The Organismal Synthesis: Holistic Science and Developmental Evolution in the English-Speaking World, 1915–1954

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Abstract In 1915, the German physiologist Jacques Loeb published a paper titled "Mechanistic Science and Metaphysical Romance." In that article, Loeb lamented that scientific research was still infected by a "romantic" approach. Despite the triumphal achievements of the sciences based on mechanistic precepts, romantic and mystical speculations abounded. Life science, Loeb added, was besieged by mysticism, vitalism, and irrationalism. "Romantic" evolutionists indulged in unsupported theories and untested conjectures. But who were these twentieth-century "romantics" really? In this chapter, it will be argued that, contrarily to Loeb's rhetoric, such a "romantic" community was not always constituted by irrational and mystical cranks. Rather, it was often composed of reflective scientists criticizing the overoptimism of the neo-Darwinian agenda and the unwarranted ambitions of the mechanistic (physicalist) approaches to biology. The chapter has three aims: First, to outline the main ideas of the early twentieth-century organicist agenda, with particular emphasis on evolutionary and developmental biology. Second, to briefly present the background and works of a few representative figures involved in the international community of organismal biology from the 1920s onward. Third, to show that aside from the neo-Darwinian synthesis, these scholars proposed an alternative synthesis between the 1920s and 1950s, a biological synthesis aiming to link studies on evolutionary and developmental biology within an organismal framework. The points of convergence and divergence between the two syntheses will be assessed. Then, the question of whether or not they were two incommensurable alternatives will be addressed.

Keywords Organicism • Evolution • Developmental biology • Heredity • Mechanism • Reductionism

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1 Introduction

“Since no discontinuity exists between the matter constituting living and non-living bodies, biology must also be mechanistic.” (Loeb 1915: 771). With this simple sentence Loeb described his agenda, and the program of the biological sciences in the years to come. In the future, he averred, all living phenomena could be successfully reduced to “…the motion of electrons, atoms, or molecules” (772). However, as Loeb pointed out, there was strong resistance to such an agenda. Not everyone accepted that science had to be mechanistic and therefore based on experiments and quantification. All those who rejected mechanistic biology were, after all, metaphysicians or reactionary “romanticists” who preferred Bergson and Nietzsche to Helmholtz and other serious physicists. These “romanticists,” Loeb added, had pretended to explain the “riddles of the universe,” but they only produced speculations and fantasies. Even worse, they swayed the masses with ideological jargon repellent to serious scientific arguments. In 1912, Loeb had published a very controversial book which included ten lectures he had given since 1893. The book, titled *The Mechanistic Conception of Life*, offered a clear and effective example of how biologists should work: from morphology to physiology, from embryology to animal behavior, from phenomena such as tropism to fertilization, Loeb showed how mechanistic science could and should be performed. At the same time, he thought he had disproved a vitalistic interpretation of life phenomena and defused the arguments of his worse enemies, the “romantic evolutionists” (see Pauly 1987).

Seven years later, a young biologist from California published two large volumes directly addressing Loeb’s provocations. The two volumes were edited under the same title: *The Unity of the Organism or the Organismal Conception of Life*. The author was William Emerson Ritter, a pupil of Joseph Leconte at Berkeley. With his synthesis of Hegel and Lamarck, Leconte would have easily been classified as a “romantic evolutionist.”[1] In contrast to Loeb, and drawing on Leconte, Ritter believed that the organism could not be reduced to its simplest physicochemical components precisely because what essentially characterized the organism was its unity and integration acquired during evolution. Once it emerged from the depths of the geological past, living organization inaugurated a new, irreducible phase in the

[1]Leconte’s evolutionary view, based on the ideas of spontaneity, creativity, and holism, was very distant from a mechanistic and determinist perspective. In his cosmic theory of transmutation, he saw the emergence of new complex unities moving from inorganic matter to human societies. The evolutionary process had to be seen as a form of embryonic development. Heterogeneity followed a state of homogeneity, as Herbert Spencer, inspired by Ernst von Baer, had argued. For Leconte, heterogeneity (diversification) was followed by a process of integration and coordination, which produced new organic unities (Stephens 1978). In other words, organisms became more complex insofar as novel instruments of organic coordination and integration appeared. Cephalization and socialization were two of these instruments that life had used to attain higher levels of integration. The unity of the organism was therefore the result of evolutionary strategies of coordination, which, once attained, produced new irreducible entities.

cosmic evolution. Life was something that the biologists had to assume as given and not try to grasp through artificial partitions and analysis. The essential nature of the organism did not lie in its inorganic components but in the way these components were articulated and functioned. When the organism was parceled out through experiment, life was irremediably gone. So, for Ritter, the Loebian mechanistic conception of life had to be replaced by an organismal conception of life, if a deeper understanding of living organization was to be sought.

This chapter aims to reconstruct the organicist tradition that Ritter, among others, articulated starting from previous and contemporary ideas. Indeed, Ritter's polemical position in relation to Loeb was not a novelty. He drew upon a vast array of old and new sources to support his view (as will be shown later on). However, Ritter's organismal conception of biology was not only a philosophical position; it also defined a community of biologists who, from different perspectives, disciplines, and places, agreed that the idea of a Loebian mechanistic biology was not a perspective worth adopting. In fact, behind what von Bertalanffy had dubbed in the early 1930s an "organismal revolution" (Esposito 2016), there were many of those Loeb disparagingly called "romanticists": a group of scientists that was active from the early twentieth century and that survived the Second World War. However, contrary to Loeb's despective view, it will be shown that this "romantic" community was not always constituted by irrational cranks or mystical eccentrics. Rather, it was a community that was often composed of critical scientists who questioned the overoptimism of the neo-Darwinian agenda and the unwarranted ambitions of the mechanistic (physicalist) approaches to biology. In short, what these biologists dubbed "organicism" was indeed a rational stance that aimed to provide a more sophisticated and realistic representation of living phenomena including evolution, development, and heredity.

Most of these "romantics" were also historically informed and philosophically knowledgeable. They explicitly connected their scientific learning with authors and doctrines of the eighteenth and nineteenth centuries: in particular, Kant and post-Kantian philosophies and many of the scientific extensions and applications springing from these (Esposito 2016). This neo-Kantian syncretic view included important tenets that Kant himself had established when reflecting on the nature of organisms and the epistemic limits to understanding them: for instance, the idea that organisms are self-organized entities that can only be understood as teleological wholes; the idea that organisms are active, creative, and purposive things, whereby causes and effects are deeply intertwined and self-directed toward their reproduction—and therefore their maintenance and adaptation (Lenoir 1982; Mensch 2013); and, as a consequence, the idea that a living organization has to be assumed and never reduced to physicochemical mechanisms, simply because, as Goethe had himself poetically observed in *Faust*: "...though fast your hand lie the parts one by one, the spirit that linked them, alas is gone..." (Goethe 1988). Indeed, the Kantian complex views were filtered and reframed through Goethe's morphological studies (see Levit and Hossfeld 2017), von Baer's embryological reflections, and many other major and lesser post-Kantian and romantic figures active throughout the nineteenth century (Lenoir 1982; Harrington 1999; Sloan 2007).

