Lamarckian Research Programs in French Biology (1900–1970)

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Abstract The situation of biology in France in the twentieth century has always been considered something of an oddity. The theories of the Darwinian Modern Synthesis and of population genetics were not included in standardized university curricula and the main research programs until the 1970s. Against the Darwinian picture that was developing abroad, French life scientists promoted various forms of Lamarckism. The aim of this chapter is to produce a general picture of these different twentieth century Lamarckian research programs which deeply structured various fields of the French life sciences, like morphology, zoology, paleontology but also microbiology and virology. We first recall the failure of the first Lamarckian program, based on a mechanistic understanding of life, and which aimed at explaining evolution in terms of cumulative adaptation through the inheritance of acquired characters. We show that during the interwar period, French Lamarckians were no longer unified in their understanding of the evolutionary process but instead defended a heterogeneous array of concepts. In particular, we examine philosopher Henri Bergson's legacy, which was pivotal in the setting up of a second Lamarckian program that started to develop in the 1940s with the work of zoologists Albert Vandel and Pierre-Paul Grassé. While it is true that the various forms of Lamarckism delayed the reception of Darwinism and, to a lesser extent, genetics, we assess their impact on the way the Modern Synthesis and molecular biology were conceived and developed in France by non-Lamarckian biologists like Georges Teissier, Philippe L'Héritier, André Lwoff, or Jacques Monod.

Keywords French biology • Lamarckism • Inheritance of acquired characters • Henri Bergson

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1 Introduction

No other scientific nation opposed Mendelian genetics, the chromosomal theory and the Evolutionary Synthesis as strongly, and during such a significant portion of the twentieth century, as France. During the same period, Lamarckian-oriented research programs were flourishing. For nearly a century, French biological thought was almost completely dominated by various forms of Lamarckism, forms that often presented substantial differences and were sometimes even theoretically incompatible. Despite these differences, all posited that the Darwinian approach was neither a satisfactory nor fruitful way of theorizing about organic evolution. Natural selection provided an explanation for the survival of the fittest but could by no means account for the *origination*—i.e., the causal/physiological formation—of the fittest. In other words, the creativity of natural selection was either denied or misunderstood.

The aim of this chapter is to provide a balanced overview of these various Lamarckian programs as well as their relationship with the programs they opposed, namely genetics and Darwinism. However, our main focus will not be to describe how these Lamarckian programs contributed—among other factors—to prevent the positive reception of these theories (this aspect will be raised briefly in the conclusion). Illuminating studies already provide detailed explanations of how and why Darwinism and genetics were ignored or opposed in France during the nineteenth and part of the twentieth century (Conry 1974; Boesiger 1998; Burian et al. 1988; Gayon 2013a, b). In this chapter, we limit our study of the Lamarckian reception and rejection of genetics and the Evolutionary Synthesis to those elements allowing us to clarify the internal logic of these Neo-Lamarckisms. We attempt to summarize the main conclusions of some of our previous works (especially Herring 2016; Loison 2010, 2011, 2012; Loison et al. 2017), by contrasting the various ways in which French life scientists theorized along Lamarckian lines and by providing a general picture of their research programs.

The terms “Lamarckism,” “Neo-Lamarckism,” and “Lamarckian” are not historiographical categories we use to retrospectively label past theories: most of the life scientists we reference abundantly made use of this vocabulary and explicitly identified themselves as Lamarckians or Neo-Lamarckians. The epistemological adequacy or inadequacy of these terms is an issue that will not be addressed here (Loison 2011: 737–741), and for the sake of clarity and concision, we will use them indiscriminately as convenient labels. The same does not apply, on the other hand, to the “research program” concept, which is a historiographical category that was not necessarily employed by the life scientists in our study. We use it to emphasize that these Lamarckisms were not merely vague and audacious speculations: most of them were designed as frameworks for concrete research intended to guide everyday work in the laboratory or in the field. In addition, it is important to note that although our characterization of the “research program” concept is similar and compatible with the concept developed at length by Imre Lakatos, we do not wish to import the whole Lakatosian philosophical apparatus into our study (Lakatos 1986).

We are utilizing a less restrictive and more common usage of the concept as a basis to examine how metaphysics, scientific theory, and practice were intertwined.

The first two sections of our study (Sects. 2 and 3) contrast two very different forms of Lamarckism. In the Sect. 2, we give a brief account of the failure of "experimental transformism," the (relatively) unified view about evolutionary dynamics shared by most French Neo-Lamarckians at the end of the nineteenth century. This first research program which focused on the issue of adaptation was unable to produce any conclusive evidence in support of the inheritance of acquired characters. Therefore, from the 1920s onwards, with no experimental evidence to back it up, all that was left of this program were doctrinal arguments against genetics and Darwinism. Section 3 is devoted to the delayed influence of Bergson's philosophy on French biological thought. It starts with a short summary of Bergson's famous metaphysical take on biological evolution, *L'Evolution créatrice* (1907), and describes how some of his ideas gradually became appealing to certain French biologists. At first quite elusive in the 1930s, references to Bergson and his "élan vital" started being used authoritatively in the 1940s and by the 1950s, zoologists Albert Vandel and Pierre-Paul Grassé were developing a vitalist and spiritualist Lamarckian program which drew heavily on some of Bergson's views. This second main form of French Lamarckism is partly responsible for the prolonged negative reception of the Modern Synthesis in France after the Second World War.

Sections 4 and 5 deal with the influence of the Lamarckian intellectual environment within French biology on research programs which did not explicitly position themselves within the Lamarckian traditions. In Sect. 4, we analyze how Vandel and especially Grassé opposed the Evolutionary Synthesis and how they interacted with some of its founders like Theodosius Dobzhansky. In France, the Modern Synthesis was at first embraced and developed solely by Georges Teissier and Philippe L'Hérétier, whose works were pivotal in the setting up of experimental population genetics (Gayon and Veuille 2001). We describe how Teissier and L'Héritier's interests, ideas, and conjectures, despite their Darwinian inclinations, were influenced by the Lamarckian atmosphere of French biology. This example perfectly shows how non-Darwinian ideas influenced the development of the Modern Synthesis, a core hypothesis of Depew's (2017).

Our fifth and last section does not concern evolution per se but instead what would come to be known as molecular biology in the 1950s. We argue that the Lamarckism of the first kind (i.e., the concept of the inheritance of acquired characters) was instrumental in the birth of two research programs at the Pasteur Institute: the one on enzymatic adaptation and the other on bacteriophagy and lysogeny (Loison et al. 2017). During the period 1890–1940, these phenomena were interpreted in terms of Lamarckian heredity. It was only in the late 1940s and 1950s, when Lysenkoism became a central bone of contention in the French community, that André Lwoff, Jacques Monod, François Jacob, and their colleagues decided to break with this tradition and produce a strictly genetic and molecular account of bacterial adaptation, namely the operon model.

2 The End of an Era: Experimental Transformism's Lack of Experimental Support

2.1 Extending "Experimental" Science to Evolution

French Neo-Lamarckism first originated as an attempt to introduce experimentation in the study of organic evolution. One of the reasons that French biologists had opposed Darwin's *Origin of Species* since the 1860s was because Darwin did not mention a single instance of the transformation of one species into another based on rigorous experimentations (Conry 1974; Loison 2010, 2011). At the time, French biology was almost completely dominated by the figures of Claude Bernard and Louis Pasteur, and thus positive scientific knowledge was believed to be obtained only through rigorous laboratory experimentation (Burian et al. 1988; Loison 2010; Gayon 2013a).

