NATURAL SELECTION AND SELF-ORGANIZATION: A DEEP DICHOTOMY IN THE STUDY OF ORGANIC FORM.

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ABSTRACT. There are two approaches in the study of organic form: the externalist and the internalist perspective. The concept of the nature of matter, on which the logical structure of these two systems of thought has been constructed, is their crucial difference. From the externalist viewpoint, living matter is a passive and a non-intrinsically ordered entity that needs an external factor (natural selection) to acquire form. From the internalist perspective, living matter is an active entity capable of exhibiting order spontaneously. Internalist theories were definitively abandoned at the beginning of twentieth century due to the mystical halo, which has always accompanied the idea of an inner factor driving morphological change. Recent studies on the physics of complexity are revealing that matter is capable of self-organization, providing strong support to the internalist view. Now an important question arises: Do we need an extended evolutionary synthesis? This question will be analyzed here.

KEY WORDS. Natural selection, self-organization, preformationism, epigenesis, genetic programme, form, function, Modern Synthesis, Evolutionary Extended Synthesis.

1. THE ORIGINS OF THE DICHOTOMY

1.1. PREFORMATIONISM AND EPIGENESIS

A crucial aspect for understanding the logical structure of the contemporary theory of evolution is that it depends on the idea that living matter is a passive and non-intrinsically ordered agent. This was the result of importing the Newtonian framework into the study of living organisms toward the end of the eighteenth century.

However, by then some people were already aware of the inability of the mechanistic framework to explain a crucial aspect of organisms, development[1].

During this time, previous to any well developed idea about the evolution of species, embryology occupied a central position in the life sciences.

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Ludus Vitalis, vol. XVIII, num. 34, 2010, pp. 25-56.

The first theories of form were based on development. There were two opposing hypotheses about development: *preformationism* and *epigenesis*. According to preformationists, the egg already contains the parts of the adult organism, but they are so tiny that we cannot see them during the early stages of ontogeny. The development from a parcel of homogeneous and transparent matter to a heterogeneous and complex organism is only apparent in this view; there is no qualitative change during ontogeny, only growth. The preformationist idea is usually illustrated in textbooks by showing a little man, or *homunculus*, in a fetal position within a spermatozoid, although this is only a caricature of preformationism. A more accurate representation of this theory would be to think of a tiny, wrinkled and considerably folded homunculus, which grows (unfolds) when the circulation of its body fluids is activated during fecundation. Preformationists did not deny that the embryo seems to undergo progressive change from homogeneity to complexity, but they claimed this change is only apparent: everything is there from the beginning.

Epigeneticists, in contrast, claimed that there are no preexisting structures in the embryo (or the gamete), and the appearance over time of structures during ontogeny is not an illusion, but a real phenomenon. Therefore, ontogeny implies not just growth, but also development. It was expected by its advocates that the improvement of microscopes would lead to the confirmation of the epigenetic theory (certainly, it was one of the reason of the fall of preformationism), by showing that structures originated *de novo* from the formless, homogeneous matter contained in the egg. Still, the actual increase in complexity of embryos raises a difficult question: what is the agency responsible of this organization? Epigeneticists were led to invoke the existence of an inner force, a vital force (*vis essentialis*). Epigenesis, then, was usually related to mysticism.

The scientists of the time, followers of the mechanistic approach tended to be preformationists because Newton's mechanical laws were not useful to explain development: "evolutionists [2] [preformationists] developed their theory because they were convinced of the impossibility of explaining form generation according to the mechanical laws— they deduced from these laws that form is not change, but just growth" (Rádl, p. 242 [3]).

Newman (2003b) also points out the inadequacy of the mechanistic approach for explaining the generation of form:

> A characteristic of most European science before the twentieth century was that, while the pre-eminence of matter and its laws of motion were acknowledged, how matter wound up assuming particular configurations and arrangements was still a mystery. The matter described by Isaac Newton, the great codifier of the science of mechanics, is inert. Although the motions of billiard balls and planets are governed by mathematically precise laws, the

> outcome of such motion is entirely dependent on the initial preparation of the system—the arbitrarily given starting position and velocity of each particle. In order for the matter in a many-body system to become organized in a complex fashion it would have to be 'set up' in an appropriate way. This is why Descartes, Newton, and the other founders of the mechanistic worldview could simultaneously be physical determinists and religious believers: God, they opined, was in the initial conditions.