The chapter, however, does not focus on the "romantic" philosophy of the organism in general but rather on evolutionary and developmental biology—in other words, on the way twentieth-century "romanticists" connected development, heredity, and evolution. Of course, ideas about what an organism is were directly related to how organisms develop, transmit their characters, and evolve. So, the general philosophy of the organism—the latter seen as an irreducible and dynamic entity—was the fundamental premise for articulating the relations between these phenomena. However, although there is a growing quantity of literature that reconstructs organicist philosophies of biology (Harrington 1999; Nicholson and Gawne 2015; Esposito 2016), little work has been done in regard to revising the ideas and models of evolution that organismal "romanticists" scholars have proposed. The undertaking is historically interesting because the very same concept of evolution that many "romanticists" held in the twentieth century had many remarkable connections with the biocentric wide perspectives maintained by some eighteenth- and nineteenth-century romantic naturalists and philosophers: what the German philosopher Adolf Trendelenburg succinctly defined as "the organic view of the world" (Beiser 2014)—especially the idea that a cosmos in permanent evolution, crossed by material forces in constant opposition, produced unexpected alterations in which new irreducible entities emerged. The cosmos followed a teleological pattern akin to an organism in its development. If the world could be seen as a complex organism, rather than a sophisticated mechanism, then the study of the organic world acquired unprecedented relevance. Such a developmental perspective was increasingly streamlined in biology insofar as embryogenetic phenomena themselves harbored the most important secrets of organic matter, including its phylogenetical transmutations. Haeckel biogenetic law represented only one variation of this larger connection between macrocosm and microcosm, and therefore, between the developing embryo and the whole history of life on earth (Gould 1977).

Starting from this very general and vague scheme, many twentieth-century "romanticists" rarely questioned certain beliefs: evolution had to be conceived as a great cosmic process in which new entities and relations constantly emerged. New structural relationship had produced, in the course of geological epochs, functional units that were irreducible to their physicochemical components. These complex units became the principal agents of organic evolution insofar as they, and not a population or species, had to be considered as the source of evolutionary change. As self-organizing, self-directed, and creative entities in an open relationship with the environment, they were extremely plastic and creative beings that could not be properly explained supposing transcendent, immaterial, vitalistic forces. Finally, these organic agents exhibited a teleological nature that could not be easily dismissed with mechanical explanations. Of course, some of these beliefs inform the discussions over the nature of the organisms ever since the eighteenth century (Bertoletti 1990)—discussions that intensified in the nineteenth century—especially in France and Germany, and that led to the successful institutionalization of biology as a professional discipline (Gusdorf 1985).

Now, the training of many biologists in Germany or German institutions toward the end of the nineteenth century makes the conceptual connection between the ideas mentioned and their revival in early twentieth century comprehensible. Some of these "romanticists" had been students of Rudolf Leuckart, Eduard Strasburger, Hans Przibram, and several other figures generally linked to the organicist world. Those who did not travel abroad had formed themselves on books and articles that contained Kantian and post-Kantian bio-philosophical ideas. In England, successful textbooks such as Balfour's *Elements of Embryology* or Sedgwick's *Student's Textbook of Zoology* were impregnated with German organicist thought (see Esposito 2016). Most of these people Loeb would have deemed "romanticists" had read Aristotle, Kant, Schelling, Lotze, and Schopenhauer directly. Many were acquainted with primary and secondary literature on eighteenth- and nineteenth-century biology. They were aware that Buffon, Blumenbach, Cuvier, Geoffroy, Goethe, and von Baer had demonstrated the profound connection between epigenesis and organicism (see Mensch 2013).[2] Finally, these "romanticists" were familiar with the sophisticated debates between neo-Darwinians and neo-Lamarckians, associating the former with mechanistic, materialist, and conservative philosophies and the latter with organicist, systemic, and progressivist positions.

This chapter focuses on a small group of these "romantic" biologists from the Anglophone world (the UK and USA) during the first five decades of the twentieth century. The figures here considered all had important institutional ties and engaged each other in discussing various aspects of their contemporary life science. They all agreed that biology was an independent and irreducible discipline that studied systemic, complex, and creative entities. They also agreed that Loeb's proposal of a pure and unrestrained mechanistic biology was a threat to a discipline, biology, which had to think more in terms of dynamic processes than in terms of inert structures, and more in terms of wholes than in terms of parts. In other words, from the beginning of the twentieth century, there was a noisy and competent international community of "romantic" biologists opposed to neo-Darwinian biologies. Figures such as E. S. Russell, John S. Haldane, D'Arcy W. Thompson, Joseph H. Woodger, William E. Ritter, Frank and Ralph Lillie, Ernest Just, and Charles M. Child constituted a little—nonexclusive—Fleckian "Denkkollektiv" proposing an alternative biological synthesis that aimed to link studies of evolutionary and developmental biology within an organismal framework. In particular, the main idea that all these biologists shared was the conviction that ontogeny "produced" or "created" phylogeny, did not "recapitulated" it, as the British embryologist Walter Garstang concisely put it in 1922.

[2]The strong association between epigenesist and organicism, and the latter with biology, should not appear surprising today. After all, the notion of "organism" was one of the central concepts of romanticism, and "biology" itself, as the French philosopher Gusdorf recognized long ago, was largely a romantic word (Gusdorf 1985).

Finally, it is important to briefly clarify the reasons why I deem Loeb's category of "romanticists" to be historically useful and pregnant, in spite of its derogative intent. First, the adjective "romantic" allows us to see the historical continuity of an old, venerable tradition that was still active in the twentieth century. Indeed, to consider "organismal biology"—or, more generally, "organicism"—as a radical break from the past not only implies doing violence to the available historical evidence but also means denying the historical awareness of the protagonists of the organicist tradition (as will be shown in the next sections). The clash between Loebians and "romanticists" was not only a disagreement about two abstract, ahistorical, philosophical undertakings; it was also, and especially, a clash between two traditions that had a long, controversial history. Secondly, the adjective "romantic" also helps to comprehend, at least more generally, why and how important boundaries between different scientific sensibilities in biology emerged, at least in regard to the first half of the twentieth century. For instance, the contrast between anti-reductionist and systemic "thought style" and a more technocratic, reductionist, and pragmatic approach. After all, especially in evolutionary biology, the clash between developmentalist views of evolution and neo-Darwinian perspectives can be seen as a part of a larger epistemological trend that involved the scientific enterprise as a whole, particularly in the context of the political and social transformations following World War II. However, it must be clear that the use of the adjective "romanticist" should not be intended as an essentialist label that includes and excludes, neatly and sharply, genuine "romanticists" from "non-romanticists." I use the notion "romantic biology" as a signpost that refers to a movement of thought, as an analytical concept denoting a particular way of interpreting life phenomena, as an instrumental label referring to a concentration of ideas articulated and disarticulated according to different contexts and conveniences, and as a name standing for a set of convictions—not always consistent—that oriented scholars of diverse places and generations toward specific views and results. In sum, in order to understand the clashes that we perceive between different ways of understanding biology during the first decades of the twentieth century, we need some tentative categories that can be used as guides or markers. Once these labels have provided us with a better view of particular historical trends, they can be dismissed in favor of more fine-grained categories.