That is why "transformism,"[1] the science of evolution, was to be based on a materialist understanding of living matter and of its various forces and had to be developed in accordance with the guiding principles of the experimental method. During the period 1880–1910, these methodological and theoretical ambitions were emphasized in several articles and books written by the most prominent biologists of the time, like Edmond Perrier (1844–1921), Gaston Bonnier (1853–1922), Julien Costantin (1857–1936), and Yves Delage (1854–1920).

Botanists were the very first to try to apply this methodology, both in the field and in the laboratory. The Bernardo-Pasteurian project of an "experimental transformism" (De Varigny 1891) developed simultaneously in several branches of biology, such as microbiology and teratology, but it was in botany that the results obtained were by far the most conclusive. In the early 1880s, Gaston Bonnier, professor of botany at the Sorbonne, launched a vast experimental program with his students and collaborators in order to establish that the morphology, anatomy and physiology of plants were dominated by abiotic parameters such as luminosity, temperature, and humidity (Bonnier 1890). Part of this research program consisted in comparative cultures. The standard protocol could be summarized as follows: cuttings of the same seedling were planted at various stations in the French Alps and Pyrenees (at altitudes of 1060–2030 m) and in his laboratory near Paris (Fontainebleau), and differences between individuals were periodically measured. After only a few weeks, he and his colleagues observed that many features of the plants had changed, and that these induced modifications could, at least in some cases, completely transform the individual so that the original species was no longer recognizable. These types of results seemed to show that natural selection was an unnecessary mechanism: by changing

[1]The anthropologist and biologist Armand de Quatrefages (1810–1892) popularized the term "transformism" [*transformisme*] during the debates surrounding the reception of Darwin's *Origin of Species*. To avoid the problems resulting from the polysemy of "evolution," he proposed that "transformism" should be preferred to designate what would later be called the evolutionary theory (see de Quatrefages 1870: 14–15). From the 1870s, "transformism" was frequently used by French scientists for almost a century.

their conditions of growth, individual organisms were capable of physiologically conforming to the new requirements and these internal modifications could in the end—it was supposed—lead to morphological evolution. The mechanism of adjustment was never clearly articulated by scientists like Bonnier and others. In general, they believed that the intimate relationship of an organism with its environment was a sufficient explanation: the physiological/nutritive working of the protoplasm was the way in which the environment affected morphology (Loison 2010).

On some occasions, Bonnier directly referenced Claude Bernard and explained that he was trying to extend Bernard's ideas and methodology to anatomy and morphology (Bonnier 1893). Bernard strictly separated morphology and anatomy from physiology (Bernard 1966 [1878]; Loison 2013b) claiming that only physiology had the potential to become a true experimental science. Physiology studied the present functioning of living beings whereas anatomy and morphology studied organisms' form and structure which were mainly the consequence of heredity, meaning they were not the result of present "determinism" and could therefore not be studied experimentally (Bernard 1966 [1878]: 341; Gayon 2013c). This led Bonnier and others to argue that Bernard's account of experimentation was too restrictive and that morphology could also be included in the realm of experimental science. Most of the French Neo-Lamarckians of this period understood "experimental" the way Bonnier did, as a category which needed to be extended in order to include transformism (Loison 2012). But in the French context, "experimental" also referred to another, substantially different, practice that also challenged Bernard's restrictive characterization. Bernard's account valued experimentation as a practice where the scientist controlled the phenomenon at stake, whereas observation was reduced to a strictly passive activity. Many zoologists felt that Bernard's intransigent and often arrogant claims amounted to an unfair characterization of their practice (Paul 1985: 98–103). In the 1860s and 1870s, zoologists were especially averse to their work being characterized as the mere "contemplation" of nature. The most influential of them, Henri Lacaze-Duthiers (1821–1901) extensively opposed Bernard's demarcation between experimentation and observation. Inspired by Ernest Chevreul's ideas, Lacaze-Duthiers argued that regardless of the type of scientific practice, the scientist's mode of reasoning would always be "experimental" (i.e., hypothetico-deductive). In other words, both nature and the laboratory presented cases requiring more than just passive observation, and therefore, zoology could be said to be experimental too.

One of Lacaze-Duthiers' students, Alfred Giard (1846–1908), was also one of the most prominent French Neo-Lamarckians around 1900 (note that Lacaze-Duthiers himself, like many of his generation, always remained skeptical about the seemingly adventurous hypothesis of organic evolution). Despite being opposed to his previous mentor on almost every possible subject, Giard nevertheless continued to support Lacaze-Duthiers' understanding of what it meant to be "experimental" (Loison 2013b). Founder of the marine station of Wimereux, in the North of France, he trained dozens of zoologists and taught them what he considered to be the principles of experimental transformism. This sort of transformism was not based on laboratory experimentation but on the careful observation of living beings in their specific "milieu" (De Bont 2010). The significant adaptation of their anatomy and behavior to the requirements of their environment was interpreted as the cumulative ongoing result of individual morpho-physiological accommodations (Loison 2010).

Hence, experimental transformism, in the context of French biology, designated two different practices. Despite their methodological disagreements, these research programs pictured the evolutionary process identically: evolution was completely reduced to changes at the level of the individual, and thus the organism was the only relevant level for studying the operations of evolutionary mechanisms. This made the inheritance of acquired characters a necessary postulate; otherwise, these induced individual modifications would have been evolutionarily irrelevant. At the beginning, this hypothesis seemed rational, as it appeared to be supported by various observations and susceptible to further experimental tests. But, as time went on, the power of these empirical arguments weakened, especially because of August Weismann's sharp criticisms (part of Weismann's texts were translated into French as soon as 1892). During the 1910s, it became clear, even for the most radical French Neo-Lamarckians, that no conclusive experimental results asserted the reality of a general process of the inheritance of acquired characters. And, because natural selection was still seen as a secondary evolutionary cause, the scientificity of transformism was once again in question.

2.2 Renouncing the Experimental Method: The Theoretical Agnosticism of the Interwar Period

Camille Limoges correctly highlighted that because of the failure of the experimental transformism research program, most French biologists of the interwar period were "led to an attitude of theoretical agnosticism" (Limoges 1998: 323). These second generation Lamarckians, in contrast to their predecessors, could no longer take the reality of the inheritance of acquired characters as given and were forced to renounce studying the mechanisms of evolution through what they conceived as the standard experimental method. This epistemological renunciation gave birth to various theoretical attitudes.

Some biologists proposed that the mechanisms of evolution could no longer be studied experimentally because they were no longer operative. This view was supported by the zoologist Maurice Caullery (1868–1958), the successor of Alfred Giard in the chair of "evolution of organized beings" at the Sorbonne (1909–1939). In his main book *Le problème de l'évolution* (1931), he argued that Lamarckian mechanisms had once been operational in the distant past but this was no longer the case and that this could explain the failure of current attempts to demonstrate the reality of Lamarckian processes. Because natural selection was still understood as of secondary importance, Caullery and others (like Jean Rostand) maintained that the main steps of phyletic adaptation were the consequence of Lamarckian mechanisms. But to do so, they had to renounce the uniformitarianist stance the previous generation of Neo-Lamarckians had adopted: the new form of Neo-Lamarckism could not be tested in the present day and had thus become a strictly ideological doctrine. In the early 1960s, Georges Teissier (1900–1972), one of the founders of experimental population genetics, recalled the pessimism that characterized French transformism during this period. According to him, during the 1920s, the issue of the mechanism of organic evolution "had become a desert that one only crossed as a tourist in a hurry because it didn't deserve much attention" (Teissier 1962: 362). Because of this apparent lack of scientificity, scientists "had become convinced that this problem did not concern them any longer and should be left to the philosophers" (Teissier 1962: 362).

