews of books and articles commented in detail the major Mendelian discoveries of this period, and underlined their importance in well-documented review articles. The volume for 1900, for instance, includes two long commentaries on De Vries' first Mendelian article by Yves Delage, the editor, and Lucien Cuénot, who thus manifested his interest in the rediscovery of Mendel for the first time. From 1901 to 1903, *L'Année Biologique* published precise and clear reviews of the most important papers and books by Bateson, Castle, Correns, Cuénot, Darbishire, Doncaster, Haecker, Tschermak, De Vries, and Wilson. In 1902, Cuénot summarized two years of worldwide Mendelian research in a 20-page review article [20]. Such an article, written by one of the most brilliant French biologists, himself active in Mendelian research, could hardly be ignored. *L'Année biologique* was the most widely read biological journal. Until 1914, this journal continued to report as fast as possible on the development of Mendelian genetics.

The *Archives de zoologie expérimentale et générale* did not include reviews, but it published most of Cuénot's important notes on the pigmentation of mice between 1902 and 1908 (see below 1.3).

The *Comptes rendus hebdomadaires des séances de l'Académie des Sciences* and the *Comptes rendus des séances de la Société de biologie et de ses filiales* played a more discrete role, but these two journals published Cuénot's articles on the genetics of cancer in mice from bertween 1908 and 1912. These periodicals also published the more ambiguous but locally influential works of Blaringhem on induced mutations in cereals, and of Delcourt/Guyénot on the nutritional and aseptic factors influencing the reproduction and evolution of lineages of *Drosophila melanogaster* (see below 1.3).

Finally, in the same period before WW I, the *Bulletin scientifique et la France et de la Belgique,* a major bastion of neo-Lamarckism, published the first (and only) French translation of Mendel's memoir on hybridization in plants [21]. At the same time, Etienne Rabaud, the editor of the journal, began to publish articles criticizing Mendelism. Thus he published big memoirs of a more or less Lamarckian inspiration by Blaringhem [22] and Guyénot [22, 100].

Two symbolic events testify to the interest of the French scientific community in Mendelian genetics before 1914. One is the attribution of the Académie des Sciences' prestigious Cuvier Prize to Cuénot in 1911. The official citation accompanying this Prize mentions clearly Cuénot's contributions to "genetics" (mentioned as such). The other symbolic event is the international Conference of Genetics that was held the same year in Paris. This conference was sponsored by the Vilmorin company. At the first Conference on Hybridization in London in 1899, Henry de Vilmorin (then head of the company) had obtained agreement that the Second Conference would be held in Paris. This did not happen because Henry died soon after the London Conference. But his son Philippe was able to organize the Fourth Conference, renamed "Conference on Genetics", in Paris, in 1911. The official patron of the Conference was the *Société Nationale d'Horticulture de France*. The sessions were held in Paris, in the building of this society (rue de Grenelle). The Conference was also "morally sustained" by the *Société de biologie*, the *Société de Botanique de France*, the *Société de Zoologie de France* and the *Société d'acclimatation de France*. The list of the personalities and institutions represented at the conference shows that almost no important institutional component of the French biological community was absent. However, the list of the French scientists who presented papers includes almost exclusively horticulturists, agricultural engineers and doctors. There were two exceptions: Blaringhem, and Delcourt and Guyénot, all of whom were young and relatively critical of Mendelian genetics. The discordance between support and effective participation is revealing. It corroborates the results of our inquiry into the periodicals: before 1914, the French biological community was reasonably well informed of the early development of Mendelism (Source for the 4th Conference of genetics: [24]).

2.2. Teaching of genetics

How did genetics enter into the curricula in France before 1930 ? This is an important issue. When a certain kind of knowledge is not properly transmitted to the following generation, there is every likelihood that it will remain marginal. The initial training of scientists plays a large part in shaping the methodological and conceptual matrix of the next generation. We think that it is at this level that the French scientific community's singular attitude towards genetics revealed most conspicuously.

Consider the textbooks, treatises and synthetic books that were exclusively devoted to genetics in English, German and French in the period 1900-1930. The following lists include only books dealing with Mendelian heredity or genetics in general. We have excluded special works on, *e.g.*, genetics of wheat, rats, etc. Full references are given in the bibliography. Nor have we mentioned books on heredity that would not be typically "Mendelian" (for instance: Julien Costantin, *L'hérédité acquise*, 1901).