2 From the UK to the USA

One year before his death, the Scottish biologist Edward Stuart Russell published one short essay on Schopenhauer's contribution to biology (1953). The essay situated Schopenhauer's ideas within a larger history of organicism, from the nineteenth century until Ralph Lillie's *General Biology and Philosophy of Organism* (1945), and included a sharp critique of contemporary biology. In particular, Russell used Schopenhauer's philosophy as an effective weapon against mechanistic approaches in developmental and evolutionary biology (i.e., neo-Darwinism).

Indeed, recovering Schopenhauer, Russell observed, was important because "...with the gradual spread of the holistic conception of the organism, the integral view has been coming back into favour" (206). In revising Schopenhauer's short essay *Über den Willen in der Natur*, Russell underscored...three main fundamental points: the law of adaptive specialization, the unity of plan, and the purposiveness of organic nature. The first refers to the correlation of organs in the overall morphological plan; i.e. all organs and functions are necessarily connected in a whole organized unity. Although this idea could be traced back to Cuvier, with his principle of the correlation of parts, Russell noted that the novelty of Schopenhauer's position lied in his interpretation of this principle in terms of the "will": the Kantian thing-in-itself, which is behind all phenomena. The second point, the unity of plan, could be linked to Geoffrey Saint-Hilaire and explains that all structures can be understood as functional adaptations. Finally, the third point refers to the teleological nature of organisms, which can be interpreted neither as an external intelligent goal nor as the result of undirected selection of variations: the organic purposive phenomena are, rather, the result of an internal drive, Schopenhauer's will, which directs and shapes the living matter. For Russell, Schopenhauer's philosophy of the organism was directly opposed to post-Darwinian insights and vitalistic tendencies: "In post Darwinian speculation on evolution—he wrote—too much stress was laid on the separate 'characters' of the organism, especially those which vary inside the species, and the primary fact of the fundamental wholeness and integral adaptive specialization of the living things was lost from sight" (1953: 206). And again, Schopenhauer would "...have rejected also any theory of dualistic vitalism, such as Driesch's theory of entelechy" (208).

Russell's historical reconstruction of Schopenhauer's bio-philosophy was therefore a polemic effort directed against mechanist and Neo-Darwinist evolutionary hypotheses and, at the same time, a strategic move aiming to demonstrate that there was a viable alternative between mechanism and vitalism—an alternative that not only found support in a venerable history but also in twentieth century biology and physiology. Such an alternative would temper overenthusiasm for genetical explanations of evolutionary diversification and, at the same time, would emphasize the importance of individual development in the processes of speciation. Such an alternative, Russell added, might also find support in the philosophical intuitions of Henry Bergson and the more recent scientific ideas of Ralph Lillie (on Bergson, see Loison and Herring 2017).

Russell was not the only scientist interested in Schopenhauer's philosophy. In Britain, the first translation of *Die Welt als Wille und Vorstellung* was published in 1883 and the translator had been the brother of the physiologist John Scott Haldane, Richard Buldon. A student of the neo-Kantian philosopher Hermann Lotze in Germany, Richard would cooperate with his brother John in diffusing Kant and post-Kantian philosophies in the UK. At a very young age, John Scott and Richard would make clear that Kantian and post-Kantian speculations were relevant to biological thinking. As they argued, stressing one of the main themes of romantic thinkers, the organism had to be comprehended through the category of *reciprocity*, where: "...every part of the organism must be conceived as actually or potentially acting on and being acted on by other parts of the environment, so as to form with them a self-conserving system" (1883: 45). Almost three decades later, John Scott introduced, in the Anglophone world, the word "organicism" as a short label for this idea[3]—a notion that, as he noted, could be found in the earlier teachings of Xavier Bichat, Von Baer, Claude Bernard, and Yves Delage—and referred to a third position between mechanistic hypotheses and vitalistic views. This position implied a whole philosophy of the organism that can be briefly summarized as following: life is a category that, in virtue of its visible properties, is irreducible to physico-chemical analyses. The organic parts are shaped and constituted in a dynamic interaction with the whole organism and its environment. These dynamic wholes have to be conceived as teleological and self-sustaining entities, able to adapt and change their form and behavior according to the external circumstances. Precisely because the organism has to be regarded as a whole self-contained unit, organic evolution has to be related to an organism's complex capacity of responding to environmental pressures.

Like Russell later on, Haldane spent his life criticizing what he saw as an over-reductionist neo-Darwinism based on hasty speculations about material inheritance (i.e., Mendelian genetics and then population genetics). And, like Russell, Haldane was heavily indebted to Kantian, Romantic, and idealist philosophies, who denied a mechanist and purely material world. Indeed, British idealists such as T. H. Green and F. H. Bradley, Haldane acknowledged, had been very important for his formation. Although he did not specify what he took from these neo-idealistic philosophies, we could advance the hypothesis that Bradley had taught him to be wary of atomistic worldviews in science (from physics to psychology), which conduced to mere abstractions taken from an absolute, organic, and dynamic whole. Green, instead, an arch-critic of Spencer's individualism, had probably taught him to be very skeptical about social Darwinism and, at the same time, to think of human society as a complex organic whole (Simhony 1991). What Green, Bradley, Kantian, and post-Kantian philosophy had certainly taught him was the old Aristotelian saying that, in the organic realm, the whole was more than the parts. Although Haldane applied such a maxim to his physiological and medical practices, he also believed that evolutionary biology and heredity had to be conceived accordingly.