But the idea that evolution had come to a halt thus rendering its experimental study impossible was not the only option explored by French biologists to account for the experimental failure of the inheritance of acquired characters. Another student of Alfred Giard's, Etienne Rabaud (1868–1956), professor of experimental biology at the Sorbonne, developed an alternative solution to this problem. Rather than renouncing the principle of uniformitarianism, he challenged the basic idea that morphological adaptation was the cornerstone of evolution. He went as far as to say that the adaptationist vision of evolution was an expression of a fundamental bias in favor of teleological explanations in the living world. Since morphological adaptations were mostly projections of the naturalist's teleological mind, it thus became irrelevant to construct a hypothesis—like the inheritance of acquired characters—to explain them (Rabaud 1922).

As it has been previously emphasized, these various forms of renunciation reduced Neo-Lamarckism to a state of explanatory impotence during the interwar period (Loison 2011). In contrast to the project of its founders, this evolutionary doctrine could no longer explain adaptation, at least in its classical morphological sense; in fact, it failed to produce any heuristic research programs whatsoever. The lack of positive arguments for Lamarckism meant that during this period most Neo-Lamarckians concentrated their efforts on producing negative arguments directed against their opponents which contributed to the specific French resistance against Mendelian genetics and the chromosomal theory.

2.3 *Demoting Genetics to Secondary Knowledge*

Richard Burian and Jean Gayon have given masterly accounts of the fate of genetics in the history of French biology to which we refer readers seeking a more detailed exposition of this reception (Burian et al. 1988; Burian and Gayon 1999, 2004; Gayon and Burian 2000). Our aim here is simply to give a broad picture of the way French Neo-Lamarckians opposed, or at least undermined, genetics.

The aforementioned scientists shared a common understanding of biological heredity. In accordance with their Bernardian framework, French biologists pictured the entire mechanism of heredity as the continuation of the physiological state of the protoplasm (Loison et al. 2017). Reproduction was reduced to the division of a mass of protoplasm in which each of the new parts preserved the nutritional dynamics of the initial entity. This developmental account of inheritance implied that acquired characters were automatically heritable and opposed all forms of particulate inheritance. By particulate inheritance, we mean all the hypothetical and sometimes speculative explanations of inheritance, from Darwin's pangenesis to Mendelian genetics, based on the existence and transmission of discrete representative particles.

From 1900 onwards, French biologists did not reject the results of Mendelism, but they argued that the phenotypic characters at stake were of secondary importance, i.e., only superficial or ornamental. Important physiological and anatomical features were not the consequence of hypothetical genes (or of any other sort of hereditary particles) but of the workings of the entire protoplasm conceived as an integrated whole. If genes existed, they should be seen as analogous to microbes (in a typical Pasteurian sense), i.e., microscopic discrete entities able to disturb the normal regulation of physiological processes and thus bring abnormal traits into existence. Félix Le Dantec (1869–1917), another student of Giard, was from the outset one of the strongest opponents to genetics and did not hesitate to write, as early as 1904, that "Mendelian heredity does not concern heredity, properly conceived, but rather a kind of *contagion* affecting the gametes" (Le Dantec 1904: 515).

Alongside Rabaud, Le Dantec was no doubt the fiercest critic of genetics, and most French biologists shared at least part of his suspicion against what they considered to be a secondary science. For instance, Caullery, who was one of the few who taught the principles of genetics during the interwar period (Burian et al. 1988), nevertheless always remained convinced that a true developmental theory of biological inheritance still needed to be conceived and that genetics was at best nothing more than a practical model (Caullery 1916: 424, 1931: 336).

This almost systematic opposition to Mendelian genetics and to the chromosomal theory—with the remarkable exception of Lucien Cuénot (Burian et al. 1988)—strengthened the received view that the problem of the mechanism of organic evolution was not to be found within the boundaries of experimental and positivist science. Therefore, the explanation for evolution was a problem for metaphysicians and philosophers, rather than for true scientists. The success of Bergson's *L'Evolution créatrice* (1907) strongly reinforced this view and contributed to the reluctance, on the biologists' part, to engage in any form of theorization in the fields of evolution and heredity.

3 Bergson's Legacy

3.1 L'Evolution créatrice

In the first decades of the twentieth century, French philosopher Henri Bergson (1859–1941) was one of the most famous intellectual figures in the world. After teaching secondary school philosophy for just under two decades, in 1898 he obtained a professorship at the *Ecole Normale Supérieure*, where he himself had studied philosophy. Two years later, he accepted the chair of Greek and Latin philosophy at the Collège de France. At this time, Bergson was already famous, renowned for his theories of time, in his own words *durée* (duration), mind, and matter (Bergson 1889, 1896) and later, the nature of laughter (Bergson 1900). His lectures were so crowded that people sometimes resorted to climbing up the walls of the prestigious Parisian institution for a chance to listen in (Soulez and Worms 1997). It was not until 1907 that Bergson reached the height of his fame after the publication, and rapid translation into several languages, of his metaphysical take on biological evolution, *L'Evolution créatrice*. The book was a huge commercial success, and Bergson's ideas were discussed in and outside of philosophical circles propelling the philosopher to international stardom (Azouvi 2007). Although many biologists dismissed Bergson's ideas as nonscientific, others from both Lamarckian (Herring 2016) and Darwinian (Gayon 2008) traditions found some of Bergson's ideas appealing, for instance, his criticism of Laplacian determinism, his idea of evolution as the progressive pursuit of certain tendencies without predetermined telos, and the coextensiveness of life and consciousness.

In his previous books, Bergson had discussed and challenged existing theories of mind, memory, and brain. In *L'Evolution créatrice*, he focused on the different biological theories of his time. Bergson was well versed in the life sciences and had read and mastered biological classics including Cuvier, Lamarck, Darwin, and Weismann as well as more contemporary works by his compatriots such as Cuénot, Delage, Giard, Le Dantec, and Perrier and by life scientists outside of France like Bateson, Cope, De Vries, Driesch, and T. H. Morgan. Bergson used a metaphor, the *élan vital*, to describe evolution as an unpredictable, unitary, and creative force, turning inert matter to its advantage and striving to free itself from material constraints. He was writing in the midst of the period Julian Huxley later called the "eclipse of Darwinism" (Huxley 1942: 22–28) during which various evolutionary theories were proposed. In the first chapter, Bergson discussed his controversial notion of the *élan vital* in relation with the four main rival theories of the time (Darwinism, mutationism, orthogenesis, and Lamarckism).

Bergson was often accused of defending a vitalistic agenda. However, he was not attempting to propose a fifth rival scientific theory, "the theory of the élan vital." Rather, the *élan vital* was a metaphor (Bergson 1907: 258) serving philosophical purposes. In fact, it was, according to Bergson, the metaphor that best expressed his metaphysical picture of life because the main characteristics of life could be subsumed under this one image. Firstly, the image of an original impetus common to all of life allowed Bergson to consider evolutionary history as a coherent whole consisting of successive divisions stemming from the same origin. He also stressed the inherently unpredictable (therefore non-teleological and nondeterministic) and creative nature of evolution. Finally, adaptation was not for Bergson—in contrast to the views of French Neo-Lamarckians of the first generation—the driving force of evolution. Changes in environment were merely contingencies, obstacles to the development of the main tendencies of evolution. Even though these environmental changes required organic innovations that some might call adaptations, these did not constitute the driving force of evolution. Evolution was not driven by external environmental causes; it was internally driven and engaged in the direction of the liberation of mind and the complexification of mental phenomena.