These two theories have been described as like *Scylla* and *Charybdis*, an episode in Greek mythology used to describe situations where one is forced to choose between two unattractive alternatives. Reconstructing the preformationist claim of the time, Gould (1977) wrote:

> [we] know that the tininess and transparency of the embryo and the crudeness of our instruments preclude any direct observation of what is really there in early stages of ontogeny; we must therefore either accept the epigenetic evidence of our raw senses or postulate what we cannot yet perceive. If we choose the former course, we avoid the *Scylla* of unseen entities but confront instead the *Charybdis* of a general theory that substitutes mystical forces for the mechanics of Newtonian science (p. 21).

Again, it is important to note that epigeneticists were not mystics. They did not deny that organisms were entirely material bodies, what they claimed was that some other force seemed to operate in living systems. Although these factors were an abstract concept; epigeneticists were not able to say exactly what they were and how they operated.

This kind of vitalism was advocated, for example, by Caspar Friedrich Wolff in his dissertation *Theoria generationis* (cited in Rádl 1988). For Wolff, the *vis essentilist* was a force which pulled the embryonic matter in different directions and with different velocities. This force, together with the tendency of organic matter to solidify, generated the form of the organism. This vital force was quantitatively and qualitatively different between species. Differences in the vital force explained differences in form between species (see Rádl, 1988). Probably it would be easier to understand this theory if we take into account that the epigeneticists did not know that organisms are made of cells; rather they saw a gelatinous homogeneous mass that took shape during development.

For epigeneticists, the *vis essentialis* is that which *gives form* to the organism during its development, it is a generative force. For Wolff, the generation of form was a law-like process; consequently, scientists should be able to explain the final forms resulting from development by investigating the laws governing this process. This vitalism is quite different from the animistic vitalism defended by Georg Ernst Stahl in his *Theoria medica vera* (cited in Ráld, 1988), a German chemist and physician influenced by the Cartesian dualism between the immaterial soul and the material body. For Stahl and the Cartesians the body is like a machine, and it is already constructed when a non-material force operates making it a living entity. This version of the *vis essentialis* is not a generative force; it is like a breath that gives life to a non-living machine.

Epigeneticists were called vitalists since the idea of an inner force driving morphological change has always had a mystical connotation, also because they were not reductionists. Any conception of organisms as whole systems not reducible to their components has been associated with the unscientific idea of a non-material force [4].

Preformationism implied that only one of the progenitors provided the germs for the following generation; for this reason, there were both ovist and spermists among this group. As the form of the offspring was already contained into one of the progenitor germs, the other progenitor only stimulated or nurtured the *homunculus*, favoring its unfolding. Preformationism thus precluded the needed for a theory of heredity. That is, preformationists were not interested in parent-offspring similarities since trait characteristics were already defined in the germ.

The fact that offspring showed resemblances to both parents was used by epigeneticists to refute preformationism. If form in the offspring varied it was because form was not preformed in the germ.

Heredity is parents-offspring resemblances. This means that heredity is the passing of *form* from one generation to the other and that it is a two-stage process: 1) the transmission stage: from the adult (parent) to the egg; 2) the generative stage: from the egg to the adult (offspring). In the first stage, parents mate to produce the embryo and in the second one, the embryo takes its form. During this pre-evolutionary era, heredity compressed the two stages. For epigeneticists, what was transmitted from generation to generation were not the parental traits, but the *vis essentialist*, the inner force responsible for generating body form. Heredity was an epigenetic process (Amundson 2007) (See the figure at the end of the article).

1.2. THE CONTROVERSY BEGINS

1830. An historical moment was to take place at the *Académie des Sciences*, Paris. During the weekly meetings organized by the *Académie*, two of the most eminent zoologists of the day, Georges Cuvier and Étienne Geoffroy Saint-Hilaire, debated before an expectant public their different views concerning the study of form. As pointed out by Appel (1987) there are several interpretations of what was the essence of the debate. It appears there were several issues at stake, some of them beyond the biological field.