Haldane argued that whereas heredity could not be reduced to independent and discrete particles, which biologists increasingly frequently named genes, evolution could not be reduced to a statistical distribution of characters fixed through a process of directionless selection. In other words, the production of new characters in evolution could not be focused on mere intracellular processes whereby the genetic material was statistically reshuffled in sexual reproduction. Rather, an evolutionary novelty had to be seen as an "…active adaptation of pre-existing life, and its transmission to descendants is a sign that in the adaptation the life of the organism itself is expressing itself" (Haldane 1935: 74). Heredity belonged to the whole striving organism, which expressed itself through efficient adaptations: "the chromosomes…of a living germ-cell are an expression of its whole life, and its further life in essential

[3]See Haldane (1917: 3).

connexion with embryonic and adult environment furnishes the only key to an understanding of their real nature" (74). While the organism could not be severed from its environment, heredity could not be severed from the whole life cycle of the organism itself. Changes in the life cycle of the individual, therefore, from the earliest stages of development to the adult life, could induce changes in the whole species. New characters arise from this individual process of adaptation during development. Haldane believed that the organism could not be understood as a passive subject of evolution, but rather must be understood as an active entity able to adjust itself according to its needs in a variable environment. Although Haldane did not mention Lamarck directly, his vision was much more akin to a Lamarckian understanding of the evolutionary process than it was to the blind mechanism of Darwinian selection.

Unlike his ambitious cogitations on physiology, Haldane never developed a full-fledged vision of evolutionary biology, of the kind his son J. B. S. developed later. However, John Scott's thinking on evolution was both informed and extended by one of his oldest friends: D'Arcy W. Thompson. Both born in Edinburgh in 1860, they shared most of educational background and interests. Both leaned toward German philosophy and science, and both polemicized, frequently between themselves, regarding materialism, vitalism, and reductionism in biology. While Thompson believed that mechanistic hypotheses could be heuristically fruitful in explaining life phenomena, Haldane remained deeply skeptical about any kind of mechanist approach. However, what they shared was a general distaste toward neo-Darwinism and Mendelian genetics. Even though Thompson had a deep respect for Darwin, he could not accept the overenthusiastic conclusion that many of his later disciples suggested: that natural selection could fully explain adaptation and morphology. And yet, although he seriously considered the works and results of Mendelian geneticists, his view about how cells worked and reproduced was strongly opposed to Mendelian models. Indeed, Thompson believed that the cell had to be understood as a dynamic "sphere of action," rather than as an entity with a static structure containing small powerful entities able to direct and form living organization: "The things which we see in the cell are less important than the actions which we recognise in the cell" (Thompson 1942: 289). Picturing the inner structure of the chromosomes would not reveal the complex function of the whole cell. As a relatively self-contained entity, the cell was a system of forces in relative equilibrium. Speaking about "hereditary substance" in cell nucleus was equivalent to saying that "...a particular portion of matter is the essential vehicle of a particular charge or distribution of energy, in which is involved the capability of producing motion, or doing the work" (1942: 288). As a consequence, for Thompson, the idea that during reproduction organisms transmitted discrete "factors" uniquely responsible for the emergence of phenotypes was a deceptive figure of speech. What was really transmitted during reproduction was a whole system of forces that would produce phenotypes according to the environmental context.

Thompson's cytological view was directly related to his evolutionary view. With Haldane, Thompson maintained that the organism could not be thought of without considering the crucial contribution of the environment. From bacteria to jellyfish, from amphibians to mammals, all organic forms were the response of physical forces and stresses coming from the environment and, more generally, from the material conditions of animal life. Depending on the size of the body, organisms had to face diverse challenges: i.e., surface tension for small organisms and gravity for the largest ones. These physical forces, in concert with what Thompson called "morphological heredity"—i.e., systems of force which engender growth rates during development—produced the different adult forms in the general course of evolution:

> The deep-seated rhythms of growth, which, as I venture to think, are the chief basis of morphological heredity, bring about similarities of form which endure in the absence of conflicting forces; but a new system of forces, introduced by altered environment and habits, impinging on those particular parts of the fabric which lie within this particular field of force, will assuredly not be long of manifesting itself in notable and inevitable modification of form (1942: 1025).

While the organism had to be conceived of as an "integral and indivisible whole," as Aristotle, Kant, Goethe, and Cuvier had taught, such integral wholes were also historical entities, as Lamarck and Darwin had showed. The organicist view, together with the awareness that life had history, conducted Thompson toward the idea that evolution was a process of holistic diachronic transformations of related *bauplans* that could be geometrically described through Cartesian grids. The transformation of whole integrated morphologies could neither be simply ascribed to natural selection nor to animal needs or vital forces. Rather, the transformations were the outcome of physical, chemical, and electrical forces that acted in concert with internal and external stimuli. Altogether, the forces influenced the growth rates of the morphological parts and therefore the overall organic form. As the title of Thompson's famous book indicates, form was the result of differential growth rates.

The relation between growth and form, and therefore between development and morphology, fostered Thompson's interest in developmental phenomena. The American physiologist Charles Manning Child and the Canadian embryologist Frank Lillie were two of his important references for understanding the relationship between growth rates and morphology. While Child had conceived of the organism as a reaction system crossed by specific patterns of metabolic activities that he dubbed "metabolic gradients," Lillie had stressed the power of the environment in relation to morphological evolution. Both had severely criticized Mendelian genetics and both had offered an alternative view according to which evolution could not be understood as change in gene frequencies but rather as changes in developmental paths related to gradients or physiological mechanisms. As I have shown elsewhere, the evolutionary ideas of Thompson were not as bizarre as many recent interpreters have claimed (Esposito 2014): rather, they were an original variation of a general view held by many embryologists and physiologists during the first half of the twentieth century—a view which can be best resumed through Walter Garstang's lucid remark: "Ontogeny does not recapitulate phylogeny: it creates it" (1922: 87). If evolution was the result of developmental changes triggered by internal or external (environmental) stimuli, then natural selection had a very secondary relevance in explaining speciation.

