Genetics
www.genetics.org

doi: 10.1534/genetics.113.154724
Genetics **October 1, 2013** vol. 195 no. 2 **295-302**

Georges Teissier (1900–1972) and the Modern Synthesis in France

Laurent Loison

+ Author Affiliations

Address for correspondence: Laboratoire SPHERE (Sciences, Philosophie, Histoire) Université Paris-7, Centre National de la Recherche Scientifique, Unité Mixte de Recherche, 7219 Paris, France. E-mail: laurentloison@yahoo.fr

Abstract

This Perspectives is devoted to the ideas of the French zoologist Georges Teissier about the mechanisms of evolution and the relations between micro- and macroevolution. Working in an almost universally neo-Lamarckian context in France, Teissier was one of the very few Darwinians there at the time of the evolutionary synthesis. The general atmosphere of French zoology during the 1920s and the 1930s will first be recalled, to understand the specific conditions in which Teissier became a zoologist. After a brief overview of his joint work with Philippe L'Héritier on the experimental genetics of *Drosophila*, this article describes the ways Teissier, during the 1950s, conceptualized the mechanisms that could allow for macroevolutionary transitions.

IT is usually acknowledged that France did not significantly participate in the elaboration of 20th century evolutionary theory, often designated The Modern Synthesis. In their classical book on the history of the synthesis, Ernst Mayr and William B. Provine devoted a whole—nonetheless small—chapter to this specific issue (**Mayr and Provine 1998**, pp. 309–328). Mayr clearly stated that "France is the only major scientific nation that did not contribute significantly to the evolutionary synthesis" (**Mayr 1998**, p. 309). In the absence of a French architect of the synthesis, Mayr and Provine asked Ernest Boesiger, a Swiss population geneticist and a former student of Georges Teissier, to tell the story of what had happened in French biology at the time of the evolutionary synthesis. Boesiger, who died in 1975, wrote a paper in 1974 that provided the firm basis of the chapter. In very strong terms, he depicted French biology as "a kind of living fossil in the rejection of modern evolutionary theories" (**Boesiger 1998**, p. 309). He insisted on the fact that, even in 1974, most French biologists and philosophers were still reluctant to accept Darwinism. As regards the period of the 1930s, Boesiger was able to think of only two exceptions: Georges Teissier and Philippe L'Héritier. He then referred to their joint research in population genetics, which was based on the new technique of the population cages with the species *Drosophila melanogaster*, and listed their contributions to this new discipline.

If Teissier and L'Héritier's works on *Drosophila* are nowadays more widely recognized than in 1974, due in particular to the efforts of Jean Gayon and Michel Veuille (**Gayon and Veuille 2001**), this recognition could have as an unintended consequence the reduction of both Teissier and L'Héritier to being simply the inventors of a useful technique, namely the population cages (see especially how Mayr presented their work in his other classical book, **Mayr 1982**, p. 574), or as the founders of a French school of population geneticists (**Gayon and Veuille 2001**). The aim of this article is to reevaluate the way Georges Teissier (1900–1972) conceived Darwinian natural selection not only as an important mechanism for evolution at the population level but more fundamentally as a general key for the unification of biology, exactly as Julian Huxley or Ernst Mayr did during the same period (1930–1970). However, starting in the early 1950s, Teissier went on to conceive a very specific understanding of the evolutionary synthesis.

In this article, I will first describe the general atmosphere of evolutionary issues in French biology at the time when Teissier started working as a zoologist, to understand *against* what he developed his joint research program with L'Héritier and afterward his general conceptions about evolution. During the 1930s and the 1940s, only a very few scientists in France could be seen as Darwinians. In addition to Teissier and L'Héritier, one may also consider Marcel Prenant, Boris Ephrussi, and the mathematician Gustave Malécot. Building on Jean Gayon and Michel Veuille's work, I will then give a quick overview of L'Héritier and Teissier's most important achievements in the field of population genetics. In the third part, I will discuss the discovery made by Teissier and L'Héritier of a case of cytoplasmic inheritance in *Drosophila*. This unexpected finding led them into the field of non-Mendelian heredity. I will then develop in detail the way Teissier finally went on to conceive the relation between microevolution and macroevolution, in light of the general context of French biology and of the development of the field of cytoplasmic inheritance.