English :

1902 : W. Bateson, *Mendel's principles of heredity; a defence by W. Bateson ... With a translation of Mendel's original papers on hybridisation* [25].

1905 : R.C. Punnett, *Mendelism* (re-issued : 1907, 1911, 1912, 1919 : 1922. German translation : 1910) [26].

1905 : Reid G.A., *The principles of heredity with some applications* [27].

1906 : Lock R.H., Recen*t Progress in the Study of variation, Heredity, and Evolution* (re-issued : 1910, 1911) [28].

1907 : Cook O.F., *Mendelism and other Methods of Descent* [29].
1908 : Bateson W., *The Methods and Scope of Genetics* [30].
1908 : Thomson J.A., *Heredity* (reissued 1919) [31].
1910 : Doncaster L. *Heredity in the Light of Recent Research* (2nd ed. 1912) [32].
1911 : Castle W.E., Her*edity in Relation to Evolution and Animal* Breeding [33].
1911 : Darbishire A.D., *Breeding and the Mendelian Discovery* [34].
1913 : Bateson W., *Problems of Genetics* [35].
1913 : Morgan T.H., *Heredity and Sex* [36].
1913 : Walter H.E., A*n Introduction to the Study of Heredity* [37].
1915 : Morgan T.H. et al., *The Mechanism of Mendelian Heredity* [38].
1915: Pearl R., *Modes of Research in Genetics*. [39]
1916 : Castle W.E., *Genetics and eugenics; a text-book for students of biology and a reference book for animal and plant breeders* (reissued : 1921, 1924, 1930, 1932) [40].
1918: Babcock E.B., and Clausen, R.E., *Genetics in Relation to Agriculture* (2^{nd} ed., 1927) [41].
1918, Babcock E.B., *Genetics laboratory manual* [42].
1919 : Morgan T.H., *The Physical Basis of Heredity* [43].
1920: Gager C.S., *Heredity and Evolution in Plants* [44].
1923: Coulter M.C, *Outline of Genetics, with Special Reference to Plant Material* 1923 [45].
1925 : Jones D.F., *Genetics in Plant and Animal Improvement* [46].
1925: Sinnott, E.W. and Dunn, L.C., *Principles of Genetics, An Elementary Text, with Problems* [47].
1925 : Morgan T.H., *Evolution and Genetics* [48].
1926 : Morgan T.H., *The Theory of the Gene* [49].
1926: Shull, A.F., *Heredity*, McGraw-Hill Company, New York [50].
1928: Altenburg, E., *How We Inherit* [51].
1928: Altenburg, E., *Instructions for Reports in Genetics, Supplement to How We Inherit* [52].
Total for English books : 28 titles.

German :
1909 : Johannsen W., *Elemente der Exakten Erblichkeitslehre* (reissued : 1913, 1926) [53].
1907 : Baur E., *Einführung in die Experimentelle Vererbungslehre* (5 reeditions between 1911 and 1922) [54].
1911 : Goldschmidt R.B., *Einführung in die Verebungswissenschaft* (re-issued : 1913, 1920, 1923, 1928) [55].
1911 : Häcker V., *Allgmeine Vererbungslehre* (reissued : 1921) [56].
1913 : Plate L. *Vererbungslehre* [57].
1913: Plate L., Handbücher der Vererbungstheorie, Engelmann, Leipzig, 1913 [58]).
1914 : Goldschmidt R.B., and Correns, C, *Vererbungslehre und Bestimmung des Geschlechts* [59].
1920 : Goldschmidt R.B., *Die Quantitative Grundlage von Vererbung und Artbildung* [60].
1920 : Goldschmidt R.B., *Der Mendelismus.* [61].
1920 : Goldschmidt R.B., *Mechanismus und Physiologie der Geschlechtsbestimmung* (English translation : 1923) [62].
1921: Baur E., Fischer E., Lenz F., *Grundriss der menschlichen Erblichkeitslehre und Rassenhygiene* [63].
1925: Plate, L., *Die Abstammungslehre* [64].