The Cuvier-Geoffroy debate is usually interpreted as addressing the problem of the relation between form and function (Rusell 1916): Is form prior to function, i.e., is the structure initially construed under the guidance of some natural laws and afterward put to use, or is function prior to form, i.e., is the structure just the result of the function it performs?

The function-follows-form position was defended by Geoffroy. He focused his attention on the regularities we can observe across taxa. These taxa exhibited different life styles and lived in different environments, so these regularities could not be explained in functional terms. They rather implied the existence of laws underlying the construction of organisms' *bauplans.*

The regularity of form ranges from similarities relatively easy to recognize, e.g., the segmental body plan of arthropods, to that harder to discern owing to extensive functional differences, e.g., the similarity between parts of fish jaws and gill arches and the ossicles of the inner ear in mammals. Geoffroy defended the existence of an underlying unity of organismal design—the Unity of Type—and his scientific commitment was to discover this unity through the study of the empirical regularities of biological form.

Cuvier held the form-follows-function position. He claimed that structure could be explained in functional terms. Cuvier defended a functionalist position, as later Darwin did, but as his emphasis was on the internal relationships between organs which constitute the organism as a whole, he distinguishes only four possible plans (Russell 1916). In contrast, Darwinists have conceived organism as an aggregate of traits (Gould and Lewontin 1979).

In Cuvier's view, these four plans were the only possible combinations. Any alteration of a plan is inconceivable, since it would break the functional harmony of the whole. According to Cuvier, the four plans were designed by God, and he used this argument against the idea of the transmutation of species (also part of the debate). Geoffroy defended the position that that different *bauplans* could be transformed one into other, supporting the idea of transmutation.

As noted by Appel (1987), the conflict between facts (positivistic empirical science) and ideas (rational science), also permeated the environment of the hall of the *Académie*. Geoffroy's morphological programme of 'philosophical anatomy' defended the centrality of ideas and the importance of synthesis. His interest in the 'unity of plan' and the search for natural laws attracted Goethe's attention, one the founders of the *Naturphilosophie* movement. For Goethe, form must not be conceived as static, but as a dynamical phenomenon: "...he was very far from the static conception of life which is at the base of pure morphology. His interest was not in *Gestalt* or fixed form, but in *Bildung* or form change" (Russell 1916, p. 49). Russell continues: "Form is of interest not in itself but only as the manifestation of the inner activity of the living system. Over development, he [Goethe] says elsewhere, there presides a formative force, a *blidende Kraft* or *Bildungstrieb*, which works out the idea of the organism" (p. 50).

The problem of whether or not there are organizing principles governing the generation of form is a very old one. Discussing this relationship, Bateson (1972, cited Emmerche and Hoffmeyer 1991) traced the roots back to Pythagoras:

> This statement came out of a very wide range of philosophic thinking, going back to Greece, and wriggling through the history of European thought over the last 2000 years. ...It all starts, I suppose, with the Pythagoreans versus their predecessors, and the argument took the shape of 'Do you ask what it's made of—earth, fire, water, etc.?' Or do you ask, 'What is its pattern?' Pythagoras stood for inquiry into *pattern* rather than to inquiry into *substance*. That controversy has gone through the ages, and the Pythagorean half of it has, until recently, been on the whole the submerged half (p. 449).

Webster (1996) discusses the continuity of Aristlotle's concepts *eidos* and *hyle* and modern biology:

> While *eidos*, according to Grene [1974], is a single, univocal concept, it is used by Aristotle in two apparently different contexts. In the first, where the sense seems to be relatively straightforward, *eidos* is contrasted with *hyle*; form as against matter ...In the traditional example of Socrates' nose, snub is the form of the matter: flesh and bone. But at another 'level', bone is the form of whatever elements compose it—earth and fire, say. As Grene notes, in this context, the concept of form functions in much the same way as the concept of organisation in modern biology. The form of an entity or process denotes its principle of organisation. Thus, systems which lend themselves to analysis in these relative terms have a double aspect. On the one hand are the 'laws' or constraints arising from the nature of the material elements of which the system is composed; on the other, the 'laws' or constraints that arise from the order or 'arrangement' of these elements (p. 3-4).

