On the Convergence of Ontogeny and Phylogeny into the Evo-Devo Theory: Why They Did not Integrate before and Why They Finally Could?

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The aim of this work is to explore the historical background of the Evo-Devo Theory, focusing on von Baer's and Haeckel's contribution to embryology and on their attitude towards Darwin's theory. Although von Baer funded modern embryology by his discovery of the mammalian egg, his doctrine of the primordial animal "types" was incompatible with evolutionism. Instead, Haeckel was a strong supporter of the Darwinian theory. According to his biogenetic law, "ontogeny recapitulates phylogeny": the embryogenesis of the individual repeats the history of the phylum which the individual belongs to. This means that evolutionary and developmental aspects of biology were very close in Haeckel's doctrine.
In 20th century, Evolutionary and Developmental Biology lied separated, mainly because molecular biology entered the former but not the latter. Since 1977, when Gould published *Ontogeny and Phylogeny*, but also thanks to the rise of epigenetics, these two fields of biology began to meet again. Thus, Haeckel's and Baer's doctrines are to be considered of great interest for the Evo-Devo Theory.

Keywords: Evo-Devo, embryology, evolution, K.E. von Baer, E. Haeckel, ontogeny.

Introduction

The aim of this paper is to understand the theoretical core of the Evo-Devo Theory. First of all, we try to define this approach as the tendency, in biological studies, to consider embryogenesis as the very moment in which evolution occurs. In order to do that, it seems necessary to use an approach which is both historical and epistemological; in this way, our recognition earns the awareness of the material[1] and the theoretical reasons that lie at the basics of the unification of Evolutionary Biology on one hand, and Developmental Biology on the other hand. Indeed, a philosophical analysis should not only understand why two different domains in Biology have converged into a new one, but also — and above all — why this unification was not possible in the past; the questions we ask is why Ch. Darwin's theory on the evolution of the species by means of natural selection seemed to be unconformable with embryology, which studied instead the way every single organism develops and changes during the time of its ontogeny.[2]

What philosophy affords to sciences is thus the possibility of acknowledgment of their historical and theoretical background: behind a series of empirical facts and experiments, we can find a nucleus of ideas which drives scientific studies all along their paths, even drowning the path itself.

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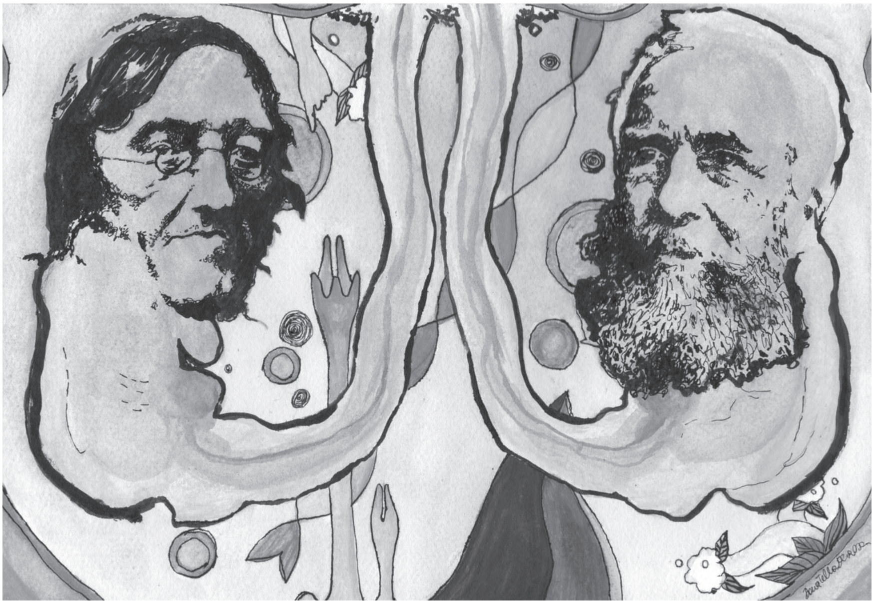
[1] By this word, we basically mean the historical conditions which lie at the basics of a scientific theory. It was thanks to K. Marx's and F. Engels' historical materialism that the study of the economical and social elements, that is just *history*, earned the status of a science. Later on, the Marxist approach got into epistemology, so that also the philosophical reflection on scientific theories was inspired by a historical method. We quote as an example of historical epistemology G. Canguilhem and M. Foucault.