Because of the strong psychological component of his evolutionary philosophy, Bergson was sympathetic, although not committed, to American Neo-Lamarckism represented by people like paleontologist Edward Drinker Cope (1840–1897) who characterized evolutionary change as internally motivated by some kind of force analogous to a psychological effort (Bergson 1907: 77–78). However, Bergson was highly critical of the French tradition of Neo-Lamarckism. He aligned himself with the life scientists who, at the time, were expressing strong doubts about the heredity of acquired characters. He concluded that even if one day it became apparent that, in some instances, acquired characters were inherited, these phenomena would be too marginal to account for the level of coordination required for the creation of complex organic structures. In addition, he was strongly opposed to the mechanistic component of the French Neo-Lamarckian philosophical framework. This did not, however, mean that he defended a teleological vision of evolution instead. The creative nature of evolution meant for Bergson that the outcome of evolution could not be predicted by deterministic mechanical laws nor by a predetermined telos, and he insisted that evolution could be directional without being teleological. He believed that the different branches of the evolutionary tree followed the same tendencies, mainly the development of higher forms of consciousness (some more successfully than others), not because of a shared goal but because of a shared origin since all of life was the result of the same unique initial impulse. This special conception of teleology involving notions of creativity and inventivity eventually made its way into French biology, but not until the first generation of French Neo-Lamarckism had definitively died out (both literally and metaphorically).

3.2 Emile Racovitza and René Jeannel: Rethinking the Lamarckian Issue of Adaptation

The failure of the experimental transformism research program broadly undermined the explanatory power of the concept of the inheritance of acquired characters during the interwar period. However, this did not mean that the ideas Bergson put forward in 1907 were positively received by French biologists. While in Britain some biologists like Arthur D. Darbishire (Wood 2015), J. A. Thomson (Bowler 1996), D'Arcy Thompson (Esposito 2013), and Darwinian zoologist Julian Huxley (Gayon 2008) showed immediate and explicit enthusiasm for some of Bergson's ideas; in France during the 1910s and the 1920s, biology was still mostly mechanistic and therefore Bergson's "élan vital" was dismissed as vitalistic and nonscientific. For instance, in his scathing review of *L'Evolution créatrice*, Félix Le Dantec described the book as a good piece of poetry but denied it any scientific value (Le Dantec 1907: 232). During the late 1930s and early 1940s, however, the attitude towards Bergson's philosophy substantially changed and his notions of "creative evolution" and of the "*élan vital*" started receiving approval from several French biologists. In 1941, Lucien Cuénot published a book that rapidly became a classic, entitled *Invention et finalité en biologie* (Cuénot 1941). Cuénot expressed his disaffection regarding the traditional mechanistic account of life and made extensive use of finalist vocabulary of inventive and creative evolution to describe living matter's puzzling ability to create purposive structures over the course of organic evolution. Cuénot's tone is often very Bergsonian, and the philosopher's name appears 14 times in the book.

Research carried out during this period on the evolution of underground creatures provides a particularly interesting case study for these changes that were gradually affecting French biological thought. Firstly, cavernicolous animals still provided what appeared to be evidence supporting adaptation via the inheritance of acquired characters, for instance, the progressive loss of functional eyes because of the Lamarckian law of use and disuse (see Bowler 2017). Secondly, biologists involved in the study of underground life gradually made use of increasingly finalist and vitalistic vocabulary in their writings. In France, "biospeology" (*biospéologie*), the science of cavernicolous life, was founded by Emile Racovitza (1868–1947) and his colleagues at the beginning of the twentieth century. Racovitza was a Romanian biologist trained in Paris and in the marine stations of Banyuls and Roscoff under the supervision of Lacaze-Duthiers. Before 1920, he spent most of his career in France where he was recognized as an exceptional naturalist. Racovitza started studying cavernicolous animals in 1904, and was quickly joined by René Jeannel (1879–1965), an entomologist who became director of the Museum of Natural History in Paris after the Second World War.

At first, Racovitza and Jeannel explained morphological adaptations to the underground environment in typical Lamarckian terms: as a result of the disuse of certain organs in the specific cavernicolous milieu, these structures had most probably gradually become atrophied through the cumulative effect of the inheritance of acquired characters (Racovitza 1907: 418, 453). However, both naturalists eventually changed their minds and became more and more interested in the idea of orthogenesis because underground evolution appeared to result from linear and oriented evolution rather than simply from adaptations. The two ideas were not seen as incompatible: because of the remarkable invariability of the underground milieu, the adaptive processes would always advance in the same direction and thus create orthogenetic lines of evolution (Racovitza 1929).[2]

Because of his involvement in the development of a speleological institute in Cluj, Racovitza's scientific activity decreased in the 1930s. In contrast, Jeannel, who had by then become a renowned entomologist, proposed a vitalist, finalist, and orthogenetic

[2]We would like to thank our friend and colleague Cristiana Oghiva-Pavie (Angers University, France) who translated for us part of Racovitza's (1929) book that was published in Romanian.

vision of evolution over the course of several significant publications (Jeannel 1950: 51–52). His 1950 book with an explicitly teleological title, *La marche de l'évolution* (*The march of evolution*), marks the definitive transition from the period of mechanistic adaptive Lamarckism (1880–1910) to a new Lamarckian program which incorporated some major aspects of Bergson's philosophy of life. In the first pages, Jeannel argued that teleological thinking had acquired new respectability mainly because of Bergson's influence. Nevertheless, Jeannel did not renounce the classical Lamarckian explanation of adaptation and even developed it a little further: he believed that the induced modification of a somatic character lead to the synthesis of specific hormones able to reach the gametes and then modify germinal genes in the same direction as the phenotypic character (Jeannel 1950: 100). He labeled this hypothetical explanation of the inheritance of acquired characters "somatic induction" (Jeannel 1950: 8). It is interesting to note that this explanation was based on Mendelian genes, a significant difference from explanations supported previously by the first Neo-Lamarckians.

Orthogenesis was still viewed as the necessary consequence of an ongoing process of adaptation, and Jeannel also recuperated the distinction made by Racovitza (1929) between two types of adaptations: specialized adaptations that significantly constrained the subsequent evolutionary potential and "séclusions" that were adaptations which reinforced the autonomy of animals (for instance, homoiothermy). The former necessarily drove evolution towards a dead-end because of excessive specialization, whereas the latter opened the door to the development of new lineages, new organic types. Jeannel used the term "relais" to label this shift from one organizational body plan to another (Jeannel 1950: 52), a concept and a term that would be pivotal in the zoologist Albert Vandel's Lamarckism.

3.3 Putting Adaptation Aside: Albert Vandel, Pierre-Paul Grassé, and the Project of a Bergsonian Theory of Evolution

Vandel (1894–1980) held the chair of Zoology at the University of Toulouse which he occupied until the end of his career. He was a specialist of terrestrial isopods and published over 150 papers on the matter covering subjects ranging from genetics to systematics and evolutionary biology, but he was mainly interested in their sexuality and geographical distribution. In 1948 Vandel became the head of a CNRS funded underground laboratory situated in a cave in the French Pyrenees (Moulis in the Arriège region) and created at the initiative of Jeannel. In his studies of cave fauna, Vandel concluded that the animals' regressed ocular organs were neither the result of the direct impact of the environment transmitted via the inheritance of acquired characters nor the result of the selection of fortuitous mutations. In fact, said Vandel, the loss of eyesight was a form of evolutionary regression, not an adaption at all (Vandel 1964: 563–564). As such Vandel was in direct opposition to Racovitza's interpretation and a lot closer to Cuénot's notion of preadaptation. Vandel belonged to a generation of life scientists beginning their career in the 1920s at the time when the first generation of French Neo-Lamarckism was declining, failing to secure new followers to carry out their experimental program. Zoologist Pierre-Paul Grassé (1895–1985) was another prominent representative of this generation. They both proposed similar yet nonequivalent versions of Neo-Lamarckism, discarding soft inheritance and focusing on internally driven and progressive evolution instead. They positioned their version of Lamarckism within a tradition inspired partly by Bergson and Jesuit paleontologist Pierre Teilhard de Chardin and motivated by conservative and religious views. Both men were respected members of the *Académie des Sciences de Paris* and had highly successful careers. Grassé comprehensively studied the anatomy, systematics, and behavior of termites and published a lifetime's worth of research on the matter in the early 1980s. In 1941, he obtained the chair of "evolution of organized beings" after Maurice Caullery's retirement. Until his death in 1985, he worked on his monumental zoological encyclopedia which ended up being published in 48 volumes and was the absolute reference for French biology students who would, up till quite recently, refer to it as "Le Grassé."