When substance is featured, pattern is not conceived as a real entity demanding an explanation, but as a by-product of substance (composition), and consequently, it is denied that there are principles of organization that govern the generation of form. That is, it is assumed that pattern can be reduced to substance.

When pattern is chosen, the two aspect of an entity are considered and it is held that pattern cannot be reduced to substance. This is a holistic position: "A form-matter analysis is, therefore, antireductive in the sense that it denies that systems of the relevant kind can be completely understood in terms of the elements of which they are composed" (Webster, 1996, p. 4).

Darwinism is a theory of substance (composition). This is quite clear from the way Darwinists deal with morphogenesis (they are commented upon later). Denying the existence of any organizing principle of structure, the agency of the generation of form is placed in the genome (their products, i.e., composition). What follows from this is a gradual elimination of any agency (generative capacity) in the living matter so as to enable natural selection to work as the creative factor in evolution. The result is a gradual reduction of morphogenesis to genes, i.e., the exclusion of development from evolutionary biology, that is, the loss of its dynamical component, the denial of the existence of organizing principles, the loss of structure as a real entity... the loss of the organism.

2. A THEORY OF FORM BASED ON NATURAL SELECTION

2.1. LOSING THE ORGANISM

At the beginning of the nineteenth century, Lamarck presented the first elaborated theory of evolution in a series of works, *Philosophie zoologique* (1809) being the most famous of them [5]. According to Lamarck, organisms are capable of changing their habits in relation to variances in the environmental conditions. These altered habits can produce a morphological change if they are sustained over a certain period of time. Then, Lamarck proposed that the morphological changes the organism has acquired during its lifetime can be passed to its offspring. An extended course of this process would explain the transmutation of species.

That organisms can alter their morphologies during their lifetimes is a fact and there was also some indirect evidence that some of these changes could be passed to the offspring, as the presence of callosities on the knees of ostriches (Waddington 1957). Despite the fact that Lamarck theory was a natural explanation, the use of some terms as *sentiment intérieur* [6] to refer to this direct relationships between the environment and the morphological changes were open to charges of vitalism.

At this time, Darwin was developing his theory of natural selection. Darwin agreed with Lamarck's idea of the transmutation of species. And as Lamarck's theory of inherited characters, Darwin's theory was only focused on explaining adaptations (the fitting of traits to environmental conditions [7]). The existence of adaptations was a long-recognized fact of central importance to biologists of the time, yet the only explanation available was a supernatural one. Natural Theologists used the existence of adaptations to develop the 'argument from design', considered the most important theological argument for the existence of God. Anyhow, Darwin strongly disagreed with the mechanism proposed by Lamarck:

> I am almost convinced (quite contrary to opinion I started with) that species are not (it is like confessing a murder) immutable. Heaven forfend me from Lamarck nonsense of a 'tendency to progression', 'adaptations from the slow willing of animals,' etc.! But the conclusion I am led to are not widely different from his; though the means of change are wholly so (in F. Darwin 1887, volume 2, p. 23, cited in Gould 2002, p. 175).

Darwin's theory of natural selection avoided the necessity of this *sentiment intérieur*, avoiding the 'weak point' of Lamarck's theory. He believed he had found "the simple way by which species become exquisitely adapted to various ends" (Gould 2002).

Darwin observed that offspring exhibited innate differences from parents and from each other. His mechanism was developed on the basis of this observation. If some innate variants could appear at any generation, if these variants differ at least slightly in the performance of some vital functions, and if there are many more newborn than can probably survive, the death of the unfit and the preservation of the fittest at any generation, i.e., the mechanism of natural selection, could mould organisms though evolution.

Darwin did not deny the capacity of organisms to adapt to their environments during their life cycles, but he gave more importance to innate variations and their sorting as an evolutionary mechanism [8]. He studied the variation related to use and disuse in domestic animals, and he accepted the inheritance of acquired characters because it was the common idea at this time, not a special feature developed by Lamarck to support his evolutionary theory.