1927 : Goldschmidt R.B., *Die Lehre von der Vererbung* [65].
1927-1939 : Baur E. Hartmann M., *Handbuch der Vererbungswissenschaft* , vols. 1-3 [66].
1928 : Goldschmidt R.B., *Physiologische Theorie der Vererbung* [67].
Total for German books : 15

French :
1919 : Blaringhem L., *Les problèmes de l'hérédité expérimentale* [68].
1921 : Rabaud E., *L'hérédité* [69]
1923 : Morgan T.H., et al., *Le mécanisme de l'hérédité mendélienne*, Lamertin, Bruxelles [70].
1924 : Guyénot E., L'hérédité [71].
1928 : Blaringhem L., *Principes et formules de l'hérédité mendélienne* [72].
1929 : Rostand J., *Les chromosomes, artisans de l'hérédité et du sexe* [73].
1930 : Rostand J., *De la mouche à l'homme*, Fasquelle [74].
Total for French books : 7.

Several lessons can be drawn from the comparison of these lists. First, the French titles are all posterior to WW I. The contrast with England and Germany is striking : 18 English titles before 1918, 7 German titles in the same period (with many new reeditions in both cases). This is not to say that the French public could find nothing on genetics in standard textbooks. Before W.W.I, the most reliable and most popular source was Cuénot's *La genèse des espèces animales*, first published in 1911, [75]. But only a fraction of this book was devoted to an exposition of the principles of Mendelian genetics. Thus our list shows at least that genetics was not in France a serious enough topic before WW I for a full textbook to be devoted to it.

Secondly, the content of the list of French textbooks of or about genetics deserves attention. One of the titles is a translation of Morgan, Sturtevant, Muller and Bridge's legendary 1915 book [38, 70]. This was indeed a remarkable book, but it was translated in Belgium, and poorly diffused in France. Blaringhem's two books [56, 72] were relatively small and he was a notorious Lamarckian. Nevertheless these books, together with Blaringhem's teaching at École Normale Supérieure and the Sorbonne allowed a certain number of students to discover the new science of genetics. Although they were written by a Lamarckian, they were certainly a much better introduction to Mendelism than Etienne Rabaud's *L'hérédité* [68], an overtly polemical and Lamarckian pamphlet. Rostand's books had a tremendous effect, but only in the 1930s. Rostand's 1929 and 1930 books [73, 74] were not properly speaking textbooks. Written by a brilliant writer who did not work in any university or research laboratory (Rostand did not need to work thanks to a considerable personal fortune), they were probably the most influential source of information on genetics for the layman. Finally, the only detailed and academically reliable textbook published in French language was Guyénot's *L'Hérédité* (1924). With its various revised editions, this book, probably one of the best introduction to genetics in any language in the first half of 20th century, was the major place where French biologists learned genetics during almost 30 years. Thus it is the only book on our list published in French by a biologist with an active research program in genetics. And in 1924, Guyénot was employed not in France, but at the University of Geneva!

The rarity of genetics textbooks in French reflects the absence of genetics in the curricula. The only places where some genetics was taught before 1930 were the following :

- In the context of Cuénot's "Certificat de biologie générale" in Nancy; this was certainly the most famous place. According to legend, in the 1920s and 1930s, there was every year a regular flux of Parisian students who used to go to Nancy to attend Cuénot' lectures on genetics.

- A few hours in Blaringhem's lectures in general biology at École Normale Supérieure.
- A dozen hours of practicals on Drosophila in Maurice Caullery's laboratory ("Laboratoire d'évolution des êtres organisés", university of Paris).
- A few hours at the Institut National d'Agronomie, in the context of a course initiated in the early 1920s, and entitled "Génétique, phytotechnie et botanique appliquée" [76 : 109].

Another sign of the poverty of the offerings of genetics in the French curriculum is given by the creation of specialized chairs. The first chairs of genetics were created in England, Germany, United States and Russia in the years 1910 to 1930 (*e.g.* Bateson, Baur, Serebrovsky). In France, the first chair of genetics was created at the Institut National d'Agronomie in 1936. It was given to Félicien Bœuf, a specialist in wheat. However the first chair of genetics in a University was created after WW II at the Sorbonne, for Boris Ephrussi.

Doctoral dissertations are also a good parameter. The first dissertation in genetics ever supported in France was Philippe L'Héritier's in 1937. It was devoted to quantitative variation in Drosophila [77, 78].

Finally, no allusion to genetics can be found in the curricula of secondary schools before WW II. This is an important aspect. Since their restoration in 1880, the priority mission of the French universities has been to train teachers for secondary schools, on the basis of national curricula, diploma, and competitions. This was a factor of rigidity, which amplified the extremely late incorporation of genetics in the French scientific curricula.