Contrary to their Lamarckian predecessors, Grassé and Vandel did not believe that the study of evolution would be possible through experimentation. For them, evolution was neither a matter of speciation nor adaptation, or rather, speciation and adaptation were not representative of the true forces at work. Both believed that the true nature of evolution—namely that it was progressive, creative, and directional—could only be discovered through the erudite study of palaeontology and comparative anatomy. True progressive evolution only arose through the creation of new organic types and therefore could only be observed at the level of the phylum. Therefore, they viewed themselves as being part of the intellectual lineage of French naturalists of the past, like Lamarck, Buffon, or Cuvier, rather than the more recent strands of Neo-Lamarckism.

For Vandel, to explain evolution was to explain the creation of absolutely novel organic types at the level of the phylum. He was explicit about the Bergsonian undertones of this claim and insisted on the unpredictability and irreversibility of evolution (Vandel 1942, 1958). He analyzed the history of life into different key stages which he called "paliers" (levels), each new level being irreducible to preceding ones. From each new level, only a few truly progressive routes appeared from which new irreducible characteristics emerged. All phyla went through the same cycle (a progressive stage, an expansive stage and gradual death) but only a few managed to break their cycle and open the path for new forms while the others gradually lost all creative potential before dying out. Human evolution, said Vandel, is currently engaged on the most advanced and progressive route (i.e., with the most creative potential). Like Jeannel, Vandel used the term "relais" to designate the progressive succession of evolutionary cycles (Vandel 1942: 82–84).[3] Vandel didn't propose any explanatory mechanism for the passage from one level to the next. He considered himself an "organicist" which he took to mean that the mechanism of evolution was to be found in "the organization of the living being itself" (Vandel 1958: 12). He speculated that processes occurring at the embryonic level may be able to account for these structural changes.

Grassé, on the other hand, emphasized the oriented nature of evolution. He conceived evolution as "progress towards a certain form which takes place, within a phylum, by adding up similarly oriented variations, completing each other for millions and millions of years" (Grassé 1973: 173). He called the form or type towards which evolution progressed, the *idiomorphon*. Grassé never clearly defined this notion; however, in his view the *idiomorphon* was first created[4] without being actualized and then, over the course of evolution, was realized through different forms within various different lineages in a manner analogous to musical variations on a same theme. Evolution progressed in the direction of the realization of the *idiomorphon* until the emergence of a new form which would become evolution's new goal. Grassé believed that to explain the advent of new organic forms, biologists would have to explain the creation of new genes and their associated enzymes, rather than mutations which were, in Grassé's opinion, merely the rearrangement or destruction of existing genes.

With no concrete evolutionary mechanism, the explanations for Vandel's and Grassé's evolutionary pictures ultimately rested on metaphysical theories. In Vandel's case, evolution rested upon Bergson's metaphor, the *élan vital*, depicting evolution as an unpredictable, irreversible creative movement; whereas Grassé's theory relied on a supernatural or spiritual force responsible for both the creation of new types and the orientation of evolution (much like in Teilhard de Chardin's theological theory of orthogenesis). Therefore, in order to establish themselves as legitimate alternatives to the Modern Synthesis despite not having a rival mechanism to propose, they launched a series of attacks against their Darwinian opponents based not only on scientific issues but also on general epistemological questions concerning the correct way to conduct a scientific investigation in evolutionary studies. These in turn raised philosophical problems about the meaning of evolution for humankind.

[3]Vandel claimed that he was inspired by Jesuit paleontologist Pierre Teilhard de Chardin's description of the law of "relais."

[4]Grassé heavily implies on several occasions that the creation of the *idiomorphon* involves, in some way or another, supernatural forces. Grassé became increasingly vocal about his catholic faith as he got older.

4 Dialogues with the Modern Synthesis: Teissier and L'Héritier in a Lamarckian milieu

4.1 A "True" Synthesis Against the Deficient Darwinian Synthesis

Vandel and Grassé repeatedly attacked their Neo-Darwinian adversaries on two main theoretical fronts which they viewed as the two fundamental components of the Modern Synthesis: adaptation via natural selection and random genetic mutations as the selected "material." Because they viewed evolution as internally driven, they rejected the idea of organisms being passively adapted by natural selection (which they took to be the Darwinian stance). They insisted that it was extremely unlikely that random mutations could give rise to complex structures such as the eye or the human brain (Vandel 1969: 269; Grassé 1973: 176–178). In addition, the chances of the highly coordinated and synchronized evolution of systems such as the eye and nervous systems resulting from random mutations were even slimmer. Therefore, either the Neo-Darwinians of the Modern Synthesis secretly regarded natural selection as a supernatural teleological force or they were unaware that this was a direct consequence of their theoretical stance. Either way, the Darwinian picture did not hold.

Vandel and Grassé claimed that these complex structures, which could not be explained within a Darwinian framework, indicated that evolution involved internal and directed processes. However, as we have already highlighted, they proposed no explanatory mechanism for evolution. Therefore, as one of us has previously argued (Herring 2016), they self-identified as Lamarckians as part of a strategy to constitute their theories as legitimate alternatives to the increasingly dominant Darwinian Synthesis. On several occasions, they wrote their own histories of evolutionary biology with Lamarck systematically cited as the father of evolutionism and the founder of biology. They made a point of identifying with a French tradition of thought in the life sciences and, on an intellectual level, they genealogically linked themselves to Lamarck, Bergson, and Pierre Teilhard de Chardin.

In addition to attacking the architects of the Modern Synthesis for the content of their theories, Vandel and Grassé claimed that the general enterprise of the Modern Synthesis represented a defective manner of conducting scientific research. The two naturalists criticized the Modern Synthesis on the grounds that it was a superficial juxtaposition of different specialist areas of knowledge with no internal logic or harmony rather than a true synthesis. True understanding of evolution required decades of erudite study of all aspects of nature including philosophical reflections. Therefore, the true synthesis was the one taking place within the minds of erudite naturalists such as themselves. However, Vandel and Grassé's depiction of the architects of the Modern Synthesis as pure specialists was not quite accurate. Neo-Darwinians like Theodosius Dobzhansky and Julian Huxley also proposed views of evolution incorporating data from a whole range of biological disciplines while being thoughtful about philosophical and metaphysical questions (for a detailed analysis of Neo-Darwinian philosophy see Delisle 2009).