Darwin argued that the two processes could operate at the same time, but that the mechanism of natural selection dominated:

> On the whole, I think we may conclude that habit, use, and disuse, have, in some cases, played a considerable part in the modification of the constitution, and of the structure of various organs; but that the effects of use and disuse have often been largely combined with, and sometimes overmastered by, the natural selection of innate differences (p. 143).

This is the same strategy that adaptationists later used to defend the primacy of natural selection in evolution:

> In natural history, all possible things happen sometimes; you generally do not support your favored phenomenon by declaring rivals impossible in theory. Rather, you acknowledge the rival but circumscribe its domain of action so narrowly that it cannot have any importance in the affairs of nature. Then, you often congratulate yourself for being such an undogmatic and ecumenical chap. We maintain that alternatives to selection for best overall design have

> generally been relegated to unimportance by this mode of argument (Gould and Lewontin 1979, p. 151).

During this time, the idea of heredity as a force was gradually replaced by the idea of heredity as a particulate material (Gayon 2000). Darwin contributed to this transition with his *Variation of Plants and Animals under Domestication* (Darwin 1868). Consistent with the conception of heredity as a force, it was argued that it changed its intensity with time: "the longer the trait had been transmitted without crossbreeding, the more powerful its hereditary force became" (Gayon 2000, p. 71). Darwin pointed out that breeders and horticulturists had observed that new traits could both rapidly be fixed or not transmitted at all. Furthermore, traits that did not pass to the following generation could reappear in the following one. According to Darwin, the constancy of a specific character was not related to how long it has persisted in a population, but with the interactions that could emerge when other variants arose.

These observations seemed to be in accordance with the idea of a particulate conception of heredity. Darwin indeed proposed a particulate theory of heredity called "pangenesis." The basic idea was not new, being previously proposed by the ancient Greeks (Terrall 2002). According to this theory, cells from different body parts were capable of producing 'gemmules', which contained 'miniature representatives' of them (Jablonka and Lamb 2000). These gemmules circulated in the blood and some of them were used to regenerate body parts. Gemmules from different body parts are stored in the reproductive cells and transmitted to the next generation.

The gemmules present in the egg were not organized in any precise way. The organization of these gemmules to form an organism took place during development.

This is another version of preformationism, or more precisely something in between preformationism and epigenesis. This time it is not the whole and completely organized organism that was passed on, but its parts contained in the gemmules. The forms of body parts are already present in the egg (as gemmules) and during the transmission stage these preformed pieces are passed onto the offspring. Still, some assembly is needed to generate the organism, and this took place during the generative stage. Here development was also a component of heredity (Amundson 2007).

2.2. LOSING THE ORGANISM A LITTLE BIT MORE

There was a great inconsistency in Darwin's proposal. Like most scientists of the time, he accepted the inheritance of acquired characters; yet this theory of inheritance is incompatible with the idea of natural selection as an organizing factor.

If individuals are capable of acquiring the optimum "trait values" for a specific environment during their lifespan, all of them will be well adapted to the environmental conditions and so could leave similar numbers of offspring, which would be independent of the trait values they exhibited when newborns. Here, there is no selection which preserves the fitter to specific environmental conditions and eliminates the unfit (i.e., those which perform their vital functions in a less efficient way). All of them are equally fit [9].

There can be a sorting process if there are more organisms than can survive, but in no case would this sorting process mould the phenotype. Natural selection could not be a creative factor—an organizing principle of living matter—if organisms are constructed in such a way that they can respond in a sufficiently active fashion to environmental changes (i.e., exhibit phenotypic plasticity [10]). This is why heredity, a marginal issue in the pre-evolutionary stage, now occupied a central role in the biological sciences. The nature of heredity would decide which of these two evolutionary theories was correct. And because development was a component of heredity, the problem of form arose again. But now (at the evolutionary stage), there would be attempts, in the form of the Darwinian programme, to resolve the problem by the mechanism of natural selection.

Weismann's theory of development was a way of resolving the incongruence in favor of natural selection. Again, Lamarck's theory was not refuted empirically. It is well known that Weismann carried out some experiments cutting off mouse tails to disprove the inheritance of acquired characters. But as Gould pointed out, these experiments "did little to combat Lamarckism, which is, as supporters parried, a theory about the inheritance of functional adaptations, not of sudden and accidental mutilations" (p. 201). Gould stressed that this was admitted already by Weismann. Weismann's rejection of Lamarckism was instead a logical deduction from his theory of development (Gould 2002).