2.3. Mendelian research

The third axis of our description of the penetration of Mendelism into France is the development of effective research along Mendelian lines. Although limited, the participation of French scientists to the development of genetics was not an absolute desert. But it had a rather specific character.

Lucien Cuénot's contributions must be mentioned in the fist place. In 1900, Cuénot (1866-1951) was 34 years old. In 1894, he had been one of the few French biologists (perhaps the only one) to opt for Weismann's version of Darwinism, in a major article entitled "The new transformist theory. Jäger, Galton, Nussmaum et Weissmann " [79]. This neo-Darwinian proclamation was followed by a series of about thirty articles, mainly devoted to phagocytosis, in which Cuénot used a conceptual framework associating natural selection with the rejection of inheritance of acquired characters [80]. In 1901 however, he switched allegiance to the mutationist theory of evolution [81], which he formulated under the form of what he would later call [82, 83, 84] the "theory of preadaptation" (for a reconstitution of this story, see 11]. This preference for mutationism is typical of the majority of the such early Mendelians as Bateson, Castle, De Vries, Goldschmidt, Johannsen, Punnett.

In the 1900 volume of *L'Année biologique*, Cuénot gave a detailed analysis of Hugo de Vries' first Mendelian paper in the *Comptes rendus des séances de l'Académie des sciences*. Interestingly enough, this review was incorporated into the chapter devoted to "heredity" [85]. In 1901, he himself began crossing strains of mice, with the intention of determining whether pigmentation is transmitted in a Mendelian fashion. Whence a first article published in 1902 [86], in which Cuénot established that the law of disjunction of characters applies to the animal kingdom. This work is contemporaneous to Bateson's similar study of the transmission of characters in guinea pigs [87].

From 1902 to 1910, Cuénot’s main contributions to genetics were the following : (1) Demonstration that independent segregation of characters applies to animals (mice) [88] ; (2) Discovery that there are multiple forms of the same Mendelian determinant (or “multiple alleles” in a modern terminology) [89, 90] ; (3) Recognition that a particular determinant can mask the normal effect of another determinant [89]. This was a first exemple of what was later called genetic interaction or epistasis ; (4) Recognition that certain combinations of factors cannot yield viable offspring (homozygous “yellow mice”) [90] ; (5) First formulation of the hypothesis that the function of a gene is related to the production of a specific “diastase” (enzyme) [91] ; (6) First Mendelian work with L. Mercier on the genetics of cancer. Cuénot’s and Mercier’s methodology consisted in combining the Mendelian technique of crossing various strains, and that of grafting of tumors. The result was that tumors of a given cellular genotype behave in a different way in function of the genotype of the surrounding tissues [93, 94, 95, 96]. This method became enormously important in physiological genetics in the 1920s and 1930s (Beadle and Ephrussi).

Taken together, these various lines of research made Cuénot one of the most active and prolific Mendelians on an international scale in the first decade of the 20th century. The overall “physiological” orientation of Cuénot's work must be emphasized. After 1912, Cuénot progressively dropped out of experimental work in genetics. There were various reasons for this. First he became increasingly involved in writing synthetic books. In 1911, he published his *Genèse des espèces animales* [75]. This book was followed by many others during the next 40 years. Furthermore, he was disconcerted by the chromosomal of heredity, which was just being formulated around 1910. He began to criticize it. Then, when he realized the tremendous advances by Morgan and his collaborators, he felt that he could no longer pretend to be *the* leading figure. Finally, in 1914, he had to leave Nancy because of the war, and he lost his strains of mice, which were absolutely crucial for his experimental work in genetics. (For more details on Cuénot and genetics, see [1]).

Other French scientists took an interest in Mendel’s laws before W.W.I. Beside a handful of botanists and agricultural scientists who just tried and verified whether Mendel’s laws applied or not in this or that particular case, Guyénot’s work deserves special attention. In 1910, Guyénot (1885-1963) began to work on strains of Drosophila in collaboration with A. Delcourt, who had observed for the first time in 1909 the occurrence of a mutant form in a strain of Drosophila [97]. The two young biologists worked under the supervision of Maurice Caullery, and they were encouraged by Etienne Rabaud. Their objective were to establish that The Mendelian methodology was vitiated by an insufficient control of the nutritional and aseptic conditions of breeding. They hoped in fact that a modification of these conditions would entail the production of mutants. The titles of their first joint papers before the war are illustrative of this purpose [22, 98, 99]. For a reason that we have not been able to elucidate, Guyénot stopped working with Delcourt stopped working with Delcourt approximately in 1913 or 1914. The war may have been the motive, but we do not know.