Zoology and evolutionary thought in France during the interwar period

It has often been proposed that Teissier was able to develop a Darwinian methodology because he was first a mathematician who had only secondarily become interested in zoology (**Sapp 1987**, p. 128; **Mayr 1998**). Mayr, on the basis of what L'Héritier told him in 1978, wrote, for example, that "Teissier was […] a mathematician with certain biological interests" (**Mayr 1998**, p. 321). This is untrue, however, and Teissier should definitely not be seen as a kind of French Ronald A. Fisher. Despite the fact that Teissier had had a very strong training in mathematics at the beginning of his curriculum, which was classical in order to enter the "Ecole Normale Supérieure," he also showed a very precocious taste for natural sciences in general, and entomology in particular. At the age of 12, he regurlarly went to the laboratory of entomology of the Museum of Natural History, in Paris, to learn about the zoology of insects (**Dorst 1975**). From 1920 to the end of his life, he spent most of his summers in the station of marine zoology of Roscoff, in French Brittany (**Figure 1**). In 1945, he became director of the station and continued as even more of a presence there, dying in Roscoff in January 1972. During his stays, he conducted very classical and typical research on the embryology of some groups of Hydrozoa (**Teissier 1922**, **1931**). In 1945, when the first chair of Genetics was at last created at the Sorbonne, it was assigned not to him but to his friend Boris Ephrussi. At the same time, Teissier succeeded the embryologist Charles Pérez in the chair of Zoology at the Sorbonne. Teissier, unlike Jacques Monod, for instance, remained deeply indebted, all his life, to the old tradition of general zoology and was recognized as one of the most brilliant French zoologists of his time.

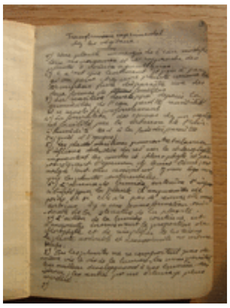
View larger version:
In this page **In a new window**
Download as PowerPoint Slide

Figure 1
Teissier had been since the very beginning a true "field naturalist." Here, in Roscoff, collecting marine invertebrates (archives of the station of Roscoff).

Due to the fact that Teissier was a true zoologist, and not a mathematician who tried to apply some abstract laws in the field of zoology, he was completely aware of the situation of the debate concerning evolutionary mechanisms in French biology during the interwar period. Mayr's main hypothesis was that Teissier (and L'Héritier) had not "been exposed to the prevailing French ideas" (**Mayr 1998**, p. 322), *i.e.*, various Lamarckian beliefs about evolutionary change and, because of this theoretical "purity," he would have been able to understand that natural selection was the best way to explain evolution. As far as I can understand the situation, it seems to me that the complete opposite is true: Teissier had thorough knowledge of zoology, due both to his training (notably in Roscoff) and to his early interest in natural sciences. As a consequence, he chose to develop experimental and Darwinian methods on purpose to address the issue of the causes of organic evolution.

In the archives of Roscoff, a few boxes of Teissier's personal and scientific papers still exist (**Toulmond 2005**). The most interesting documents may well be two small notebooks that contain reading notes written by Teissier in 1917 and 1918 (Teissier was only 17 years old when he started writing them). In the first notebook, he summed up the content of 27 scientific articles dealing with various problems in the fields of zoology and botany (most of the papers he read had been published in the *Revue générale des sciences* or in the *Comptes rendus de l'Académie des sciences*). In particular, some of these articles were devoted to what was called at the time "experimental transformism," *i.e.*, research programs of Lamarckian inspiration founded on the idea that physiologically induced modifications could be inherited (**Figure 2**). The second notebook concerns Hugo De Vries's theory of evolution by mutation. Teissier read the French edition of De Vries's book *Species and Varieties* in 1918. This book was translated from English in 1909 by the neo-Lamarckian botanist Louis Blaringhem (**De Vries 1909**). These notebooks are convincing evidence that Teissier had been from the very beginning completely familiar with the

French neo-Lamarckian context and that his interest in biology was not at all secondary. Thus the issue of the reason behind his total acceptance of Darwinism, in contrast to his peers, remains an open one.



View larger version:
In this page In a new window
Download as PowerPoint Slide

Figure 2
Reading notes of Teissier in 1917. Here, the summary of an article entitled "Experimental transformism in plants." Experimental transformism was the dominant neo-Lamarckian program in French biology during 1880–1920 (archives of the station of Roscoff).

Camille Limoges has suggested that, between 1920 and 1950, a kind of "theoretical agnosticism" prevailed in French biology about the way evolution proceeded (**Limoges 1998**, p. 323). In a previous study, I have argued that this precise period should be seen as a junction between two major forms of neo-Lamarckisms (**Loison 2011**). From the early 1880s to the late 1910s, a materialistic and adaptive Lamarckian theory was dominant: organisms were seen as machines transformed by the direct effect of their powerful milieu because of the efficiency of the inheritance of acquired characters. During the interwar period, however, the reality of soft inheritance was strongly challenged, and finally scientists had to accept—even in France—that this kind of heredity did not exist, at least in present-day nature. At the end of this very confused period, another kind of transformism started to develop, which was a much more orthogenic and vitalist Lamarckism. For people like Albert Vandel or Pierre-Paul Grassé, both contemporaries of Teissier, organic transformations were driven from the inside, due to some sort of spiritual forces.