Some important discoveries in the new field of cell biology inspired Weismann's theory of development. Firstly, it was recognized that organisms are made of cells and that cells come only from other cells. This already made implausible the theory of pangenesis, the idea that gemmules coming from any part of the organism could enter in the gametes (Jablonka and Lamb 2000). It was also discovered that cells had a nucleus which contained some filaments (later called chromosomes). And it was discovered also that cell divided by mitosis, where the filaments were replicated and each cell received one copy of each. The observation of chromosome duplication and distribution of a copy to each cell raised the possibility that chromosomes were the material bearers of form.

Weismann defended a mosaic theory of development. According to this theory, the fertilized egg possessed hereditary particles in its nucleus which contained all the information needed to reproduce the organism (this was called the 'germ plasm'). Cellular division during development unequally distributed these determinants between cells. Then, cell differentiation was the result of the unequal division of the germ plasm during development.

Roux advocated this theory as well. He had obtained experimental evidence in support of this hypothesis. Roux killed one of the two blastomeres of frog embryos with a hot needle. He observed that only half of the embryo was developed at the neurula stage. This observation supported the mosaicist idea that specific somatic cells only contained part of the germ plasm and then, they were not able to form body parts normally generated by other cells.

But if differentiated somatic cells contained an incomplete set of these determinants, how is possible to reproduce an organism in the next generation? The only answer to this question was that early in development, some cells with still a complete set of determinants are sequestered (encapsulated) and then protected from any alteration other parts of the organism could experience (these cell were called the germ cells). By this way, nature assured the reproduction of new organisms in the next generation.

Weismann found some empirical evidence supporting his logical deduction from the mosaic theory of development. He observed that during the earliest stages of *Drosophila* development the first embryonic cells to form, by covering with membrane the nuclei of the posterior pole of the syncytium, will become the reproductive cells (Goodwin 1994).

The sequestration of the germ cells is what made the inheritance of acquired characteristics impossible. Note that Weismann did not deny that organisms can respond directly to their environmental conditions; this was a fact that could be not avoided. What he argued was that Lamarckism (inheritance of acquired characters) was logically impossible under the hypothesis of the germ plasm. Again, Weismann's preference for his theory was despite the fact that some phenomena were better explained by the alternative theory.

Thus, the idea that form is contained somehow in hereditary particles was retained in the theory developed by Weismann [11], revealing the influence of Darwin's theory of inheritance. But now what was defended was still another version of preformationism. It was not assert that the nucleus contained a miniature representation of the organism; it was claimed that hereditary particles possessed the instructions to reproduce a whole organism. This privileged the mechanistic conception of living matter as a passive agent. The form of the organism is completely determined (preformed) by the hereditary particles carried in its germ plasm.

The body (the soma) is no more than the vehicle of transmission of these particles to the next generation.

Weismann's doctrine of the germ plasm allowed natural selection to be the creative factor in evolution, providing the mechanistic explanation of form; this was called Neo-Darwinism.

These hereditary particles determine differentiation. Still, as in Darwin's theory of pangenesis, the final form of the organism came into being during development, where the characteristic distribution of these determinants was established. Thus, development was a component of heredity in the Roux-Weismann mosaic theory (Amundson 2007).

But what governs development? Roux was explicit regarding the cause of development. According to him, differential growth was an adaptation that arose by the action of natural selection (Russell 1916, p. 331). However, where is this developmental information 'stored' if the hereditary particles just contain information to make the organism's trait? (As we will see, the discovery of DNA structure provided a supposed explanation.)

The alternative to mosaic development was the regulative theory defended by Driesch. For Driesch, in no way was form predetermined in the embryo. For him, the self-regulation observed in the embryo so as to form a whole organism after the removal of part of its material, could not be explained in mechanistic terms. In particular, there is no machine that remains a whole after the removal of some of its parts.