[2] The first one who used the terms "ontogeny" and "phylogeny" was E. Haeckel (1874); by these words, he meant to refer to the process who leads to the formation of an organism on one hand, and to the history of the genealogy of a phylum on the other hand.



«Heterochrony», Donatella De Rosa, 2011

As the theme of our analysis concerns von Baer's embryology, which has been linked to *teleology* and to vitalism, it may be useful to underline that our recognition is not committed with ethics, but it is just an epistemological study on biological vitalism. The role of teleology in biology is very subtle: by his theory, Darwin (1859; 1871) succeeded in expunging it, as history — and of course, phylogeny is linked to historical processes — has not a *goal* to reach, it is just stochastic and connected to chance. The fact that Evolutionary Biology is not committed anymore with finalism, since the publication of the theory of evolution of the species, doesn't mean that life sciences don't need it at all. We will ask then why embryology requires a teleological category to study developmental processes and what finalism affords to the domain of ontogeny. Thus, the reason why Evolutionary Biology and Developmental Biology never really met in the 19th century seems to be connected with the intricate role that teleology plays in life sciences and, of course, with the lack of embryogenetic studies in Evolutionary Biology (Morange, 2011).

The subject of life sciences is analyzed from two different perspectives, ontogeny and phylogeny; someone may ask which is the relationship between these two domains, either they're linked to one another into a *causal* nexus (Haeckel, 1874) or they are just two different ways to study the stages which lead organisms through individual and specific history. Indeed, Haeckel (1874) suggests that ontogeny was the recapitulation of phylogeny; his approach unifies these two domains, but it expires into a non-scientific and extremely ideological[3] theory; it will be then necessary to understand why he stated the existence of a link between them and why this statement was not worth the title of a science; however, as the Evo-Devo Theory actually unifies ontogeny and phylogeny, we will ask why it is now possible to conceive these two segments of the study of the organisms as deeply connected one another. The Evo-Devo Theory is then

[3] For the sense of the *ideological* in epistemology, we mean what L. Althusser's stated in his "Philosophie et philosophie spontanée des savants" (1974).

committed with the eccentric statement of Haeckel's biogenetical fundamental law for what concerns the inspiration, but it makes use of experimental studies (Carroll, 2008), which really support this unification.

The reason why we want to analyze under a theoretical and a historical perspective this mutual integration lies in the misconstruction of the role of finalism in biology on one hand, and in the confusion that concerns von Baer and Haeckel's different approaches to embryology on the other hand. Indeed, as Darwin quotes both of them, J. Huxley (1939) writes about their theories as if they were identical. This shows a serious misunderstanding that we want to dissipate: von Baer's embryological studies lead to the refusal of the evolutionary theory and are supported by the epistemological category of *difference*, whereas Haeckel's statements represent yet a great intuition of the *unity* of nature and an enormous adhesion to Evolutionism, but they are just metaphysic thoughts.

The aim of our recognitions is thus to understand what von Baer and what Haeckel offered to embryology in 19th century, which was the relationship between ontogeny and phylogeny at that time, and what the Evo-Devo Theory inherits from its theoretical background.

Before all that, a review of the embryological debate before 19th century and the doctrines of von Baer and Haeckel seem to be useful to answer our questions.