The failure of the first form of adaptive Lamarckism was emphasized and summed up in 1931 by the zoologist Maurice Caullery, in his very famous book *The Problem of Evolution* (**Caullery 1931**). To Caullery, like many other French scientists at that time, while the fact of evolution was indisputable, the way that evolution proceeded, however, remained unknown, and even worse, might be unknowable (**Loison 2011**, p. 722). The absence of evidence in favor of the inheritance of acquired characters forced him to propose that most of the morphological evolution—at least in animals—had occurred in the past. Hence, it followed that evolutionary processes could no longer be studied in modern laboratories. This epistemological renunciation considerably stengthened the distinction between microevolution and macroevolution in French thought. In this view, microevolution, the kind intensively studied by Morgan and his associates using the genetical variations of *Drosophila*, could not be a key to understanding past major evolutionary patterns (**Caullery 1931**, pp. 341–348). Of course, just before the emergence of the evolutionary synthesis, this attitude was common in most Western countries (**Gould 2002**). But in France, the separation between micro- and macroevolution was an absolute one. That is the main reason why the second form of neo-Lamarckism was based on the idea that phyletic evolution rested on a complete specific cause, which was not related to any kind of microevolutionary mechanisms (**Loison 2011**).

In 1932, when Teissier started his collaboration with L'Héritier, he was fully aware that for most of his colleagues, evolution could no longer be studied in the laboratory. In 1945, he critized this attitude in very strong and explicit terms (**Teissier 1945a**, p. 3):

> **If no serious biologist can nowadays doubt the reality of evolution, most sincerely believe, because they did not study the issue themselves, that its mechanism remains unknown. Others, imbued with indefensible prejudices, are going a step further and maintain that it is unknowable, the "evolutionary forces" that have undoubtedly acted in a distant past having long since disappeared from our weakened world.[1]**

Against this ideological bias, Teissier repeated again and again that evolution could be experimentally studied and that microevolution was a decisive enough factor to understanding macroevolution. For example, a few pages after his sharp criticism, he wrote (**Teissier 1945a**, p. 5):

> **There is no "macroevolution" and no "microevolution" which could be explainable in two different ways, one of which must remain eternally inaccessible; there is the [the only one form of] evolution that we have to explain.**

During the 1930s and the 1940s Teissier's epistemological positioning, which was first made explicit by him in 1938 (**Teissier 1938**), is very close to the one that was at the basis of the evolutionary synthesis. Reading nowadays most of Teissier's papers on evolutionary dynamics gives one the impression that there is no substantial difference between Teissier's claims and the ones Ernst Mayr defended during the 1940s and the 1950s. Both of them argued that a species was nothing more than a set of populations where individuals were interfertile. Both of them supported the view that macroevolution was only the long-term effect of microevolutionary mechanisms that took place at the population level (**Teissier 1945a**,**b**).

The main difference between someone like Mayr and Teissier is that the latter, since 1932, had been active in the field of genetics. Because of this direct involvement, Teissier always considered that genetics was the ultimate discipline to scientifically address the issue of evolutionary mechanisms, including its analysis by experiments. That is why, to him, every significant improvement in the knowledge of heredity should transform the general structure of the evolutionary synthesis. In the next section, I give a short overview of his joint work with Philippe L'Héritier, which founded experimental population genetics, in order to observe how Teissier directly addressed, on an experimental basis, the issue of the importance and limits of natural selection for evolution. In the third and main section of this article, I will explain how the development of cytoplasmic genetics made Teissier rethink his position about the relationship between micro- and macroevolution.

The early works of Teissier and L'Héritier in the field of population genetics (1932–1938): an overview

In 2001, Jean Gayon and Michel Veuille published a significant and insightful study of the early history of the French school of population genetics, a school that had been initiated by the joint research of Teissier and L'Héritier from 1932 to 1938. This 25-page-long paper gives a full picture of the story, and here, I will only give its main conclusions.

1. First, Gayon and Veuille argue that the contribution of this school was acknowledged by at least some of the founding fathers of the synthesis. For example, they insist on the fact that Sewall Wright devoted one chapter of the third edition of his book Evolution and the Genetics of Natural Populations (**Wright 1977**) to L'Héritier and Teissier's results on natural selection in the laboratory (**Gayon and Veuille 2001**, p. 77).