The biologist and philosopher H. Woodger offered another variation on Garstang's theme. Born in 1894, Woodger is one of the most fascinating theoretical biologists of the...first half of the twentieth century (See Nicholson and Gawne 2014). As an admirer of Haldane's organicism, Woodger believed that such a philosophical position had to be related to the view that the living entities had to be understood through three general concepts: functionality (organisms are entities that are always functioning), morphology (this functioning is always related to a particular structure), and environment (function and structure work, directly or indirectly, always in reference to what surrounds the organism). As he explained: "Just as the organism is more than the sum of its material parts, so it is more than a bundle of functions. Just as its parts are organized and unified, so are it functions in reality not separable but all interconnected and integrated, as to result, in the living animal, in one great function—the behaviour of the animal as a whole" (1924: 457). On D'Arcy Thompson's advice (Esposito 2016), Woodger undertook a short period of research leave at the Vienna Vivarium in Austria. This institution, headed by Hans Przibram, was, as Pouvreau recorded, "characterized by the opposition to Darwinian and neo-Darwinian theories, accepting, of course, evolution, but denying the idea that natural selection alone could explain evolution... the dominant conception was that the organism had to be conceived as a system in an active relationship with its environment, and that the organic morphogenesis had to be seen as the result of epigenetic processes..." (Pouvreau 2006: 13). An enthusiast of Thompson's morphological ideas, Przibram had been a pupil of the physiologist Rudolf Leuckart—a deep admirer, in turn, of Kantian philosophy (Lenoir 1982). In the vibrant environment of Vienna, Woodger would learn about systemic thinking through the scientific and philosophical discussion that took place between Paul Weiss and Ludwig von Bertalanffy (Drack and Apfalter 2007). However, one of the concepts that most attracted Woodger's interest was the notion of "hierarchy" in an organic system and how it relates to heredity, development, and, eventually, evolution. Organisms, after all, could be conceptualized as hierarchal systems whereby causes and effects, intra and extra level, were deeply connected. Woodger believed that a solid concept of biological hierarchy could solve different conceptual issues related to dichotomies such as inborn and acquired characters and, therefore, could provide a larger, more sophisticated context in which the process of speciation could be framed. Indeed, Woodger believed that the term "heredity" had to be eliminated, in favor of a different conceptualization of the transmission and manifestation of characters. In order to do that, Woodger distinguished between intrinsic (or immanent) and relational properties. When we think about a hierarchical organization, we assume that the parts have specific relations with other parts, which may or not be static or dynamic. Thus, while intrinsic properties were those characters (phenotypes) which were transmitted with relative constancy generation after generation, the relational properties had to be considered as new characters generated during development, representing the engine of novelty in evolution. In other words, the intrinsic properties were none other than previous acquired relational properties:

> If two cells, which are assumed to have "equal" nuclei behave differently in the same environment, we should say that they differed intrinsically in their cytoplasm, since their relations are supposed to be the same. But that intrinsic cytoplasmatic difference may have been acquired in consequence of relational differences during development, and would therefore be an acquired relational property. But since it now persists in spite of changed relations (since by hypothesis both cells are in the same environment now) we should have to call it an acquired intrinsic property (Woodger 1930: 15).

The dialectic between relational and intrinsic properties could explain how novelty can be generated over time, supposing that the acquired relational properties were consequence of developmental changes. The unit of evolution, therefore, could not be the population, but rather the individual organism, which, during development, reproduced patterns and structures typical to its own species and, at the same time, small or large variations triggered by environmental stresses. Of course, Woodger never offered a full-fledged evolutionary theory. He was mainly concerned with defining what an organism was. Nevertheless, he reached the conclusion that it was within an organized, hierarchical, and dynamic entity that new relations between parts in a whole could be acquired during development. After all, Woodger argued: "Development is a process in which with temporal passage new spatial parts come into being all with the same genetic endowment." (Woodger 1929: 376). More specifically, he maintained that both embryogenesis and evolution were two forms of development: "We speak of individual development and evolutionary development as two examples of development" (Woodger, 1930:391), and yet, "Developmental theories, whether individual or racial, do not deal with characters but with processes, i.e. with organisms as events in relation to the events constituting their enviroment" (Woodger, 1930: 423). As a consequence, evolution, as a specific form of development, was characterized by the temporal emergence of new modes of living organization. Although Woodger admitted that he could not find any convincing hypothesis about how these new modes of organization actually occurred, he concluded that evolution itself had to be eventually conceived as a dynamic, not "uniform", epigenetic event (Woodger, 1030:427).

While for Russell the French philosopher Henri Bergson, with his conception of elan and creative evolution, could make sense of the essential productivity of the organic matter, Woodger found in Whitehead's process philosophy the correct inspiration for a new philosophy of the organism. In the Romantic spirit of Whitehead, who in 1925 wrote that: "nature is a process of expansive development... nature is a structure of evolving processes" (Whitehead 1925: 135), Woodger felt that evolution could be seen as a process in which new relations and hierarchies come into being ("concretions" in Whitehead's terminology). The dialectic between relational and intrinsic properties involved a Whiteheadian evolutionary process, going from the structuring of novelty to the fixation of the characters. When Russell noticed in his *The Interpretation of Development and Heredity* (1930) that evolution could not be explained as being the result of blind mutation and selection, but rather as systemic alterations of developmental paths, he was only stressing one central tenet advanced by what I call "romantic biologists": the largely shared belief that ontogeny produced phylogeny—which is quite different from the more famous, and probably more controversial, argument that ontogeny recapitulates phylogeny. Indeed, while in the latter phylogeny produced ontogeny, in the former it was ontogeny which produced evolution. For Woodger after all, the origins of evolutionary novelties depended on hierarchical changes along the ontogenetical processes. Evolution was the overall drama in which the creativity of each individual organisms was staged.

In 1954, Russell felt that new findings supported this idea, and many of the new proposals came from the USA (in particular, he mentions Joseph Lillie and William Ritter). The future of organicism could be glimpsed, in its newest developments, in the USA.

3 From the USA to the UK

In the chapter on Schopenhauer's biology, Russell had concluded that the history of organicism could count on one important recent contribution from the USA: Ralph Lillie's *General Biology and Philosophy of Organism* (1945). Lillie was a physiologist based at the University of Chicago from 1924. Until his retirement, he had often published in philosophy journals. Indeed, *General Biology* was a compilation of different papers Lillie had published from the 1920s onward, for a general public. The influence of Whitehead and Bergson, as well as the references to D'Arcy Thompson, Russell, and Ritter and many organicists, makes Lillie's monograph an excellent instance of what Loeb understood with "romantic evolutionism." The book tackled what Lillie considered the most important and controversial topic of general biology: the difference between living and non-living systems—the former deemed to be the evolutionary consequence of the latter. Indeed, life was a particular kind of emergent organization from matter—an irreducible organization which implied directionality. In general, Lille believed that there were two principal tendencies in the organic nature: a conservative and an active side. Conservation and transformation are two sides of the same coin. For instance, Lillie maintained that there could be no creativity in evolution without a general framework of regularity and permanence. Living entities were very conservative systems. Complex mechanisms of reproduction guaranteed the continuity of the species. However, the regularity of biological systems did not imply their complete predictability and determinism. The process of embryogenesis, although highly stable, could also be highly creative. Using Whitehead's terminology, Lillie defined development as a process of concrescence "...in which a variety of materials come together to form a closely unified whole" (Lillie 1945: 23). Life, Lillie added, quoting Bernard, is creation: such intrinsic creativity of the living systems had to be linked to the capacity of life to transcend regularity under environmental stresses: "This dependence of local development (i.e. of special parts and organs) on local physical conditions is an intimate one, and experimental alterations of these conditions (by excision or displacement of parts, chemical influence, transplantation, etc.) produces correspondingly constant changes in development" (Lillie 1945: 203). Although environmental pressures could trigger changes in the organism's developmental path, the real issue was to understand the origin of novelty in evolution: "What constitutes the real biological problem is... the tendency toward novelty, synthesis and higher organization, as seen both in individual development and in evolution" (Lillie 1945: 204). Lillie did not have a clear answer to this problem. He believed, however, that speciation had to be somehow related to a psychical directive factor:

> The factors of evolutionary diversification still remain essentially unknown, but the selection of purely fortuitous variations does not seem to be a sufficient explanation for the origin of the more complex adaptive characters. The entrance of some directive or integrative factor seems to be required (Lillie 1945: 47–48).