1. Preformationism and Epigenesis

The history of the embryological doctrines is marked by the opposition of two different ideas on the development of the embryos: preformationism and epigenesis. Since the 17th century, when microscope was used in life sciences (Solinas, 1967), embryologists started to explain the processes of the development of the organisms through the metaphor of the *emboîtement*: it means that embryogenesis was seen as a progressive dimensional augmentation of a whole being which was yet formed in all its parts. This conception is deeply connected to *mechanism*. Indeed, in the 17th century mechanist philosophies started to emerge, such as R. Descartes' and, above all, G.W. Leibniz's metaphysics; thus, it was possible to gaze at the material which gives rise to a new organism thanks to an innovative instrument, through which you could observe something very similar to a living being, that moved by itself and looked as a little man. Actually, as the instruments were not so sophisticated and accurate, a remarkable role was played by the observer's imagination, that led him to conceive this little being as an incredibly small animal, that was then called *animalculus*. Thus, a mechanic conception, together with the Christian idea of creation, suggested that all organisms had been created by God since the origin of time and put one into another, so that they could grow all along generations and come into being *seriatim*. The process that led to birth was then just an *accretion*, not yet a real formation: organisms existed, completely preformed in all their parts, since ever; they only needed to be led to rise. Preformationist doctrines imposed to think on the origin of individual life in terms of *development*, which means that a living being, already formed, came to life by the explication of a pre-existing morphologic structure (Canguilhem et al., 1962). This development happened step by step, all along a homogeneous time and in a completely mechanic way; according to preformationism, the process of accretion concerned only quantitative parameters, as qualitative ones — such as the acquisition of a *form*[4] — were already set since creation and, for this, unsusceptible of any modification.

[4] In the sense of figure or silhouette.

Yet this was the problem: modification. Preformationism was questioned by its incapacity to explain the fact that, sometimes, very weird organisms came to life. What was called *monstrum* was just an erratic form of an ordinary living being, peculiar in its body, abnormal in relation to the others to which it was supposed to look like. If every animal had been created according to an ideal form, that was the species[5], morphologic and physiologic aberration weren't presumed to be possible. All possible ways of being would be created and set by God, in order to be realized through development. Sexual intercourses were thus reduced to a bare activation of a mechanic process, which did not admit any change, any deviation from the pre-set course of accretion. As indeed modifications were real and monsters actually came to life, preformationism experienced a crisis, as it was unable to explain this kind of abnormalities.

So, it was necessary to use different theoretic instruments: all what happened before birth was not to be thought as a developmental process as we conceive it today, but rather as a real *formation* of a structure which did not exist before. It dealt with the construction, step by step, of a figure through a temporal factor which was not homogeneous nor mechanically pre-set anymore, but totally free, so that during the period of morphogenesis, organisms could create themselves, yet according to the ideal form of the species, but they could also undergo aberration and could experience new settings, realizing unpredictable structures.

Whereas preformationism didn't admit any news, epigenesis[6] was a theoretical explanation that permitted to conceive the genesis of organisms through the epistemological category of *novelty* (Turriziani Colonna, 2011). A non-mechanic process was the only way to explain how a living being could create itself either according to a prototypic structural form and introducing and experiencing new possibilities in the body setting.

It is clear that epigenesis represents a mode of realizing a form that is not involved into any mechanic view, but it is rather *wide* and free; it conceives the time before birth as a progressive self-construction of the structure of the body and admits that any sort of aberration can occur to deviate the course of morphogenesis towards a form which can either be functional and healthy — even if anomalous — or it can be monstrous, pathological and unhealthy. Whereas preformationism could not experience any new path besides the ones pre-set into a mechanic development, epigenesis refused mechanism and admitted every possible aberration. The former explanation was the only one that could save embryology from absurdity.

However, a conception like this could eventually miss accounting the preservation and the perpetuation of the species. How could be possible that from a man arose another man and not a different animal? What was there to maintain the reproduction according to a *specific* criterion? Indeed, organisms commonly generate offspring similar to parents in relation to characters, which are maintained through generations. Nevertheless, sometimes abnormality occurs. Epigenesis must then account *stableness* but also *variation*.

On its own, this concept could yet explain exhaustively the attitude to variation, but it needed a theoretical means to legitimate the maintenance of the species through generations, otherwise it would be totally anarchist. So, the way to justify this lied in the idea of *natural goal*, which involves teleology. Epigenesis is thus connected to the idea that there is a goal to reach (Turriziani Colonna, 2011), so that a germ can form an adult organism, which displays the characters typical of the species it belongs to. Without a goal in the process, morphogenesis

[5] Preformationism was deeply connected to creationism: all living beings had been created and distributed among prototypic forms, the species, always identical to themselves since ever and for ever.

[6] Epi-genesis means exactly formation by assembling parts step by step, according to a sequential process.

would be totally disorderly and left to accident, thus proceeding by chance. Instead, the idea of a goal is theoretically useful for the embryological reflection.