2. Population cages—the experimental device that was developed during this period—were conceived by L'Héritier during his stay in the United States in 1931–1932. This visit was devoted to the study of American genetics, and the idea had come to him just before he had returned to Europe (**Gayon and Veuille 2001**, p. 79). L'Héritier was a skilled woodworker and was able to build the first model of population cages himself when he returned to Paris. At first, these cages were not designed for the study of competition between genes, but to measure and compare the ability of flies from different origins to establish themselves in a given milieu (**L'Héritier 1981**, p. 337). The idea of using this device for testing natural selection came only later, from Teissier (**Gayon and Veuille 2001**, p. 83). In population cages ("demometers"), food was periodically renewed and this allowed the study of the kinetics by which competing strains approached demographic equilibrium and of the parameters of a population in equilibrium (**Burian and Gayon 1999**, p. 319).

3. Numerous experiments allowed L'Héritier and Teissier to show that natural selection could be studied in the laboratory. In particular, they brought substantial pieces of evidence that:

    - Fitness coefficients could not be seen as constant but depended on the frequency of the alleles in the population studied (**Gayon and Veuille 2001**, pp. 86–87). Thus, selection is frequency dependent.

    - In some cases, they were able to demonstrate, for the very first time, the fact of heterozygote advantage (**Gayon and Veuille**

2001, p. 88). Before them, this mechanism had only been suggested by Fisher from purely mathematical considerations.

4. From a more general point of view, their ultimate purpose during this very active period was to show that natural selection acted to maintain variability in populations, *i.e.*, that genetic polymorphism was maintained actively (**Gayon and Veuille 2001**, pp. 90–91). At that time, as Gayon and Veuille insisted, “genetic polymorphism was still commonly thought of as [a] ‘transient polymorphism’ that affected alleles on their way to fixation or elimination” (**Gayon and Veuille 2001**, p. 88).

In 1938, L’Héritier was appointed professor of zoology in Strasbourg, an event that ended his collaboration with Teissier (**L’Héritier 1981**, p. 339). Teissier decided to continue the population cage project, and, after World War II, established in Paris and afterward in Gif-sur-Yvette, a school of population geneticists. His students (including Charles Bocquet, Maxime Lamotte, Claudine Petit, and Ernest Boesiger) were more concerned with aspects of natural population than L’Héritier and he had been (**Gayon and Veuille 2001**, p. 91).

The above provides a general overview of Teissier and L’Héritier’s main achievements. What we need to understand is that, during the 1930s, their work built the foundation of research in population genetics and helped to establish this discipline as an experimental practice. Teissier’s concern with Darwinism was a direct one: in his empirical work, Teissier was daily interested in the ways natural selection could transform genetic characteristics of a given population. As we have seen, Teissier’s whole approach to evolution was contrary to the one prevalent in French zoology at that time, when most of the zoologists, during the 1920s and 1930s, believed that evolution could not be approached experimentally.

What is the relationship between microevolution and macroevolution? An unorthodox answer

Richard Burian and Jean Gayon, in a series of papers, have proposed a very convincing reconstruction of the tortuous history of French genetics for the period 1900–1960 (**Burian *et al.* 1988**; **Burian and Gayon 1999**; **Gayon and Burian 2000**). In their first joint study, published in 1988 with the collaboration of Doris Zallen, they insisted on an accidental event that was of some importance in the course of this history. They pointed out that in order to count the thousands of flies grown in the population cages, L’Héritier and Teissier used carbon dioxide as an anesthetic, first photographing the flies and then doing their counts from the resulting pictures. In 1937, the two biologists discovered that certain strains of flies were sensitive to the carbon dioxide and were killed by light doses (**L’Héritier and Teissier 1937**). From 1937 to 1944, Teissier and L’Héritier published together five papers on what seems to be the very first case of a cytoplasmically inherited characteristic ever documented in animals: the sensitivity to carbon dioxide in *Drosophila melanogaster* (**Burian *et al.* 1988**, pp. 377–378).

After the end of the war, when Teissier formed a genuine research school focused on the maintenance of genetic polymorphism, L’Héritier developed this research program in his new laboratory at Gif-sur-Yvette, near Paris, and then in Clermont-Ferrand where he ended his career. Between 1945 and 1955, French biology was fascinated by cytoplasmic inheritance, as **Burian and Gayon (1999)** have emphasized. Jan Sapp has also showed that, during this precise period, the concept of plasmagenes was discussed favorably, at least oustide American biology (**Sapp 1987**). The idea that some kinds of nonnuclear genes could exist was found very attractive by most of the French biologists of the time, L’Héritier included, who formed the concept of “génoïde” to explain maternal inheritance in flies (**L’Héritier 1949**). Despite the fact that Teissier did not work on cytoplasmic inheritance after 1944, he nontheless remained very interested in this new field, which to him was only an extension of classical genetics.