Like Russell, and Richard Semon, or Richard Hering before him, Lillie played with the mnemonic theory of heredity (Esposito 2013). Although there were different versions of such theory, the common denominator was that the characters of the organisms could be analogically explained as "engrams": mnemonic traces engraved in the germinal matter. These traces were produced through an organism's interaction with the environment and were reproduced during development, just as a phonograph reproduced the traces of a vinyl record. However, Lillie recognized that the "engrams" could only be used as analogical or metaphorical concepts for explaining heredity and could not really explain the emergence of novelties in evolution. Even though the causes of evolutionary change were far from being understood, apart from the general descriptive dialectic between conservation and novelty that organisms exhibit over geological eras, what the biologist could surely maintain was that evolution referred to the historical process of the emergence of new organized entities. For Lillie, the evolutionary process that Lloyd Morgan had proposed in his influential *Emergent Evolution* (1923) described very clearly the generation of irreducible novelties—of new levels of systemic organization—which could be simply the result of accidental combinations in the physical world or teleological assortments in the organic world.

Not surprisingly, Loeb despised Lillie's speculations, which he considered as too mystical or "Bergsonian." But Loeb also scorned the work of Lillie's elder brother, Frank Lillie (Manning 1985). A pupil of Charles Otis Whitman at the University of Chicago,[4] Frank replaced Whitman as director at the Marine Biological Laboratory at Woods Hole in 1908. Like Ralph, Frank was deeply critical of mechanistic and reductionist approaches in the life sciences. And, like Haldane, Thompson, Russell, or Woodger, Frank shared the same uneasiness toward particulate theories of heredity. Indeed, he distinguished between the latter and physiological theories of heredity: the first pertaining to the study of the transmission of characters within populations and the other concerning the development of those characters in individual organisms. As he clarified, for example, the observed differences in the color of mammals' fur did not simply result from the presence or absence of some supposed determinants in the germ cells but from physiological and developmental mechanisms: "the development or inheritance of color… can certainly not be due to the presence of black or brown or red or yellow determinants in the germ, assumed for theoretical purposes by some students of heredity, but to a specific power of oxidation of the protoplasm" (Lillie 1914: 248). The visible characters, after all, could not be merely

[4]Whitman, in turn, had been a student of Leuckart in Leipzig.

related to some postulated elements but had to be conceived of as the unique result of different physiological processes happening in different times and contexts during the whole process of embryogenesis.

The studies and experiments Lillie started to perform from the 1930s onward on feather development in Brown Leghorn fowl—the very same studies that had fascinated D'Arcy Thompson—showed that the inheritance of morphology and pigments (feather patterns) were related to hormones and growth rates in different regions. Lillie injected hormones and showed that this could produce particular pigment patterns, depending on the growth rates and the quantities administered: "As rate of growth is a fixed property of the different feathers tracts...it is possible to produce birds by means of suitable administration of female hormone, with female feathers in the slowly growing tracts, and feathers of male characters in the more rapidly growing tracts" (Lillie and Juhn 1932: 177). In observing variations in, and the transmission of, plumage patterns, Lillie was following to some degree the example of his mentor, Charles Whitman, who had previously studied the evolution of pigeons through the observation of plumage patterns (Gould 2002). However, while Whitman used his observations as evidence to support an orthogenetic theory of evolution, Lillie saw plumage patterns as a window onto physiological heredity. But in spite of their differences, both believed that development was "...the more general problem of biology" (Whitman 1919). The nature of development, with its law-like processes and teleological patterns, mirrored evolution. Ontogeny and phylogeny, after all, had not to be considered as two distinct phenomena insofar as the nomological, linear, and seemingly teleological direction of evolution mimicked the nomological, linear, and teleological direction of individual development. Indeed, Lillie maintained that development was the proper window through which to observe evolution (Gilbert 2003).

Although Lillie did not develop any theory about how these changes could be transmitted, one of his students, the zoologist Ernest Just, did. Just followed a similar career path of many American biologists during the late nineteenth and early twentieth century. After the PhD at the University of Chicago, he complemented his formation at Dohrn Zoological Station in Naples and at Kaiser-Wilhelm-Institut für Biologie in Berlin. In 1939, Just published the *Biology of the Cell Surface*, an ambitious book showing the importance of cytoplasm in controlling development in interaction with the cell nucleus. The book begins with Goethe's short poem "on the contrary (to the physicists)" which anticipates the whole monograph's content: "Natur hat weder Kern, Noch Schale, Alles ist sie mit einem Male" (that can be translated as "Nature has neither core nor shell. But is all at once"). To Just, the poem expressed the intuition that organisms are constituted of parts, but the parts, in turn, are shaped and articulated into the whole, so that neither parts nor the whole could be thought independently from each other. Just also applied the poem's idea to his cytological theory: nucleus and cytoplasm were both responsible for the expression of hereditary characters and the generation of novelties in evolution. In the cell, there was neither core nor shell, but all is at once.[5]

[5]For a recent revisitation of some of Just's biological ideas, see Byrnes and Newman (2014).

In particular, Just speculated that the crucial differences among species had to be related to differences in the structure and function of the cell surface, rather than structural changes in the chromosomes. Thus, environmental stimuli could produce changes in the ectoplasm (the outer region of the cytoplasm) that, in turn, could modify the nucleic substance and therefore could be transmitted to the following generations. As he explained: "…species arose through changes in the structure and behaviour of the ectoplasm. In the differentiation of ectoplasm from ground-substance we thus seek the cause of evolution" (Just 1939: 361). If heredity manifested itself during the embryogenetic process, then both heredity and evolution had to be understood through the analysis of embryogenesis—and the latter, in turn, revealed that the developing organism and the environment were "…one reacting system" (Just 1933: 23). In other words, the proper engine of evolution was the dynamic dialectic between environmental pressures and cellular alterations.