Anyway, we need to remind that, between two alternative approaches, we cannot choose decidedly one or another: it is so far more fruitful to analyze both possibilities and to use theoretical instruments taken from both. As an example, we can quote C. Bonnet's peculiar doctrine: he thought that germs were completely preformed, but their development happened according to a *differential accretion* of the different parts of the body. In this way, he could explain the occurrence of abnormalities in relation to a temporal factor, which was not uniform; because of that, the temporal parameter sometimes could happen to work in the wrong way in regulating the whole process, thus causing morphological aberrations. It seems, then, that a hybrid approach to life sciences and, in this peculiar case, to embryology, is the best way to understand (Canguilhem *et al.*, 1962) how organisms create themselves during their whole existence, obeying to their specific morphogenesis and sometimes experiencing new paths.

2. Von Baer's Non-Evolutionist Doctrine

As we just have seen, since the 17th century embryology was influenced by mechanism and, later, by the discovery of the theoretical benefits of the ideas of *variation* and *goal*. Thus, preformationism and epigenesis enriched each other with these epistemological categories, which came to represent the main ideas in theoretical embryology. At the beginning of the 19th century, then, embryology was a teleological domain, deeply connected to the idea of species as something unavoidable to explain the maintenance of similarity all along generations. Moreover, as in life sciences the idea of a historical *progression* was been thought, another doctrine entered embryology: the one about *recapitulation*, that eventually occurred during the process of formation of new organisms, which were then supposed to retrace, all along their morphogenesis, the stages accomplished by the species they belonged to. There would be a *parallelism* between the process that leads to the formation of each individual — *ontogeny* — and the history of the phylum the individual belongs to — *phylogeny*. Thus, every single step you could isolate on one domain had a correspondent on the other one. The idea of recapitulation first occurred in J.F. Meckel and A.E.R.A. Serres' doctrines (Gould, 1977).

In 19th century, above all, a very remarkable theory has been elaborated: Ch. Darwin's one. Evolutionary Biology represents the theoretical condition to think on recapitulation, because this last one needs the concept of history as a category of analysis in life sciences. Thus, we want to understand which was the relationship between Darwin's theory and embryological doctrines all along 19th century, when the ideas of evolution and recapitulation arose. By questioning this complex relationship in the past, we will then try to understand the same relationship in the present, in reference to the Evo-Devo Theory.

Embryological studies are marked by an essential discovery, which concerns the identification of the *ovum* in mammals as the beginning of all biological processes. This discovery is due to K.E. von Baer (1827), a Baltic scientist that attended to medicine, biology, embryology, geography and anthropology. In 1827 he published *The ovi mammalium et de hominis genesi*, to report his studies on the ovum. Someone may ask what makes his discovery innovative compared to all the descriptions of eggs published before, as for example the one by N. Stensen. Indeed, the criterion which makes von Baer's studies the actual discovery of the ovum lies first of all in (Leikola, 1993; Turriziani Colonna, 2011) the locus where this biological structure was found, but also in the fact that behind a series of observation there must be a conceptual framework which permits to think on empirical descriptions as the confirmation of a theory.[7] It was now, in 19th century, that anatomists studied the feminine genital structures in different animals, to search what was the basic element that launched the process of formation of the embryo. The question was if this element was fluid or corpuscular; all along the history if life sciences, scientists had thought that fecundation happened thanks to two principles, the masculine one which constituted the formal factor, and the feminine one which represented the material element. Since Aristotle, the masculine principle was conceived as a fertilizing *power*, and the feminine one was supposed to be both the *receptacle* and the nourishing *matter* of embryogenesis. Medical schools in the antiques reposed on a conception of the body as a mixture of different fluids, whose harmony caused a state of good health, whereas the dominance of one of them above the others determined illness. Thus, inside the body there were several fluid substances — *humours* — responsible for our corporal status and mood. According to this paradigm[8], also embryogenesis was then conceived as a process caused by fluid elements: no corpuscular matter could cause any biological process. This means that, within this "fluidist" paradigm, the idea of an egg as the principle of human life was completely absurd, even if it was from the egg that life started in other animals, such as birds, fishes and so on. Observers never thought, until they did not use microscope, that life, in mammals, could be produced by an egg; in 17th century, indeed, N. Stensen — a preformationist — stated that human life developed from the egg. Despite this affirmation, his statement was deeply linked to the idea that, inside the egg, the organism was completely preformed and ready to be accrued. The idea of the ovum[9] is instead connected, on one hand, to a corpuscular conception that was actually stated by von Baer[10], on the other hand to epigenesis: thus, the ovum was a biological structure, but it was not yet an organism, because no preformation could occur. The ovum represented the beginning of life, that is the beginning of a *formational* process. In the discovery of the ovum, published in 1827, all these new conceptual elements lie.