In the early 1950s, he decided to reconsider his position about macroevolutionary dynamics in light of the new developments of nonchromosomal heredity. In 1952, he published a paper soberly entitled “Population Dynamics and Taxonomy” in the *Annales de la Société Royale Zoologique de Belgique* (**Teissier 1952**). The first part of the text is faithful to his previous position about the way biologists should understand what a species is: nothing more than a set of genetically related individuals. The second part is much more surprising, and Teissier adressed the problem of supraspecific categories in taxonomy. He then considered that the classical unformitarianist principle of strict continuity between micro- and macroevolution was at best only a stopgap. Due to the fact that genetics had undergone major changes during the 1940s, Teissier thought it was necessary to include this new knowledge in the modern synthesis itself. That is why, in the second part of the paper, he made two propositions in order to extend the genetical basis of the evolutionary synthesis. The first was to take into account the new mechanism of gene duplication. According to Teissier, gene duplications during phylogeny could be responsible for at least part of some major morphological transitions in animals. This view was neither original nor unique to Teissier: many biologists were interested in this possibility at the time. Teissier, however, also thought that this solution was not a fully satisfactory one and therefore developed a very bold speculation in the last pages of his paper. The ideas he put forth in these last pages were indeed his own and did not represent the classical view of Darwinians, contrary to what he had expressed in the first part of the text (**Teissier 1952**, p. 37).

To Teissier, the recent discovery of different cases of nonnuclear heredity in various species was the most significant achievement in the field of heredity during the late 1940s. In contrast to most of the biologists who were interested in these results at that time, he did not see them as being in opposition to classical genetics, but only as an extension of the science of inheritance. His general purpose was to examine the possible consequences, at the scale of macroevolution, of the existence of such mechanisms of cytoplasmic heredity (**Teissier 1952**, p. 40). It is interesting to note that in its general shape, Teissier's thought process was similar to those of Niles Eldredge and Stephen Jay Gould when they first proposed, in the early 1970s, their model of punctuated equilibria (**Eldredge and Gould 1972**): in both cases, the question of the structure of macroevolutionary changes was adressed in light of what was known in terms of microevolutionary mechanisms (cytoplasmic inheritance for Teissier, Mayr's allopatric theory of speciation for Eldredge and Gould; **Gould 2002**, pp. 777–781).

Taking into account the new concept of the plasmagene, Teissier tried to use it to explain marcoevolutionary changes in phylogeny. The concept of the plasmagene, *i.e.*, a cytoplasmic semiautonomous gene, had been, as we have seen, developed during the 1930s and the 1940s to explain some unorthodox cases of non-Mendelian inheritance. It was then discussed at length, at least by scientists in Europe, between 1945 and 1955, but afterward was forgotten during the rapid growth of molecular biology (**Sapp 1987**). It is also important to mention here that during the first half of the 20th century, most embryologists were not interested in genetics as they were convinced that the main features of a living thing were not controlled by the nucleus but by the cytoplasma (**Sapp 1987**). Teissier's first works were the ones of an embryologist (**Teissier 1931**) and he was of course aware of this very classical distinction between nucleus and cytoplasma. After World War II, his friend and colleague Boris Ephrussi demonstrated that the ability to use oxygen—a very essential function—was determined in yeast by cytoplasmic particles. It is not surprising, therefore, that it seemed completely reasonable to Teissier to assign to the cytoplasm the function of controlling the development of the main characteristics of an individual, its general "baupläne."

Accordingly, he then proposed that the major evolutionary transitions could be the consequence of the temporary transformation of plasmagenes into nuclear genes. Teissier explained his unorthodox idea as follows (**Teissier 1952**, p. 43):

> **"We know that specific crisis periods exist in evolution, when the latter speeds up and seems to look for its direction in multiple divergent attempts. We also know that these periods coincide, most of the time, if not always, with major changes in environmental conditions and with the correlative appearance of new types of adaptation very different from the ones prevalent before. In such moments, when the very basis of the physiological functioning has to be changed in order for life to remain possible, it could be of decisive importance that plasmagenes, which govern this functioning are transformed in a favorable way. I think that they could only do so quickly enough if they entered the selective competition by becoming nuclear. As long as the difficult time of trials and tests […] goes on, these genes would stay subjected to the Mendelian discipline, only capable, in the period of time when the survival or the extinction of the lineage is decided, of giving every chance to the final acquisition of a new adaptive type.**
>
> **Once the new adaptation is acquired by privileged forms and then becomes indisputable, it would be definitively reinforced by the crossing in the cytoplasma of the genes […] which control it. There, from now on protected from the chromosomal adventures, they would continue a more discrete but also safer life than the nuclear genes, the only ones […] which would be responsible for the diversification of a new group. Later, much later, the cycle could start again for the conquest of a new domain, and so on until**