What we do know is that in 1913 Guyénot began to work on new strains of Drosophila given him by T.H. Morgan. In 1917, he published the result of his personal research, which had taken the form of a doctoral dissertation, published in the *Bulletin biologique de la France et de la Belgique*, with the support of Étienne Rabaud, the journal’s editor [100]. Rabaud had hoped studies like those of Guyénot and Delcourt would help establish the limits of Morgan's methodology, and would provide support for his avowed Lamarckism. Guyénot had succeeded in controlling the experimental conditions of breeding of Drosophila and in raising them aseptically. But after observing 400,000 flies, he concluded that the progeny of mutants did not change in an altered environment, and new mutants appeared regularly in a constant environment. In his dissertation, Guyénot remained rather cautious about the obvious anti-lamarckian argument that it allowed. But soon after, in an independent article, he acknowledged that his study provided unambiguous support of Morgan's work : "J'ai pu, grâce à l'obligeance de T.H. Morgan, avoir entre les mains un certain nombre de mutations sur lesquelles ont porté ses recherches. Après avoir rendu aseptiques les élevages de ces lignées, j'ai pu refaire la plupart des croisements déjà réalisés par les auteurs américains et me convaincre, par moi-même, et d'après des pourcentages considérables, de la légitimité des résultats anoncés" [101 : 234]. After this episode, Guyénot fell out with his mentor Rabaud, who engaged him in violent polemics, and found a position at the University of Geneva (Switzerland). Guyénot's early work, protected by several patrons at the Sorbonne, led him to become a major European geneticist in later life. The early work is exemplary of the attitude of French biologists to Mendelian genetics in the first two decades of the 20th century. This attitude consisted in taking Mendelism seriously, but with the idea of submitting it to the test of a methodology and a conceptual framework manifestly inspired by three national glories: Claude Bernard (physiology, esp. physiology of nutrition), Pasteur (asepsis of strains), and Lamarck (inheritance of acquired characters). In passing, it must be observed that all the Drosophilists, including Morgan, adopted the standardized techniques of control of asepsis and nutrition developed by Guyénot.

One last negative characteristic of French genetic research in the period 1900-1930 is the following. French biologists contributed nothing to the chromosomal interpretation of genetic phenomena. Moreover, this total absence is in good agreement with the fact that the French were even less involved in genetic research in the period 1914-1935 than during the first two decades of the century. In other words, the French did not play a significant role in genetic research during the chromosomal phase of the history of genetics. We will return shortly to this aspect in the explanatory part of this paper.

We can summarize our descriptive narrative of the penetration of Mendelism into the French biological community before 1930 in three formulae: (1) French biologists were, at least at the beginning, well informed; (2) They did not find it necessary to teach genetics; (3) some of them participated brilliantly, but in isolation, in the Mendelian phase of genetic research, but they were thoroughly alienated from the chromosomal theory of heredity.

3. Resistance to Mendelism : Explanatory hypotheses

How can one explain the long continuation of the wholesale resistance of the French biological community to genetics in the first three decades of 20th century ? In previous papers we have already examined several possible causes in detail [1, 15]. Here we would like to propose a more systematic classification and articulation of these causes. It would be nonsensical to point out just *one* cause. It is preferable to speak of a bundle of unfavorable circumstances, none of which was decisive in itself, but which acted together synergistically to reinforce the resistance.

A first category of causes can be classified as "intellectual factors". We think here of a cluster of cognitive preferences and of traditions of thinking and working. This category includes three main components. The first is the predominance of a general conception of the nature of science. A large number of French biologists, and, more generally, of French scientists under the 3rd Republic (1870-1940), adhered to a positivistic conception of science. By “positivism”, we mean a conception of science which favors facts over “hypotheses”, in virtue of Auguste Comte’s “law of the three states” of the development of any human knowledge : whereas in the “metaphysical” (or second) state, explanation is founded on verbal and fictitious entities, in the positivistic or scientific state, explanation consists in gathering facts under laws.