The contribution given by von Baer to embryology is not only experimental, but also theoretical. As he was in Berlin, he got acquainted with the "theory of the types" elaborated by G. Cuvier (Russell, 1916). This idea lies within a creationist paradigm and states that there are four archetypal settings of corporal structures. The theory of the types implies that no transition among types is possible, that is to refuse any change in phylogeny: there is not, actually, any sort of historical conception within this idea. According to this view, four types would have been created since the beginning of time and organisms come to birth within the scheme of a type, which represents the morphological criterion of distribution of the species in relation to their structural affinity. Although naturalists were elaborating transformist doctrines, Cuvier and von

[7] In the French epistemology, A. Koyré (1957) asserted that, in sciences, the actual core was represented by metaphysic ideas and theoretical speculation.

[8] T. Kuhn spoke about "scientific paradigm" in his "The Structure of Scientific Revolutions" (1962); he meant by this term a structure of thought in which scientific communities lied for a certain period of time and that only allowed to think on facts in relation to a series of epistemological categories. The paradigm creates a sort of mental domain out of that it is not possible to trespass: you cannot exceed the paradigm in which you are relegated, that is influenced by historical, material, social and economical factors of the time.

[9] When we speak about von Baer's discovery, we say *ovum*, as it was written in Latin, as we conceive this word as a scientific term, in which the awareness of the novelty lies.

[10] Just a little time before von Baer's discovery, A. von Haller used to say — still within a fluidist paradigm — that the principle from which life started was the solidification into an egg of a fluid element.

Baer proposed their theory, which implied the opposite view: there never had been nor it was possible that species changed all along time, on the contrary they were static and fixed for ever within the type they belonged to. Actually, according to von Baer — who was, of course, out of the paradigm of evolutionist — little changes could eventually occur (Baer, 1828), but they did not lead to a complete transformation of the species one into another, nor at all to a transition from a type to another. Whereas in Cuvier the theory of the types concerned only morphology, in von Baer it was connected also with a dynamic view, as it was involved in embryogenesis: the type is the way the parts of an organism are set together; it establishes the modality of the whole process of morphogenesis, which undergoes the domain of the type. Thus, someone may conceive this idea as a topological scheme that influences ontogeny, just like a goal that pre-exists the effect and towards which the process is completely oriented.

Although von Baer's embryology imposed to him a refusal of evolutionism, it is clear that the contribution he gave to this domain is huge, not only in relation to his discovery of the ovum, but also because he showed the gravity of the role of a goal — played by the idea of type in his doctrine — within the domain of embryology, as he also wrote in his "Ueber den Zweck in den Vorgangen der Natur" (1876). Moreover, Von Baer conceived embryogenesis as a progressive growth of individuality, which happens by self-construction — Umbildung in German; the whole process involves *differentiation*, that is studied through quantitative methods. Also for this reason, someone may judge his embryological doctrines as a complex system, rich of insights that survived until the present, even if it imposes the refusal of evolutionism. Indeed, a historic epistemology must appreciate the merits a doctrine has, although it obliges to experience ideas that are nowadays considered false. Actually, evolutionism is the only way one can understand biological processes; nevertheless, von Baer's embryology involves non-evolutionism, but this is not enough to refuse the whole conceptual system he elaborated, because there are many ideas in it, which is useful to understand how embryogenesis occurs (De Beer, 1930). We may say that there are no true nor false ideas in sciences: one may rather say that a theory *works*, but it is necessary to remind that behind all that, a very complex history has led to conceive it. Every theoretical effort produced good theories, together with other ideas which have later been refused by experiments, but this doesn't mean that there was nothing interesting and useful in someone's doctrines such as in von Baer's.