Driesch had experimental evidence in support of his hypothesis. To the astonishment of mechanicists, he obtained a whole sea urchin larvae from blastomeres separated at two and four-celled stages. He presented a series of arguments against the mechanistic (mosaic) theory of development and argued that another causal factor must be operating in livings beings, which confers on them the property of 'wholeness' and makes them different to machines.

Unfortunately, the alternative again was tainted with the mystical halo of vitalism. Driesch called this other causal factor 'entelechy,' asserting it to be 'natural,' though not a form of matter or energy. Entelechy was proposed to order matter, to be the cause of development.

By the end of the nineteenth century it had been demonstrated that there was not a differential division of the nuclear material; all cells contained the same amount. This fact was inconsistent with the mosaic theory of development. Despite this, the roots of the mechanistic paradigm grew deeper well into the new century and the alternatives were abandoned. Mechanicism has remained the dominant paradigm in biology and the alternative theories are seen as old-fashioned and irrelevant at present.

During the last seventy years the usefulness of this approach has been clearly reflected in the great advances of molecular biology such as the elucidation of the structure of the DNA, the genetic code, the mechanism of protein synthesis and the function of many proteins.

2.3. LOSING THE ORGANISM DEFINITIVELY

The elimination of development as a component of heredity and, consequently, its exclusion for the study of evolution, is attributed to Morgan (Allen 1986; Amundson 2007; Robert 2004; van der Weele 1999). In previous years, geneticists studied the transmission stage of heredity, and embryologists the generative stage, and it was generally accepted that heredity was composed of these two components.

Anyhow, once divided, the study of these two stages and the coining of names for the resulting fields: 1) genetics, the study of transmission genetics (Mendelism), and 2) developmental genetics, the study of the physiological action of genes in embryogenesis (Morgan 1926, cited in Amundson 2007, p. 151), a strong competition arose among researchers about which field was more relevant for the study of evolution (and worthy of being financed). And the rivalry was translated to a competition for the term 'heredity'.

This "struggle for power and authority" (Sapp 1983 p. 312) was won by the geneticists. Then, as pointed by Amundson (2007), the new definition of heredity as transmission genetics was a stipulation, not a decision based on empirical observation.

Morgan, a previous advocate for the importance of developmental mechanisms in the generation of form, was gradually convinced by the experiments carried out by Mendel, that the genes directly determined an organism's traits. He agreed that complex developmental processed took place during embryogenesis, but seems to have thought that, in some way, genes governed these processes. In this case, it would be rightly said that genes were the cause of form (Amundson 2007).

This idea was called the genetic programme for development [12]. This hypothesis definitely put the agency to construct an organism entirely in the genome; it purportedly contains information both about how to construct body parts and how to organize them: "DNA provides the programme which controls the development of the embryo and brings about epigenesis" (Wolpert 1991).

Developmental mechanisms are needed to obtain the end product but these mechanisms are governed by genes. Therefore, development is no more than another trait that could be molded by natural selection to generate optimal reproductive machines.

Again, Morgan's preference for his definition of heredity was a choice, not an objective decision determined by empirical facts: "Morgan kept the disciplines of genetics and embryology officially separate, securing funding for the former and helping to establish its central position in American biology" (Robert 2004, p. 60). It is important to mention also that he did this for pragmatic reasons (Allen 1986). The study of development has always been a very complex enterprise, and the success of genetic experiments with *Drosophila* surely made it a more attractive research line for scientists than *Entwicklungsmechanik* (developmental mechanics) at the beginning of the twentieth century.

At this time, genes were still hypothetical entities, so Morgan did not explain how genes managed to control development. However, his decision to privilege the study of transmission genetics was astonishingly influential and triggered the flourishing of this new field and the associated gene-centred view in evolutionary biology that still prevails.

Later in the century, this arranged cleavage between development and heredity, was followed by a serious (empirically based) attempt to exclude development from the study of evolution.