This view of science was endorsed by those scientists who founded the *Société de biologie* in 1848 [102 : 61-67], a society which remained the most active and fertile in the field of life sciences in France until WW II. Comtian positivism was also extremely influential among those who founded the modern French educational system at the end of the 19th century, as for instance Marcellin Berthelot (the well-known chemist and minister of public instruction), or Emile Durkheim (sociologist, and general inspector of public instruction). One of the most frequent arguments that was used in the anti-Mendelian polemics of the beginning of the century was that the conception of genes as “hypothetical units”, that is invisible entities which nevertheless had the value of hereditary determinants —whatever their physical nature—, was contrary to the “experimental method”. Félix Le Dantec or Etienne Rabaud [103, 104], for instance, were opposed to the Mendelians' way of explaining hereditary phenomena through a kind of reasoning that conferred a causal role to entities that were in fact no more than a convenient symbolic notation. For them, such an attitude was not scientific, but typically verbal, empty and “metaphysical”. The following texts provide a particularly clear example of this kind of prose : “La notation symbolique a rendu, rend et rendra de grands services ; elle en rendra d’autant plus que l’on évitera d’attribuer aux symboles une valeur explicative… La conception ne nous apprend rien sur la nature et la marche des procesus héréditaires : sa précision n’est qu’une précision verbale, la solution qu’elle apporte n’est qu’une soulution illusoire ; elle est l’opposé d’une conception fondée sur la méthode expérimentale” [103 : 148-149]. “L’œuvre de Mendel est d’une importance capitale ; ses expériences cruciales éclairent d’un grand jour les phénomènes de l’hérédité. Toutefois, on ne peut dire que Mendel ait exprimé, ni suggéré une conception de l’hérédité. Les résultats expérimentaux, exposés de façon claire à l’aide d’une notation symbolique, posent nettement le problème. Mais ces résultats ne ne sont pas une théorie… C’est par une véritable usurpation que Morgan et son école prétendent accaparer Mendel : en se donnant comme ses successeurs exclusifs, ils risquent simplement de le compromettre. Les faits mendéliens restent, et tout les confirme ; la théorie de Morgan ne soutient pas l’examen. Passe encore si elle n’était qu’un conte ingénieux et ingénu ; mais elle prétend exprimer la réalité… En contradiction avec les principes les plus élémentaires de la méthode expérimentale, la théorie donne à croire que le problème entier de l’hérédité consiste à inventer des ‘gènes’ et à localiser sur des chromosomes… Ai point de départ, des hypothèses sans fondement sérieux. Dès lors la recherche s’éternise dans une voie sans issue” [103 : 140-141].

Second intellectual factor : the same anti-Mendelian authors pray for the coming of a “physiological theory of inheritance” [e.g. 57, 90, 91], that is to say : a physical-chemical theory, integrated in a global conception of the cellular metabolism : “Le mécanisme de l’hérédité, mécanisme complexe, est évidemment lié à toute la physiologie cellulaire. L’assimilation, les conditions etles processus suivant lesquels elle s’effectue dominent le problème. Aux faits épars suivant lesquels elle s’effectue dominent le problème. Aux faits épars que nous possédons, il faut en ajouter d’autres : c’est en cela que constitue le travail urgent de la Génétique. Il importe, en définitive, de faire passer la Génétique morphologiuqe du terrain, où elle s'enlise, au terrain physico-chimique, autrement vaste et fécond ; il importe de ne point s'attarder dans l'emploi de la méthode verbale, simple cliquetis de mots évidemment stérile, et de mettre en œuvre la méthode expérimentale, qui donne aux recherches la seule direction capable d'aboutir à des résultats utiles" [90 : 149-150]. Two authors serve as ritual fetishes in support of this rhetoric : Lamarck, of course, but also and probably more significantly, Claude Bernard, who had invited biologists to treat heredity not as a cause, but as a physiological effect (for more details on Bernard and heredity, see [3]).

Finally, these anti-Mendelian arguments come in the context of a French biological and medical tradition which never assigned cytology and cell theory as important a role as it was given in Germany, England and US. This poor development of cytology was not decisively negative in the first phase of the history of genetics, the properly Mendelian phase. In England, after all, cell theory and cytology were not highly developed (witness Bateson and his reactions to the chromosome theory). But the underdevelopment of cytology became a major obstacle when genetics was turned into a chromosomal theory of heredity. Then the objections about the non-physiological character of the new biological discipline increased. Morgan's genetics was charged with two opposite defects: on the one hand it was purely morphological, therefore purely descriptive; on the other hand, because of its unfounded causal pretensions (genes as hereditary "determinants"), it reified verbal entities that had no definite physical status.