3. Haeckel's Insights

Whereas von Baer's theoretical biology is marked by the epistemological category of *difference*, E. Haeckel's contribution to embryology represents the statement of *unity* in nature. Indeed, his reflection was influenced by E.G. Saint-Hilaire's doctrines, who thought that all organisms were linked within a natural framework; thus, all forms in nature could be reduced to one, which described a sole type. Someone could notice that there has been a sort of gemination: both in France and in the German lands, two different epistemological domains on life sciences were set one against another (Russell, 1916). Cuvier proposed that there was a difference among morphological types, while Saint-Hilaire suggested that no difference could be found, as all kinds of organisms could be reduced to a simple type, which he then called zootype, in order to focus on the deep unity characterizing the natural domain. In the same way, von Baer explained by the theory of types that four different forms were possible in morphology, so that animals could be distinguished by their structural organisation; instead, Haeckel thought that all animals belonged to a single type which included all structural schemes: he focused on *similarity* rather than looking at differences.

Haeckel's biological doctrines are completely different from the ones elaborated by von Baer, not only because the two authors adopted alternative epistemological categories to analyze organisms, but also because their attitude towards Darwin's theory was different. Whereas von Baer was not evolutionist, and indeed he couldn't approve that species transformed, because of his theoretical assertion on the theory of types — which excluded the possibility that organisms could evolve by trespassing the type's borders[11] — Haeckel was a strong supporter of Darwin's theory and actually he entered evolutionism into Germany. His intellectual appeal is marked by the enthusiasm for materialism, which led him to support *monism* (Toffoletto, 1945): every spiritual skill that organisms realize is just the effect of material functions; there is no actual spirit, nor extra-corporal mind, as everything exists is matter and every behaviour is caused by matter itself. Thus, Haeckel could see in Darwin's theory on evolution of the species the instrument to support his monistic materialism, as it suggested that there had been no creation *ex nihilo*, but life seemed to have his roots in matter, that evolves into organic structures. Someone could state that Haeckel's support to evolutionism lies in an ideological materialist background. By this assertion, we want to distinguish between what is conceived as intrinsically scientific and what is to be considered instead as non-scientific; actually, L. Althusser's Marxist epistemology (1974) is marked by this same distinction, through that the author gives a definition of the *ideological* as the whole of ideas elaborated within a non-scientific domain, influenced by cultural elements such as religions, economic and social structures and so on. Not only the ideological is non-scientific, but it is also pre-scientific, in the sense that it is an element which precedes the actual scientific elaboration of a theory or it anyway lies in opposition to that: it is thus necessary to draw an epistemological "coupure" — which he takes from G. Bachelard's philosophical vocabulary — between what is to be conceived as scientific and what is instead merely ideological. Then, we can state that Haeckel's support to evolutionism seems to be marked by an ideological necessity, as he was searching for a scientific theory which proved his materialist monism.

Despite all this, Haeckel's contribution to theoretical biology is enormous, although debated a lot (Gould, 1977). He was indeed a zoologist and he attended to embryology too; thanks to the theory of evolution, he could draw — as Meckel (1811) and Serres (1860), had done before — a parallelism between the history of the genealogy of the species and the process of embryogenesis of the individuals. (This same parallelism has been proposed also by Garstang (1922) and Severtsov (1927); but we won't discuss in this paper). *Ontogeny recapitulates phylogeny*: through this formula Haeckel expressed the biogenetical fundamental law. Actually, what makes the difference between Haeckel's assertion and Meckel-Serres' is the fact that, whereas in Meckel-Serres' insight there only was a parallelism between the two elements, in the German embryologist's law we can find the concept of a *link* which really connected ontogeny to phylogeny within a *circular* relationship. Although Haeckel's enthusiasm for Darwin's theory, we must state that the theoretical element thanks to which he could assert this *causal* link lies rather in Lamarck's doctrine of the heredity of the acquired characters (Haeckel, 1874). The idea of recapitulation risks to fall onto a new preformationism, in the sense that it does not admit the possibility of any change; instead, Haeckel knows that changes occur and he understands that it is not possible to miss the essential importance of this phenomenon; thus, he explains