Just had also been a student of the physiologist Charles Manning Child, a colleague of Lillie's brothers at the University of Chicago. As one of the last students of the organicist physiologist Rudolf Leuckart in Leipzig, Child maintained his criticism of any reductionist theory of heredity until the end of his life. He believed that the phenomena of animal regeneration could reveal the essence of development and, therefore, the origins of variation in evolution. In order to explain the origin of order in embryogenesis, Child introduced the concept of "metabolic gradient." He observed that cellular organization followed a specific path along the axis of the organic bodies (whether radial, bilateral, or spherical morphological symmetries), and this path could be understood as a physiological gradient orienting cellular differentiation and specialization. Thus, organisms were crossed by metabolic gradients which directed and dictated growth rates in different regions. His experiments performed on *Planarias* and *Tubularias* showed that gradients established axes of activity that were directly related to metabolic rates. Reproduction, for instance, was interpreted by Child as the reestablishment, in sexual or asexual reproduction, of a new metabolic gradient. If the organism was a collection of integrated metabolic gradients forming dynamic tensions, heredity had to be conceived of as the capacity of an individual organism to produce a new whole. In other words, the organism had to be seen as a "system of reaction" capable of transmitting specific potentialities which could trigger, in the right context, new waves of metabolic gradients. Child therefore concluded, as against Weismannians and Mendelians, that the unity of heredity had to be the whole developing organism: "the original specific reaction system in which the gradient arises is the fundamental reaction system of the species, the basis of inheritance and development" (Child 1911: 152).

If the whole developing organism had to be considered as a unity of inheritance, it followed that morphological changes in evolution had to be ascribed to changes in the whole reaction system. As Child argued: "Evolution is not directly concerned with morphological characters, but with the physico-chemical constitution of the reaction system, and so with the rate and character of its reactions and the conditions under which they occur" (Child 1915: 205). The very notion of "acquired characters" had to be reconceptualized as the structural changes experienced by the reaction system due to the continuous pressure of external stimuli. Despite the evidence, Child added, "...it is difficult to understand how biologists can continue to maintain the distinction between soma and germ plasm, and to content themselves with the assertion that natural selection is adequate to account for adaptation in the organic world" (Child 1915: 205). Evolution, therefore, was to him all that followed from structural and functional changes in the developing embryos.

Child's view was taken further by one of his friends in southern California, William Emerson Ritter, the same scholar who, as already mentioned, had challenged Loeb's mechanistic views in 1919. In 1903, Ritter had founded a small marine zoological station on the shores of San Diego. Child spent his research summers there, where he could count on a rich marine flora and fauna upon which he could perform his experiments relating to animal regeneration and development. Like Child, Ritter spent an important part of his formative years in Europe. He had befriended Child at the Dohrn Marine zoological station before concluding his research trip in Berlin. With Child, Ritter was preoccupied with the fact that an important tradition in biology, which he dubbed "organismal biology," was at risk of disappearing due to the extraordinary appeal of reductionist and mechanistic approaches in the biosciences. The proliferation of particulate theories of heredity, as well as neo-Darwinian hypotheses, overshadowed more traditional ideas and methods that could provide a deeper understanding of life phenomena. As we have seen, in order to contrast this dangerous tendency that Loeb had clearly expressed in his 1912 *Mechanistic Conception of Life*, Ritter published the two volumes titled the *Organismal Conception of Life* (1919). The books included the history, philosophy, and scientific content of organismal biology, and an informed criticism of what Ritter called "elementalism"; i.e., the idea that life processes are best understood when reduced to their simplest components. To "elementalism" Ritter opposed "organismalism", which regarded living organisms as active and reactive irreducible systems that could never be understood as a collection of physicochemical properties. Ritter's historical narrative, in emphasizing this philosophical intuition, started with Aristotle, passed through Cuvier, and the French comparative anatomists, and concluded with the American embryological school, which principally included C. Whitman, F. Lillie, E. Wilson, and C. Child.

The volumes also included philosophical reflections. As previously mentioned, Ritter had been influenced by his mentor, Leconte, at Berkeley. However, he had also been influenced by the neo-Kantian philosopher Josiah Royce, while studying at Harvard. Ritter believed that Royce's idealism was a good candidate for explaining how organic unity was the manifestation and, at the same time, the result of psychic integration (Ritter 1919, vol. II). In an article published in 1928, Ritter complemented his biological synthesis with the British philosopher Alfred Whitehead, who, while at Harvard, had developed a new philosophy that he had dubbed "process or organic philosophy": a metaphysical stance which Whitehead compared to the nineteenth-century romantic critiques against eighteenth-century materialism (Whitehead 1925). Ritter's article aimed to offer a new updated and synthetic view on organismal biology. He recognized the general contributions of Haldane and Russell to organicism and argued that the organismal approach had to be completed with Jan Smuts' and Lloyd Morgan's conception of emergent evolution. Synthesizing the intuitions of the "emergentists," Ritter restated the idea that evolution was a creative and productive process that could not be understood as a mere mechanical process.

While Ritter took seriously Whitehead's process philosophy, he was also engaged in a strenuous conceptual struggle against Mendelian biology, which he considered to be at odds with the evidence provided by organismal biologists. As Ritter explained, in criticizing Bateson's Mendelism and its relation to evolution: "My main reason for believing the enterprise will never be carried through, seriously, is that the organismal standpoint has already advanced so far on secure observational and experimental and inductive foundations, that the scientific uselessness if not folly of such elementalistic systems will deter working biologists from spending their time on them" (Ritter 1919, vol. 2: 22). In fact, with Lillie and Child, he believed that the developing organism, as a reaction system, had to be thought of as the unit of inheritance and, consequently, as the privileged site of investigation for understanding evolution. Ritter believed that the organism could not be separated into heredity and development because heredity was equivalent with the developing reaction system. In an unpublished manuscript titled "Biology Greater than Evolution" (undated, but probably dating from the 1920s; see Esposito 2016), he complained that neo-Darwinians pretended to explain variations only through the modification of the whole "race" (population), overlooking the individual, developing organism, which was the veritable source of novelty in evolution. Thus, Ritter maintained, although Darwinian biology had been essential for our understanding of life on earth, it needed to be complemented with the essential tenet that the individual organism was the veritable source of variation and, therefore, speciation. While heredity studies had to focus on what Ritter called "descriptive ontogenesis"—i.e., observing the way morphological characters emerge during development—evolutionary biology had to rely on empirical and experimental investigations of the whole reaction system. In short, Ritter underscored Child's intuition that evolution was the consequence of functional and structural changes in the reaction systems during development.

In 1931, Ritter traveled to London to chair a session at the Second International Congress of the History of Science. The session included, among others, most of the British organicists: Russell, Woodger, Haldane, Joseph Needham, and D'Arcy Thompson attended and talked about the relationships between physics and biology. This was one of the last occasions on which most of the Anglophone organismal biologists were gathered together. Indeed, 20 years later, while Russell was writing his chapter on Schopenhauer's bio-philosophy, many of the most important organismal biologists from both sides of the Atlantic Ocean had died and the reductionist and mechanist approaches in biology had largely overshadowed the organismal conception of life. The organism itself, as a self-contained, self-organized, dynamic, and creative entity, was reframed in terms of molecules and their interactions and, later, in terms of information encoded within macromolecules. The functional and teleological phenomena could be understood as epiphenomena of purely adaptive mechanisms. Evolution could be simply explained in terms of changes in gene frequencies within a population. A biology based on processes and activities was translated into a biology rooted in structures. In the increasingly technocratic life sciences emerging during the Cold War, the Loebian dream of a biology freed of "romanticists" was generally realized (although never totally achieved).