A second category of factors unfavorable to genetics in France consisted in the weak interaction between theoretical biological research and agricultural and horticultural research. As often noted in the present meeting, and in many previous studies, the countries in which Mendelism flourished best were those were agricultural and horticulturist engineering was strongly coupled with experimental biology at the turn of the 20th century (Britain, Germany, Scandinavian countries, Holland, US). In France, in spite of the efforts of the Vilmorin Company [14], this link was not successfully constituted before the creation of the Institut National de la Recherche Agronomique (1921).

A third important factor, although retrospectively sympathetic to a modern reader, must be mentioned. The eugenic ideology was poorly developed and integrated in France. Again, historians commonly agree that there is a strong coincidence between the extent to which a country accepted eugenics and the extent to which it provided a climate favorable to the early development of genetics.

A fourth category of cause must be mentioned. Institutional factors also played a role. The primary charge of French universities under the third Republic was (and remains today) to provide the best possible training to secondary schools teachers, on the basis of national programs, diploma and competitions. This was certainly not a primary cause of resistance to Mendelism, but a factor in the rigidity that amplified the effects of the debates over the new science of genetics. In a highly centralized university system, it is unlikely that a poorly practiced and controversial science would be seriously transmitted.

4. Epilogue : after 1930

In the thirties, French biology entered into genetics through two parallel pathways : experimental and theoretical genetics of populations, and physiological genetics.

The second line of research was brilliantly illustrated by the work of Boris Ephrussi. We will not detail here this particular story (see [1, 2, 4, 6, 8, 9, 15, 105]). We just want to mention that Ephussi's remarkable accomplishments and recognition in the domain of physiological genetics can be better understood under the light of some of the sources of resistance to genetics that we have mentioned earlier in this paper. First the predominance of a "physiological" approach to heredity is patent (but this time, it is not only words, it is a real and fruitful research program). Secohndly, Ephrussi developed his research program, not in a university, but at the Institut de Biologie Physico-Chimique, also known as the "Rotschild Foundation". This institution was entirely devoted to research. His founder, Edmond de Rothschild was an overt admirer of Claude Bernard, whom he had known. Thirdly, Ephrussi's program was also supported by the Rockefeller Foundation. This gave it an international dimension. Ephrussi's work on eye pigmentation was immediately preceded by a stay in Morgan's lab at Cal Tech. From there he came back to Paris with George Beadle, who signed with him all the key papers of 1935-37 on the genetic control of eye pigmentation in Drosophila.

The other line of genetic research that was developed in France in the thirties was population genetics. Although this episode has been largely neglected by standard historiography of science, it now appears that it was important [78, 106]. Experimental population genetics was indeed initiated in France, with the pioneer works of Philippe L'Héritier and Georges Teissier. In approximately the same time (ending thirties) Gustave Malécot wrote his legendary dissertation on the foundations of theoretical population genetics, which he proposed to reconstruct with the help of the calculus of probability, rather than mathematical statistics. In a sense, these two lines of research seem to be less in continuity with the story we have reconstituted in this paper. However they have also something to tell us about the particular way the French entered into the realm of genetics. Institutional factors must be mentioned. Philippe L'Héritier conceived the idea of populations cages when he was in US in 1932. He went there with a Rockefeller fellowship in order to learn genetics. There he had the occasion to hear Fisher, Haldane, Wright at the Sixth International Conference of Genetics of Ithaca. He returned to France with the project of testing their models on an appropriate experimental system. All things considered, this entrance of a young French biologist into the domain genetics resembles that of Ephrussi. Intellectual factors certainly played also a role. Population genetics developed as an expansion of the most central Mendelian kernel of classical genetics. However this expansion involves a major mathematical aptitude. All along the 20th century, France kept a major reputation in mathematics. Teissier and L'Héritier had their first training in mathematics. Malécot always remained a mathematician. It comes as no surprise, then, that population genetics was more easily developed in France in the thirties than more traditional areas of genetics.

In conclusion we can safely say that the paths by which genetics entered securely into the traditions of French science in the nineteen-thirties were certainly not typical of the paths followed elsewhere. Rather, they drew on particular strengths of French science –physiology and mathematics – that had either fostered the French resistance to Mendelism or been largely indifferent to it.

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