[11] Nowadays biologists focus on the idea of *structural bonds*: it deals with all the genetic factors that regulate morphogenesis obeying to a given topological setting.

the historical rising of new species, together with the occurrence of variations, through the idea of *terminal addition*: it deals with the incoming of novelties during the process of recapitulation of the past forms. Moreover, if a monstrous organism comes to life, that weird breeding may be due to what is called the "stop of the development" — indeed, this idea was elaborated within a preformationist paradigm which did not let to think on any news occurring: weird organisms' existence could only be explained by the idea of a premature stop. As life evolves through history and ontogeny recapitulates phylogeny, the only way to explain how new species appeared was to admit that any new character occurred, it was included in future embryogenesis, so that history earned and repeated all the novelties happened in the processes of individual genesis. This idea is indeed the Lamarckian transformationist doctrine, which represents the actual *cause* of recapitulation. Whereas the concept of parallelism doesn't involve that one process can cause the other, the idea of recapitulation needs to search for a cause which links ontologically the two aspects of evolution: the one that concerns the species and the one that concerns the individuals. Thus, in the Lamarckian statement of the heredity of acquired characters, Haeckel could find the theoretical instrument through which he could think on recapitulation.

By means of his biological fundamental law, Haeckel could connect not only embryology to comparative anatomy, but also to paleontology (Haeckel, 1974). As history is completely accidental and the process of fossilization utterly contingent and left to chance, a huge part of organic forms was missing within the fossil repertory. Thus, the scientist could eventually use the acknowledgments taken from a certain domain and transpose them into another: such was the case of the theory of the Gastrea. As there was a lack in paleontology for what concerns the first steps of evolution of life, it was possible — according to Haeckel's doctrine of recapitulation - to suppose that there would have existed an organism, called Gastrea, which corresponds to the *gastrula* (one of the first steps of embryogenesis); this statement was possible solely thanks to the idea of parallelism and causal correspondence between ontogeny and phylogeny. Anyway, all this is just ideological: since De Beer critics (1930), scientists nowadays refuse Haeckel's doctrine in its details — but Gould (1977) focuses on the theoretical importance of Haeckel's thought for a better understanding of the mechanisms of evolution and the Evo-Devo Theory lies in the same intellectual path of Gould. It is then useful to distinguish between the doctrine itself, which is doubtlessly non-scientific, and the *insights* included in all his reflection on organic processes.

To justify his law from delicate objections, Haeckel had to think on the ideas of *heterotopy* and *heterochrony* on one hand, and to the one of *cenogenesis* on the other. It happens sometimes that a character shown by an embryo doesn't have a correspondence through historical evolution of the species it belongs to; indeed, this character seems to be an adaptation to the uterine milieu. Thus, the German embryologist explained this phenomenon calling it cenogenetic adaptation (Haeckel, 1874). Moreover, during the process of embryogenesis it may happen that a character rises in a locus which is not the same in future, in the post-natal organism: this is what Haeckel (1874) called heterotopy. The phenomenon of heterochrony was instead explained as the rising of a character during ontogeny at a time which does not correspond to the time when it appeared during phylogeny; this hiatus needed to be justified, or it would have represented an element of feebleness in the biogenetical law. The fact is that Haeckel did not eventually perceive the relevance these ideas of his had within embryological studies; he proposed them just to avoid that his law would be considered wrong, as he noticed that these phenomena occurred sometimes.

Heterotopy, heterochrony and cenogenesis represent an enormous contribution to embryology, as they work as an epistemological instrument to think on phenomena that often happen during the process that lead to the formation of organisms. Even if they have no real relevance within Haeckel's doctrine, which was not scientific at all, they are extremely useful in a theoretical sense, as they are epistemological categories for the study of life sciences; these concepts were then stressed by De Beer (1930), who criticised Haeckel, and later on by Gould (1977), who tried to rehabilitate Haeckel's doctrine of recapitulation and who started the studies leading to the Evo-Devo Theory (Turriziani Colonna, 2011).

Moreover, nowadays developmental genetics shows that there are a lot of genes that do not codify straight for proteins, but they regulate all these morphogenetic processes. Genetic regulation then occurs according to spatial and temporal parameters, which can be conceived both by quantitative analysis offered by genetics and by these ideas of heterotopy and heterochrony. All these studies lead us to appreciate the contribution afforded to embryology by Haeckel.