The Neo-Darwinians did not feel threatened by these repeated attacks that spanned decades (from Vandel and Grassé's early careers in the 1940s until the late 1970s in Vandel's case and as late as the mid-1980s for Grassé). Therefore, interactions between both parties were quite rare, with a few notable exceptions. For example, in 1947, two architects of the Synthesis, geneticist John B. S. Haldane and paleontologist George G. Simpson, attended a colloquium in Paris on the relations between paleontology and transformism, organized by the Sorbonne's professor of paleontology, Jean Piveteau. The two Darwinians were up against, among others, Cuénot, Grassé, and Teilhard de Chardin who all claimed in one way or the other that evolution was directional and that the picture proposed by the Modern Synthesis failed to account for this directionality. While Simpson attempted to debunk once and for all the orthogenetic view of evolution (Simpson 1950), Haldane admitted that Darwinism did not yet manage to explain all evolutionary phenomena which did not mean that it should be abandoned (Haldane 1950). Despite this genuine attempt to create a dialogue between both parties, neither side convinced the other. Another example is the interaction between Dobzhansky and Grassé. In 1975, Dobzhansky wrote a scathing albeit respectful review (Dobzhansky 1975) of Grassé's main book on evolution *L'Evolution du vivant* (Grassé 1973) later translated into English (Grasse 1977). Dobzhansky admitted that Grassé counted among the "great modern biologists" (Dobzhansky and Boesiger 1983: 17) of his time and that *L'Evolution du vivant* demonstrated undeniable brilliance but maintained that Grassé's poor understanding of the relationship between genotype and phenotype meant that the main theses presented in the book needed to be dismissed (Dobzhansky and Boesiger 1983: 158–159).

These critiques did not deter Grassé and his anti-Darwinism seems to have grown stronger as he grew older: by 1980 he was comparing Darwinism to an incurable disease (Grassé 1980: 150). Vandel's and Grassé's hostility towards Darwinism was tied with their philosophical and ideological views. They believed that humans represented the highest point and most progressive route of organic evolution. As such, humans summarized all the organic levels below them. Therefore, true erudition, true knowledge of as many aspects of evolution as possible, is the only way to grasp the complexity of human evolution and this would not be achieved through an enterprise like the Modern Synthesis. They also proposed that humans represented the only route for evolution because evolution currently took place on an exclusively spiritual level. Therefore, their erudite synthesis could provide the means for evolution on a spiritual level to progress. An important consequence of Vandel's and Grassé's theories of human evolution was that humans were responsible for their own evolution. This was incompatible with the Darwinian idea that evolution originated in blind mutations: in other words chance. Organisms could not be passive and evolution had to be progressive, creative, and directional for humans to be able to take evolution into their own hands.

4.2 "Ne dédarwinisons pas": Teissier's and L'Héritier's Commitment to Darwinism

In the mid-twentieth century, French biology was thus deeply committed to a renewed form of Bergsonian-oriented Lamarckism; Grassé and Vandel being its main representatives. However, despite the dominance of Lamarckian ideas, not all French biologists were opposed to the core concepts of the Modern Synthesis. Two in particular stood out through their work and teachings from the 1930s to the 1970s: Georges Teissier and Philippe L'Héritier (1906–1994).

When Mayr and Provine asked Ernest Boesiger, a Swiss population geneticist and a former student of Teissier, to recount what had happened in France at the time of the Synthesis, Boesiger could think of only two biologists involved in a genuinely Darwinian research program: Teissier and L'Héritier (Boesiger 1998). Teissier and L'Héritier are still remembered today because of their collaborative work in population genetics (Mayr 1982: 574). In the 1930s, they provided the first experimental evidence for natural selection. Based on the new population cage technique applied to the species *Drosophila melanogaster*, they were able to precisely measure the various parameters controlling competitive interactions among individuals (Burian and Gayon 1999; Gayon and Veuille 2001).

Jean Gayon and Michel Veuille's in-depth study of Teissier's and L'Héritier's joint work reconstructs in great detail the origins of this French school of population genetics. In particular, Gayon and Veuille explain how these two French geneticists were able to show that selection is frequency dependent: fitness coefficients are not constant but depend on the frequency of the alleles in the studied population. They were also the very first to demonstrate heterozygote advantage, which was a purely mathematical hypothesis before then (Gayon and Veuille 2001: 86–88).

In a recent paper, one of us opposed the pervasive idea, first put forward by Mayr (Mayr 1998: 321), that Teissier was not affected by the Lamarckian atmosphere of French biology because he started out as a mathematician (Loison 2013a). On the contrary, the evidence demonstrates that Teissier was from the outset a true zoologist who was very much aware of what was at stake with the different evolutionary explanations available during the interwar period (Lamarckism, mutationism, orthogenesis, etc.). For example, in personal notebooks he kept between the ages of 17 and 18, Teissier summarized biological articles published in French academic journals and discussed at length issues such as adaptation, evolution, "experimental transformism," etc.

Here, we would like to put the emphasis on another aspect of Teissier's and L'Héritier's commitment to Darwinism: their involvement in popularizing Darwinian thought. Teissier and L'Héritier were of course aware of the generalized hostility towards Mendelian genetics and Darwinism (broadly speaking) within French biology, and they knew that publishing experimental data in the nascent field of population genetics would not be enough to change their colleagues' minds, especially because of the complex mathematical component of this abstract discipline (most French biologists were still at this time "naturalists," i.e., field biologists with erudite knowledge of systematics, but with no specific interest in abstraction and theorization).

As a result, Teissier and L'Héritier gave several talks in a wide set of circumstances which were sometimes explicitly devoted to reaching a wide audience of biologists beyond disciplinary boundaries. Both of them also made a point of publishing papers in non-specialized journals, for instance *L'Année biologique*, the *Revue de l'Encyclopédie française*, or *La Pensée*. They believed their colleagues' rejection of Darwinism originated, above all, from a misunderstanding of the central concepts of population genetics and thus of the emerging Synthesis. To counter this trend, Teissier published two articles in 1945 (Teissier 1945a, b) in which he proposed a more comprehensible account of these concepts. The central claim of these papers was that evolution could only be understood as a strictly gradual process. In other words, there was no need for any kind of "internal" or "vitalist" principle or force driving evolution: macroevolution was conceived as nothing more than the long-lasting consequences of microevolutionary mechanisms.

Teissier's and L'Heritier's pedagogical concerns were also apparent in their experimental work. The experiments they devised in order to demonstrate the selective advantage of the loss of wings for insects living in windy environments aimed to confirm Darwin's speculations on the matter (Gayon 2014) and thus convince their peers of the efficiency of natural selection.

In 1962, *L'Année biologique* published a series of conferences on organic evolution. Most of the contributors—including Grassé—were at least skeptical about the possibility of using nothing but spontaneous mutations and natural selection to explain long-term evolutionary transformations. In his talk, Jean Rostand agreed with Vandel about the inadequacy of the Modern Synthesis and he concluded saying that a "dedarwinization" (*dédarwinisation*) of the evolutionary theory was in order (Rostand 1962: 356). Despite the overwhelming, almost universal, hostility towards the Synthesis from his French peers, their reluctance to accept it, and their unwillingness to rigorously study its principles, Teissier continued to push his own Darwinian agenda and programmatically concluded his own contribution: "Oh, and I almost forgot: we must not dedarwinize" (Teissier 1962: 374; our translation).

4.3 Beyond (Population) Genetics: Plasmagenes, Non-Mendelian Inheritance, and the Issue of Macroevolution

Despite their indisputable commitment to Darwinism, Teissier and L'Héritier also showed interest in certain aspects of inheritance and evolution that did not belong to the classical Mendelian–Darwinian account of evolution. Here, we would like to briefly sketch these unorthodox dimensions of their work and emphasize their connections with the predominantly Lamarckian atmosphere of French zoology during the 1930s and 1940s.