> **the end of life…"**

Even if these ideas of Teissier's did not leave a lasting legacy, this passage deserves consideration in detail, because it addresses several important issues both of the history and of the philosophy of biology. I will divide my comments into four groups.

1. The mechanism postulated by Teissier stipulated that microevolution and macroevolution were not initiated by the same type of genetic mechanisms: mutations of nuclear genes for microevolution, mutations of plasmagenes for macroevolution. Such an explanation reintroduced an ontological demarcation between micro- and macroevolution and was very different from the classical uniformitarianism of the synthesis.

2. This explanation should absolutely not be seen as a one-off extravagance. Teissier remained faithful to it throughout the 1950s and the 1960s, until 1967 (**Teissier 1958**, pp. 74–75). A few years before he died, he was still interested in the mechanism he proposed in 1952 and believed that it was a way to unify micro- and macroevolution (**Teissier 1967**, p. 19):

    > If the differences that exist between the content of my first intervention on that topic in 1938 and the content of my articles and conferences in 1962 could be seen as substantial, it is because in between, improvements in genetics have been so important that they had not yet been completely taken into account; for example, as I noted in 1952, some new facts in bacterial genetics can help unify the contradictory interpretations of the causes of *trans*-specific evolution.

3. Even if this explanation, in retrospect, seems very unorthodox, it is not a non-Darwinian one: evolutionary change remains determined in its direction by natural selection, whatever type of genes (cytoplasmic or nuclear) natural selection acts on.

4. With the recent development of epigenetic inheritance, the question of the compatibility of this kind of inheritance and the theoretical structure of the synthesis becomes frequently asked (**Jablonka and Lamb 2010**; **Gissis and Jablonka 2011**). Teissier shows us that he had considered the possibility of an "extended synthesis" from an early date. His 1952 paper also indicates that the relations between soft inheritance and the evolutionary synthesis is a complex one and could be considered in many different theoretical ways. Furthermore, because his mechanism implied that periodically, evolutionary change was strengthened and accelerated, Teissier's ideas were relevant to what would later become the problem of evolvability (**Pigliucci and Müller 2010**, pp. 333–399).

Conclusion

The final version of Teissier's synthesis must be seen in the French tradition specifically, in its general structure, for two main reasons. First, it reactivated the old distinction between micro- and macroevolution, a distinction of prime importance for French biologists during the interwar period. Second, it did so based on the development of the field of cytoplasmic inheritance, a field that was recognized as very promising by most of the French geneticists and molecular biologists after World War II.

Nevertheless, before 1952, Teissier's ideas about evolution were very close to the ones supported by Dobzhansky, Mayr, and Simpson. Indeed, in several articles, from the late 1930s to the early 1960s, Teissier presented himself as one of the founders of the synthesis (**Teissier 1962a**, p. 363; **Tessier 1962b**, p. 16). He was personally acquainted with Haldane and Wright, both of whom came to Paris to visit him on different occasions (**Gayon and Veuille 2001**). Furthermore, in 1935 he corresponded abundantly with Julian Huxley in order to agree on a common terminology for relative growth and allometry. It was during this period that Huxley and Teissier originated the term "allometry" (**Gayon 2000**, p. 754). Finally, and most importantly, we have seen that Teissier's joint work with L'Héritier was a major contribution to the genetic basis of the synthesis. Thus, the question that remains regarding Teissier is the following: why is he not—and never has been—considered as a founder of the evolutionary synthesis?

I have discussed this issue on several occasions with Richard Burian and Jean Gayon. Upon careful consideration, I now believe that two reasons could explain not only why Teissier has not been considered as a founder, but also why this judgement is accurate.

The first reason is circumstantial: Teissier was unable to speak or write in English (**Gayon and Veuille 2001**, p. 92). Throughout his career, he published 189 scientific articles. Only three of them were translated and published in English. Only one of these three papers concerns evolution. After World War II, the English language definitively imposed itself as the international scientific language and, very quickly, articles or books which were not in English were ignored at the international scale. During the 1950s, Teissier, by sticking with French, unlike Ephrussi for example, progressively isolated himself from the international community (**Picard 1990**, p. 141).