4. Why Evo Finally Met Devo

The aim of our paper was to understand the theoretical basics on which the Evo-Devo Theory lies. We analysed von Baer's and Haeckel's embryological doctrines and the relationship they established with the evolutionary theory. It was not easy for embryology to conciliate with evolutionism because of a series of theoretical issues: first of all because it lacked of a functional biology (Morange, 2011). Moreover, whereas in phylogeny no goals can be found, in ontogeny the idea of a goal is instead necessary to understand how embryogenesis proceeds; finally, von Baer's theory of the types averted him from accepting evolutionism (Turriziani Colonna, 2011). Thus, we saw why integration between these two domains wasn't theoretically possible and why von Baer's doctrine was not conformable with the Darwinian point of view. We may ask now why at a certain point the two disciplines — Evolutionary Biology and Developmental Biology — met, creating a new domain. Whereas ontogeny and phylogeny were causally connected only in the ideological doctrine thought by Haeckel, nowadays they are linked into a really scientific background (such as the discovery of the Hox genes), which is nourished by both segments of biology.

Indeed, we may consider Heackel's ideas as a whole of insights that are now confirmed. Biologists in fact speak about the zootype (Minelli, 2007) — as an echo of the unity of type taught by Saint-Hilare, Haeckel and generally by the German Naturphilosophie — to focus on the deep unity existing in nature; it is possible to conceive a topological structure which is the same in all animals, or at least it looks very *similar* all along the different species. This is then the sense of the epistemological category of similarity. Moreover, the integration between Evolutionary Biology and Developmental Biology was realized thanks to the discovery of a group of genes which regulates the development of the embryo: they have been called homeogenes and they have been studied after 1980s. These homeotic genes (Gilbert, 2003) — or just hox genes — are responsible for all phenomena of homeosis[12], that is the transformation of a part of the body into another and it concerns, as in the case of some insects which have been studied, segments that are conceived as *analogous*. All this means that corporal topology is regulated by quantitative factors — homeogenes — that influence the whole setting of the parts which form an organism. Living beings must then be considered the result of a series of processes that involve two main parameters: space and time, which are influenced and may be modified by hox genes.

[12] The first who spoke about homeotic changes was W. Bateson, 1894.

Thus, one can recognize — and appreciate — in this idea the two concepts of heterotopy and heterocrony thought by Haeckel, that is considered the author whose doctrines lie at the basics of the Evo-Devo Theory. Since the time when geneticists started to study the processes of regulation driven also by homeogenes, it happened that the two domains of ontogeny and phylogeny began to be thought as *really* connected.

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Об объединении онтогенеза и филогенеза в теорию Evo-Devo: почему интеграции не была осуществлена раньше, и почему она стала возможна теперь?

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Целью данной статьи является анализ исторических предпосылок теории Evo-Devo. Основное внимание в ней сосредоточено на вкладе работ К.Э. фон Бэра и Э. Геккеля в формирование эмбриологии и отношении этих ученых к теории Дарвина. Бэр, впервые описавший яйцеклетку млекопитающих, считается основателем современной эмбриологии, но его учение о первоначальных типах животных оказывается совершенно несовместимым с дарвинизмом. Э. Геккель, напротив, был убежденным сторонником дарвиновской теории. Согласно его биогенетическому закону, онтогенез повторяет филогенез, т. е. эмбриогенез индивидуумов повторяет историю типа, к которому данный индивидуум принадлежит. Таким образом, концепция Э. Геккеля сближала эволюционные аспекты и биологию развития.

На протяжении большей части XX в. эволюционная биология и биология развития существовали независимо друг от друга. Во многом это разделение определялось тем, что молекулярная биология стала составной частью первой, но не второй. С 1977 г., когда С. Гулд опубликовал свой труд «Онтогенез и филогенез», а также и благодаря развитию эпигенетики, эти две области биологии снова начали сближаться. Таким образом, концепции Бэра и Геккеля представляют огромный интерес для истории Evo-Devo.

Ключевые слова: Evo-Devo, эмбриология, эволюция, К.Е. фон Бэр, Э. Геккель, онтогенез.