Jan Sapp has documented in detail how, after the setting up of the standard Mendelian account, some heterodox geneticists deliberately decided to focus on non-Mendelian aspects of inheritance (Sapp 1987). Among the various scientists in his study (Sonneborn, Goldschmidt, Spemann, Wettstein, Ephrussi, Nanney, etc.), Sapp includes L'Héritier and his work on cytoplasmic maternal inheritance in *Drosophila melanogaster*. Beyond their foundational work in experimental population genetics, Teissier, and especially L'Héritier, were also key figures of the debate surrounding the concept of the plasmagene and cytoplasmic inheritance during the period 1940–1960.

In 1937, while they were carrying out their experimental study of natural selection, L'Héritier and Teissier discovered that in certain strains of flies, light doses of carbon dioxide were fatal (L'Héritier and Teissier 1937). They coauthored a series of papers on the patterns of transmission of this unusual sensitivity. After the end of the war, when Teissier started a genuine research school focused on the maintenance of genetic polymorphism (Gayon and Veuille 2001), L'Héritier chose to devote all his time to developing research on what appeared to be the first case of a cytoplasmically inherited character ever documented in animals (Burian et al. 1988: 377–378).

Our aim here is not to reconstruct the history of L'Héritier's research program in the field of cytoplasmic and/or nonchromosomal heredity, but to emphasize that his results directly impacted on his (and Teissier's) understanding of the evolutionary process. As we have just seen, during the 1930s and 1940s, Teissier was strongly committed to a gradualism typical among the synthesists: in several publications, he repeatedly stated that the distinction between micro- and macroevolution should not be seen as qualitative (Teissier 1938: 11, 1945a: 5). He firmly believed that population genetics was the only relevant basis for the Modern Synthesis (Teissier 1945a: 3), i.e., that the causal forces of the evolutionary process could be analyzed quantitatively and experimentally.

In the early 1950s, things started to shift. The rapid emergence of what would later be called epigenetics[5] forced Teissier and L'Héritier to rethink, at least in part, the issue of gradualism and the relationship between micro- and macroevolution. Epigenetics was not understood as a new field, but rather as a mere addition or extension to classic genetics (Teissier 1952: 40). Since they saw genetics as a pivotal foundation of the Synthesis, a significant change in genetics meant that a change in the structure of the Evolutionary Theory would be needed (Loison 2013a). Both of them were also perfectly aware of the critical judgements of most embryologists against genetics who viewed Mendelian nuclear genes as being involved in

[5]As early as in the late 1950s and early 1960s, L'Héritier used the term "epigenetics" [*épigéné tique*] to denote this emerging field. Not only did he use the term, but he also proposed a definition which already fitted with our modern understanding of the concept (and despite the fact that, of course, molecular processes like DNA methylation were still completely unknown at the time): "The second [hereditary mechanism] [...] only modifies the modes of expression of encoded structures [...]. To designate this second type of hereditary mechanism, the term epigenetics has been proposed and seems well chosen." (L'Héritier 1962: 16, our translation).

nonessential characters, whereas the main organizational structures of the body were controlled by the cytoplasm.

As Jan Sapp (1987: 141–142) has rightly noted, around 1950, L'Héritier came to oppose the standard Darwinian interpretation of inheritance which, to him, was far too narrow because it did not take into account cytoplasmic heredity (L'Héritier 1955: 494). L'Héritier saw cytoplasmic heredity as a major component in the control of the body plan, and, as such, a plausible key factor in the process of macroevolution (thereby partially decoupled from microevolution).

In 1952, Teissier—and this is even more surprising—also published a paper in which he detailed a speculative account of the working of plasmagenes which could potentially explain major morphological transitions (Teissier 1952). On the basis of the knowledge available at the time, he thought that it was plausible that no essential differences existed between nuclear genes and cytoplasmic plasmagenes. In his view, plasmagenes controlled the physiological functioning of living beings. Teissier proposed that during the event of major changes in environmental conditions, plasmagenes temporarily became nuclear genes: as such, they would be able to evolve rather quickly in an adaptive way because "they entered the selective competition" (Teissier 1952: 43; our translation). In other words, Teissier here reintroduced an ontological demarcation between micro- and macroevolution, a position far from the classical uniformitarianism of the Synthesis.

L'Hérititier's and Teissier's heterodox position underlines the specificity of the French context: at the time of the Synthesis, French biology was under the domination of Lamarckian–Bergsonian thought which prioritized the separation between adaptation and true evolution and which tended to favor non-Mendelian modes of heredity: these two main characteristics were central to L'Héritier's and Teissier's rethinking of the structure of the Evolutionary Synthesis.

5 Lamarckism and the French School of Molecular Biology

In the twentieth century, most of the various forms of Lamarckism which developed in French biology had not been very productive: they contributed to the delayed reception of genetics and Darwinism and largely pushed French research into intellectual dead ends. In Lakatos' terms, these Lamarckian research programs were "regressive" (Lakatos 1986): whatever their starting points, they could not be made to relate meaningfully to empirical data. In the field of biology (i.e., if we exclude disciplines such as psychology and the like), only one Lamarckian program could be viewed as "progressive": the one that paved the way to what is usually called "the French school of molecular biology" (Morange 1998). Our aim here is to present how the first Lamarckian accounts of the phenomena of enzymatic adaptation and lysogeny were indeed fruitful starting points in the history of Pasteurian molecular biology.

This French school included people like François Jacob, André Lwoff, and Jacques Monod and its main contribution to the birth of molecular biology consisted in the setting up of the first model of genetic regulation based on experimental evidence, namely the operon model (Loison and Morange 2017). It is acknowledged that this model was formed at the intersection between two lines of research in microbiology: enzymatic adaptation (Monod) and lysogeny (Jacob, Lwoff). A recent study seeks to document how certain forms of Lamarckian explanations of variation and heredity contributed to the shaping of early debates on enzymatic adaptation and lysogeny in the Pasteur Institute (Loison et al. 2017). We would like to present here a summary of our most important findings.

5.1 Lamarckian Explanations of Enzymatic Adaptation and Lysogeny at the Pasteur Institute: An Overview

Since the late 1890s, it was known that some cells were able to produce specific enzymes if the appropriate substrate was present in the culture medium (Loison 2013c). In 1930, the Finnish microbiologist Henning Karström distinguished between this type of enzyme, which he called "adaptive enzymes," and the "constitutive enzymes," which were continuously synthesized by cells whatever the composition of the medium. With the work of Emile Duclaux (1840–1904) and Frédéric Diénert, the Pasteur Institute was at the forefront of research on what would become enzymatic adaptation during the interwar period.

In the late 1890s, Duclaux was working on two types of fungi: *Aspergillus glaucus* and *Penicillium glaucum* (Duclaux 1899: 83–93). He observed that some enzymes (like "saccharase") would only be produced and secreted in the culture medium in the presence of certain substrates (like saccharose). His student, Diénert, started working on yeast that would later become the most commonly used organism in experiments in the emerging field of enzymatic adaptation research. Diénert's results suggested that the substrate could directly and adaptively transform the enzymes that were already present in the cytoplasm (Diénert 1900: 68). He thought of enzymatic adaptation in terms of "physiological acclimatization," i.e., within a global Lamarckian framework (Diénert 1900: 71). Duclaux himself was convinced of the efficiency of the inheritance of acquired characters in the adaptation of microbes to varying conditions. He was in particular very interested in the plasticity of the protoplasm. Enzymatic adaptation was one key component of the adaptive ability of cells and was seen as the first step in a process of Lamarckian transformation (Duclaux 1898: 605).