4 Conclusion

Mayr's famous distinction between typological and population thinking can help us in introducing the opposition between developmental and neo-Darwinian views of evolution (Mayr 1982). In the first case, the individual is the most significant source and unit of evolutionary change, while in the latter the population is the main site of evolutionary novelties. The "romanticists" I have introduced in this chapter definitely uphold the first alternative and criticize the second. We can also contextualize Mayr's dichotomy within Bowler's narrative about non-Darwinian revolution. Bowler showed how nineteenth-century developmental traditions survived well into the twentieth century, challenging and often even overwhelming neo-Darwinian hypotheses. Orthogenesis and other transformist theories proliferated at the end the nineteenth century and continued to be accepted and updated until a certain consensus was reached with the modern synthesis after the 1950s—at least in the Anglophone world (Bowler 1988, 1994). Indeed, throughout the first decades of the twentieth century development continued to be a powerful metaphor for understanding phylogeny. The orderly and teleological processes of embryogenic development worked as a powerful metaphor for evolutionary thinking. However, as we have seen, the developmentalist perspective advanced by these "romanticists" was neither equivalent with Ernst Haeckel's biogenetic law nor represented a variant of orthogenetic evolution, but rather endorsed Walter Garstang's idea according to which ontogeny does not recapitulate phylogeny, it creates it. While in the biogenetic law ontogeny is a mirror of phylogeny, and in many cases its outcome, in the latter phylogeny was the product of ontogeny. In other words, the creative site of evolutionary diversification was the individual developing organism. In that sense, this perspective is closer to contemporary evo-devo than nineteenth-century recapitulationist theories.

But Mayr's philosophical dichotomy and Bowler's historical thesis needs to be linked to even larger epistemological trends in biology (and beyond) during the late nineteenth century and the first half of the twentieth. As shown, accepting or rejecting a theory (neo-Darwinism or developmentalism) means accepting or discarding a certain kind of biology and therefore a specific way to explore, understand, or explain life phenomena. The philosophy of the organism that many "romanticists" defended was definitely at odds with the idea that organisms were the outcome of relatively independent characters. If the organisms had to be conceived of as integrated, systemic, and creative wholes, evolution could only be the consequence of the dynamic activity of these wholes taken individually. The clash between alternative understandings of evolution was much deeper than an empirical or theoretical conflict between rival hypotheses. The real issue behind developmentalists and neo-Darwinians lay in the different tendencies regarding how to perceive the organism and what biology as a discipline should be. And this, in turn, was linked to a host of social and political concerns involving mechanist and materialist world views, often connected with conservative scientific or anti-scientific ventures (eugenics, social Darwinism, racial biology, etc.). Indeed, social progress and democracy, Manning Child and Edwin Conklin averred, were directly rooted in biological principles of organic integration and coordination (Child 1924; Conklin 1938). And, as Ralph Lillie lamented: "What the pure mechanist contends is that past conditions determine present conditions completely and unconditionally, and he extends this kind of determinism to human behaviour." However, as Lillie added, "the present is part of the general creative advance of nature" (Lillie 1945: 169). In short, to some biologists, organicism guaranteed democracy and free will. Mechanism only involved fatalism and despotism. For others, the opposite was true. In the twentieth-century discussions over the nature of biological phenomena, vague notions such as mechanism, determinism, reductionism, physicalism, etc., were not mere philosophical options supporting neutral views about development and evolution; rather, they also worked, frequently, as premises for political positioning (Esposito 2016).

Now, if after the 1940s, the "romanticists'" views gradually fell in the background, in favor of neo-Darwinian hypotheses (supported by new disciplines such as population genetics, increasingly paralleled by a deeper understanding of the hereditary mechanism through molecular biology), then the question is: why did that happen? The question is particularly relevant because, in the last few decades, the consensus about the neo-Darwinian synthesis has been eroded in favor of a new form of developmental evolutionism (evo-devo), and novel versions of organicist philosophies have again entered onto the stage. As Meloni (2016) has recently stressed, new versions of soft heredity, in concert with notions such as the reactive genome, have made the classic paradigm of the modern synthesis problematic at least. The overreaching perspective offered by the developmental system theory, or by the complex epigenetical models of gene expression, is certainly closer to the systemic view of the "romanticists" than the adaptationist models of the modern synthesizers. The organismic system approach defended by Callebaut et al. (2007) or evo-devo's agenda based on the intuition that the processes of growth in development offer a privileged window for observing evolutionary changes is perfectly in line with the visions of the individuals I have here presented. Of course, differences and similarities between early twentieth-century organicisms and more recent organicist proposals need to be handled with care. We should avoid "Whiggish" historical interpretations, suggesting, even implicitly, that past reconstructions fit, or support, contemporary research programs, as Pigliucci seems to argue with his critical remarks of this chapter (Pigliucci 2017). Indeed, the chapter does not have the ambition to foster a contemporary revival of what I have called "romantic biology." It would be an anachronistic and purely nostalgic attempt without any chance to succeed. The meaning of this historical exercise of recovering different twentieth-century traditions in biology, at least within the scopes of this volume, is to figure out how Darwinism itself developed and changed through, and against, his critical detractors.

Although a comprehensive answer to the question about why "romanticists" became a small minority after the Second World War goes beyond the aims of this chapter, there are at least two related hypotheses which could be profitably explored. First, the postwar anti-Lysenko campaign in the Western bloc has certainly prevented the development and diffusion of hypotheses that smelled of Lamarckism (Esposito 2015). It is not very difficult to realize how organicist conceptions, such as those of Ritter or Russell, were seen to be dangerously closer to Lysenko than neo-Darwinism. Secondly, the pessimistic epistemology of the organicists, who dismissed the possibility that the behavior of creative and unpredictable entities such as organisms could be successfully forecasted and controlled. In an increasingly technocratic environment, in which science has had to play a decisive role in managing and controlling reality, the holistic philosophies that animated romantic views of life and evolution were perceived as useless conjectures or indulgently aristocratic speculations in a world broken by socialist threats and capitalist excesses. In short, anti-Lamarckian models, based on unilineal and simpler representations of heredity and evolution, matched better with the more utilitarian expectations of the postwar biomedical establishment, epistemically and politically. In the 1950s, while Russell was recovering Schopenhauer's bio-philosophy, hoping to dismiss mechanistic ideals and neo-Darwinian views, he did not realize that the world around him had radically changed. In this new scientific world, where controlling was more important than understanding, there was increasingly little space and patience for "romanticist" speculations on the real nature of life.

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