The second reason is more essential. The history of the modern synthesis has its own landmarks: *Genetics and the Origin of Species* (**Dobzhansky 1937**), *Systematics and the Origin of Species* (**Mayr 1942**), and *Tempo and Mode in Evolution* (**Simpson 1944**). All these landmarks are not experimental results or concepts, but books; each of these books presents a synthetic approach (from the point of view of genetics, systematics, and paleontology). What Teissier never produced was precisely that: a general book in which to elaborate on his personal comprehension of the relations between genetics and natural selection. Teissier said on several occasions that he hoped to write such a book but he never succeeded in carrying it through (**Dorst 1975**). It must be emphasized here that when Ernst Mayr and Georges Gaylord Simpson published their own books in the relatively peaceful conditions existing in the United States during World War II, Teissier was busily involved with the work of the French Resistance, as he had important functions in the movement of the FTP (“Francs-Tireurs et Partisans”). Soon after the end of the war, he became professor of zoology at the Sorbonne, and thereupon, the director of two laboratories: the laboratory of zoology in Paris and the marine station of Roscoff. From 1946 to 1950, he was also the director of the new “Centre National pour la Recherche Scientifique” (CNRS). Finally, from 1951 to 1965, he was appointed director of the new laboratory of evolutionary genetics at Gif-sur-Yvette, near Paris. His personal and administrative situation helps to understand why he never found the time to write his own book. When he retired in October 1971, his death came too quickly to carry out the project. Even if he could have written the book during the 1970s, the time of the “classical” synthesis had passed, and the evolutionary synthesis was beginning to be challenged from other different perspectives. As was the case for many others, Teissier must, in the end, be considered a secondary but nonetheless important figure in the foundation of the modern synthesis.

Acknowledgments

Some of the ideas developed here were first discussed in Teissier’s laboratory at Gif-sur-Yvette, where Yves Carton, Pierre Capy, and I organized a colloquium in September 2012. I thank all the participants in this workshop. I also thank Richard Burian and Jean Gayon for kindly discussing some of these topics with me on several occasions in 2011 and 2012. Last but not least, I am very grateful to André Toulmond, a former director of the marine station of Roscoff, for his precious help when I came to Roscoff to study Teissier’s archives.

Footnotes

↵1 All translations are mine.

Communicating editor: A. S. Wilkins

Literature Cited

Boesiger E., 1998 Evolutionary biology in France at the time of the evolutionary synthesis, pp. 309–321 in *The Evolutionary Synthesis*, edited by E. Mayr and W. B. Provine, Harvard University Press, Cambridge, MA.

Burian R. M., Gayon J., 1999 The French School of Genetics: from physiological and population genetics to regulatory molecular genetics. *Annu. Rev. Genet.* **33**: 313–349. CrossRef Medline Google Scholar

Burian R. M., Gayon J., Zallen D., 1988 The singular fate of genetics in the history of French biology, 1900–1940. *J. Hist. Biol.* **21**(3): 357–402. CrossRef Medline Google Scholar

Caullery M., 1931 *Le problème de l’évolution*, Payot, Paris. Google Scholar

De Vries H., 1909 *Espèces et variétés, Leur naissance par mutation*, Alcan, Paris. Google Scholar

Dobzhansky T., 1937 *Genetics and the Origin of Species*, Columbia University Press, New York. Google Scholar

Dorst J., 1975 *Notice sur la vie et l'œuvre de Georges Teissier*, Palais de l'Institut, Paris. Google Scholar

Eldredge, N., and S. J. Gould, 1972 Punctuated equilibria: an alternative to phyletic gradualism, pp. 82–115 in *Models in Paleobiology*, edited by T. J. M. Schopf. Freeman, Cooper & Co., San Francisco.

Gayon J., 2000 History of the concept of allometry. *Am. Zool.* **40**: 748–758. CrossRef Google Scholar

Gayon J., Burian R.M., 2000 France in the era of Mendelism (1900–1930). C. R. Acad. Sci., Sciences de la vie 323: 1097–1106. Google Scholar

Gayon, J., and M. Veuille, 2001 The genetics of experimental populations: L'Héritier and Teissier's populations cages, pp. 77–102 in *Thinking About Evolution: Historical Philosophical, and Political Perspectives*, edited by R. Singh, C. Krimbas, D. Paul, J. Beatty. Cambridge University Press, Cambridge, UK.