The phenomenon of lysogeny was extensively studied in the Pasteur Institute, much more than that of enzymatic adaptation. Lysogeny was a puzzling phenomenon—after exposure to bacteriophages (bacterial viruses), some strains of bacteria seemed to be able to hereditarily transmit the ability to produce these viruses to their progeny—and during the interwar period, several microbiologists proposed hypothetical mechanisms to explain it. Physician and microbiologist, Eugène Wollman (1883–1943) played a prominent role in the debate about lysogeny and bacteriophagy. In the 1920s and

1930s, in close collaboration with his wife Elisabeth, he developed the idea that lysogeny could be thought of in terms of the theory of pangenesis proposed by Darwin (Gayon and Burian 2017). He later came to the conclusion that the virus was integrated in the genetic material of the bacterium in a latent nonpathogenic form: as such, lysogeny was explicitly viewed as an indisputable example of the inheritance of acquired characters (Loison et al. 2017).

It is obvious that Duclaux or Wollman were not committed to Lamarckism in the same way as Le Dantec or Perrier were. However, it remains the case that their Lamarckian inclinations were explicit, and that this framework helped put the phenomena of enzymatic adaptation and lysogeny on the Parisian–Pasteurian agenda.

5.2 Breaking with Lamarckism, Fighting Against Lysenkoism: The Rise of the Operon Model in Context

The Lamarckian connotations surrounding enzymatic adaptation and lysogeny were of course well known by Monod, Lwoff, and Jacob when they took up these research programs. For example, André Lwoff (1902–1994) was a close friend of the Wollmans and as a young researcher, during the interwar period, he often discussed the problem of the mechanism of lysogeny with Eugène Wollman (Loison et al. 2017).

After the Second World War and the death of the Wollmans,[6] Lwoff decided to take part in the debate on lysogeny. Lysogeny represented a challenge for the Pasteurian group because: (1) it seemed to escape any kind of experimental determinism (to such an extent that Max Delbrück, the head of the famous "phage group," contested the very existence of the phenomenon); (2) it seemed to offer strong evidence supporting the typical Lamarckian account of heredity. Quite the same was true of enzymatic adaptation.

The challenge was even greater because of the beginning of the "Lysenko affair" at the end of 1948 (Loison 2014: 15–19). Many French intellectuals who at the time shared affinities with the communist party tried to support Lysenko's claims about heredity, despite knowing next to nothing on the subject. The young Monod described Lysenkoism as nonscientific, (Monod 1948) and this led to a series of vehement attacks from one of Lysenko's main supporters, the famous poet, novelist, and editor Louis Aragon (born Louis Andrieux).

The Pasteurians were deeply affected by what they perceived as the devastating eruption of irrationality in science. Years later, Jacob claimed that one of the reasons he chose to become involved in genetics was his determination to fight Lysenkoism. In his own words, "to do genetics was [. . .] to insist on substituting

[6]Because of their Jewish origins, they were arrested by the French police and deported to Auschwitz in December 1943 where they died (Gayon and Burian 2017).

reason for intolerance and fanaticism" (Jacob 1998: 32). It was, therefore, essential that enzymatic adaptation on the one hand and lysogeny on the other be entirely explicable in strictly genetic terms.

As a consequence, Lwoff and later Jacob—who entered the Pasteur Institute at the end of 1950—were careful never to use the term "inheritance of acquired characters" when they described, and later explained, lysogeny (Loison et al. 2017). Monod was also deeply committed to putting aside any teleological component in his account of enzymatic adaptation. For this reason, he imposed a shift in the vocabulary. He convinced the main participants of the debate to use "enzymatic induction" rather than "enzymatic adaptation" in order to avoid any confusion about the molecular role of the substrate: it acts as an inducer of a preexisting genetic machinery, not as a template directly modeling enzymes (Monod et al. 1953).

The operon model was the main result of the close collaboration between Monod and Jacob which started in 1957 (Judson 1996; Morange 1998). It provided a unified explanation of lysogeny and enzymatic adaptation in which both phenomena are understood exclusively in molecular and genetic terms (operator, repression, structural gene, regulator gene, transcription, translation, etc.). Indisputably, it marked the defeat in microbiology of both traditional adaptive Lamarckism and Lysenkoism. Nevertheless, as historians we are duty-bound to note that the outcome of history should not obscure its origins. If enzymatic adaptation and lysogeny became central topics in the hands of Monod, Jacob, and Lwoff, it is because they had previously been developed by people like Duclaux, Diénert, and especially the Wollmans. Therefore, the Lamarckian dimension of these first works has to be valued as a positive and perhaps necessary contribution in the tortuous course of the works which culminated in the joint article published by Jacob and Monod in 1961 (Jacob and Monod 1961).

6 Conclusion

French biology was traversed by several forms of Lamarckism during the twentieth century. Our aim here was to provide a synthetic description of the main Lamarckian programs and to contrast them. We have seen that these Lamarckisms exhibited substantial differences: what does the spiritualist–teleological Lamarckism of Grassé have in common with the materialist–mechanist one of Le Dantec or Rabaud? Almost nothing, except their shared belief that Darwinism—i.e., natural selection—proposed a completely unsatisfactory evolutionary mechanism, incapable of accounting for the different trajectories of evolution over millions of years. French Lamarckisms were consistently anti-Darwinian. Why such a rejection of Darwin?

Jean Gayon and Richard Burian have provided the key insights to properly tackle this difficult question (Burian et al. 1988; Gayon 2013a). Firstly, when *The Origin of Species* was translated into French (1862), the names of Claude Bernard and Louis Pasteur already stood for the kind of *excellence* valued by their colleagues. Biology was seen as a science that took place in the laboratory, by means of the experimental method. Darwin did not propose anything resembling an experimental case of transformation of one species into another. Therefore, "transformism" was developed against Darwinism in accordance with the French epistemological requirement of an experimental basis (Loison 2010). Secondly, French biology was greatly influenced by Auguste Comte's positivism for more than a century (1840–1940). Therefore, empirical facts were seen as the true material of science and theoretical speculation was always considered suspicious. Thirdly, the excessive centralization of the French academic system during this period must be taken into account. A handful of Parisian bosses were responsible for virtually all major decisions affecting the orientation of French research, thus putting the whole scientific community at the mercy of their decisions and personal inclinations.

This specific situation was reinforced by the relative isolation of part of the French community. After the end of the golden age of French zoology and anatomy (i.e., after the death of Georges Cuvier), French biologists did not show much interest in foreign science. For instance, because they had their own marine laboratories (like Roscoff or Banyuls), they did not feel the need to go to the marine station in Naples which attracted many international scientists. This prevented the development of fruitful and lasting relations between French scientists and their European contemporaries for decades. This isolation also resulted from their lack of familiarity with foreign languages, especially German and English. When English became the international scientific language, French biologists resisted as strongly as possible (even defender of the Modern Synthesis Georges Teissier, for example, was unable to speak or write in English).

In the late 1940s, when biologists like Vandel or Grassé reached the top of the academic system, French isolation had increased further because of the Second World War. It took time before French biology fully reconnected with the international science scene. In 1967, Charles Bocquet was appointed professor at the Sorbonne in the chair of "evolution of organized beings." This position was created in 1888 for Alfred Giard. After his death, Giard was succeeded by Caullery, and Caullery by Grassé. Bocquet, a former colleague of Teissier and himself an eminent population geneticist (Carton 2014), was thereby the very first Darwinian to hold this position. Although in the late 1970s, and until his death in 1985, Grassé was still publishing vehement anti-Darwinian pamphlets (Grassé 1971, 1980),[7] he was increasingly isolated and could be described as the last veteran of radically anti-Darwinian Lamarckism in France. Indeed, the 1970s were the period during which disciplines concerned with evolution finally got to grips with the Modern Synthesis in France, and Lamarckian research programs were no longer seen as promising fields.

[7]In 1985, year of his death, Grassé was working on some new material, a book he would have entitled *La Face cachée de l'évolution* (The hidden side of evolution).

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