Gissis S. B., Jablonka E. (Editors), 2011 *Transformations of Lamarckism. From Subtle Fluids to Molecular Biology. Vienna Series in Theoretical Biology*. MIT Press, Cambridge, MA. Google Scholar

Gould S. J., 2002 *The Structure of Evolutionary Theory*, The Belknap Press of Harvard University Press, Cambridge, MA. Google Scholar

Jablonka, E., and M. J. Lamb, 2010 Transgenerational epigenetic inheritance, 137–174 in *Evolution: The Extended Synthesis*, edited by M. Pigliucci and G. B. Müller. MIT Press, Cambridge, MA.

L'Héritier, P., 1949 Génoïde sensibilisant la Drosophile à l'anhydride carbonique, pp. 113–122 in *Unités biologiques douées de continuité génétique*, edited by A. Lwoff. CNRS, Paris.

L'Héritier P., 1981 Souvenirs d'un généticien. *Rev. Synth.* **102**: 331–350. Google Scholar

L'Héritier P., Teissier G., 1937 Une anomalie physiologique héréditaire chez la Drosophile. *C.R. Acad. Sc.* **205**: 1099–1101. Google Scholar

Limoges, C., 1998 A second glance at evolutionary biology in France, pp. 322–328 in *The Evolutionary Synthesis*, edited by E. Mayr and W. B. Provine. Harvard University Press, Cambridge, MA.

Loison L., 2011 French Roots of French Neo-Lamarckisms, 1879–1985. *J. Hist. Biol.* **44**(4): 713–744. CrossRef Medline Google Scholar

Mayr E., 1942 *Systematics and the Origin of Species*, Columbia University Press, New York. Google Scholar

Mayr E., 1982 *The Growth of Biological Thought: Diversity, Evolution and Inheritance*, Harvard University Press, Cambridge, MA. Google Scholar

Mayr, E., 1998 The arrival of Neo-Darwinism in France, pp. 321–322 in *The Evolutionary Synthesis*, edited by E. Mayr and W. B. Provine. Harvard University Press, Cambridge, MA.

Mayr E., Provine W. B., 1998 *The Evolutionary Synthesis*, Harvard University Press, Cambridge, MA. Google Scholar

Picard J.-F., 1990 *La république des savants: La recherche française et le CNRS*, Flammarion, Paris. Google Scholar

Pigliucci M., Müller G. B., 2010 *Evolution: The Extended Synthesis*, MIT Press, Cambridge, MA. Google Scholar

Sapp J., 1987 *Beyond the Gene. Cytoplasmic Inheritance and the Struggle for Authority in Genetics*, Oxford University Press, Oxford, UK. Google Scholar

Simpson G. G., 1944 *Tempo and Mode in Evolution*, Columbia University Press, New York. Google Scholar

Teissier G., 1922 Sur le développement et la valeur morphologique du gonophore de *Dynamena pumila* L. *Bulletin de la Société Zoologique de France* **47**: 259–263. Google Scholar

Teissier G., 1931 Etude expérimentale du développement de quelques Hydraires. *Annales des Sciences Naturelles. Zoologie* **14**: 5–60. Google Scholar

Teissier, G., 1938 Une controverse sur l'évolution, intervention de M. Georges Teissier. *Revue de l'Encyclopédie Française*, 11–14.

Teissier G., 1945a Mécanisme de l'évolution. *Pensee* **2**: 3–19. Google Scholar

Teissier G., 1945b Mécanisme de l'évolution. *Pensee* **3**: 15–31. Google Scholar

Teissier G., 1952 Dynamique des populations et taxonomie. *Annales de la Société Royale Zoologique de Belgique* **83**: 23–44. Google Scholar

Teissier G., 1958 *Titres et travaux scientifiques de Georges Teissier*, Prieur et Robin, Paris. Google Scholar

Teissier G., 1962a Transformisme d'aujourd'hui. *Annee Biol.* **4**(1): 359–374.
Google Scholar

Teissier, G., 1962b *Supplément aux titres et travaux scientifiques de Georges Teissier*. Paris, Robin et Mareuge.

Teissier, G., 1967 *Titres et travaux scientifiques de Georges Teissier*, *Supplément*. Paris, Robin et Mareuge.

Toulmond, A., 2005 Un biologiste engagé dans son siècle: Georges Teissier (1900–1972). Available at: **http://www.sb-roscoff.fr/images/stories/GT-internet.pdf**

Wright S., 1977 Experimental results and evolutionary deductions. *Evolution and the Genetics of Natural Populations*, **Vol. 3**. Chicago University Press, Chicago.
Google Scholar

Related articles

Issue Highlights:
ISSUE HIGHLIGHTS
Genetics October 2013 195:NP
Full Text **Full Text (PDF)**