3. THE GENETIC PROGRAMME FOR DEVELOPMENT

3.1. THE GENETIC PROGRAMME VERSION 1.0

The discovery of the genetic code during the 1950s and 1960s (Depew and Weber 1996) gave material identity to Weismann's hereditary particles (de Vries' pangenes, Johansen's genes) reinforcing the mechanistic explanation of form. These particles were identified as segments of DNA. The explanation already formulated by Weismann remained the same, but actualized using new terms. Now, the idea was that form is encoded in the DNA sequence. These segments of DNA coded for proteins and proteins regulate the organism's metabolism, and thus all biological processes. In effect, it was assumed that different DNA sequences produced different proteins which produced different forms.

In the Roux-Weismann theory, development was a component of heredity, so that developmental processes caused the differential division of the germ plasm, distributing the trait's determinants in the right way and finally producing the organism. This theory, having been disproved (see above) led to a paradox: If all cells contain the same genes, how is possible that genes could explain the differentiation of body parts? This was called the "developmental paradox."

A possible solution to the paradox was presented by de Vries in his book *Intracellular Pangenesis* (1889). The empirical data in support of his idea came approximately a century later, with the publication of the *lac operon* model by Jacob and Monod (1961).

De Vries postulated that all cells contain all the particles needed to make an organism, but just some particles migrate from the nucleus to the cytoplasm where they are expressed. Thus, the formation of different body parts would be explained by differential expression of the same nuclear content.

Jacob and Monod offered a mechanism by which differential expression of genes took place. They discovered that there exist genetic sequences with different functions and that these sequences work together as a unit to regulate the expression of specific genes. They described the unit involved in the synthesis of three proteins related to the metabolism of lactose in *Escherichia coli*, calling this genetic unit the *lac operon*. This operon is composed of two promoters, one operator and three structural (protein-coding) genes. Two different molecules facilitate the expression of the three structural genes, binding to their respective promoters. A third molecule, a lactose repressor, binds to the operator sequence interfering with the binding to one of the promoters, and consequently, repressing transcription. Other substances are capable of interacting with these binding molecules, promoting or repressing transcription [13].

The result is that the expression of the structural genes can be turned on and off according to the presence or absence of different molecules.

Then, they suggested that the operon model of genetic regulation could resolve the developmental paradox and that the genome contained both the blueprint and a programme to run it: "The discovery of regulator and operator genes, reveals that the genome contains not only a series of blue-prints, but a co-ordinated programme of protein synthesis and means of controlling its execution" (Jacob and Monod 1961). This view makes biology into a subdivision of chemistry (Salthe, pers. comm.).

How is form generated? The idea is that materials produced by genes have inherently the specificity required to self-assemble the different constituents of the organism: from the lowest level (protein folding) to the uppermost level (formation of organs). It is very important to note that self-assembly and self-organization are two different processes of pattern formation (Halley and Winkler 2008). The major difference is that self-assembly is a process tending towards thermodynamic equilibrium, where self-organization take places in systems far form equilibrium. Whereas self-assembly is a phenomenon long time recognized, self organization was demonstrated in the eighties [14].

Then, it was proposed that self-assembly would explain: 1) the development of an organism, specifically cells from different regions of the embryo, with different sets of active genes, produce different sets of substances that generate the different body parts, and 2) the morphological differences between species, specifically different species posses different genes which produce different substances responsible for forming different organisms (or different amounts of the same substances).

Morphogenesis is held to be like a crystallization process: "Monod's text [15] is very explicit about the causal logic involved in the view of organisms as genetically directed self-assembly systems. For him, they are 'chemical machines' whose structure is generated by a process 'strictly comparable to molecular crystallization'" (Webster and Goodwin 1996 p. 132).

3.1.1. ARE ORGANISMS LIKE CRYSTALS?

The fundamental assumption behind this theory is a one substance-one form relationship:

> Monod makes it quite clear that genetic determination requires that the structure generated at each level of the hierarchy [of the organism] be uniquely specified by the properties of the constituents at the lower level, so that any form is causally reducible to the primary protein structure of its constituents and hence to the historically given information in the nucleic acid sequence of the DNA" (Webster and Goodwin 1996, p. 132-133).

Curiously the assumption is not true even for inorganic matter. It is well known that diamond and graphite have different structures (and properties) but both are composed by the same substance, carbon. And it is not true at the most fundamental level in cells. The three-dimensional structure of a protein (which confers its function) is not uniquely determined by its amino acid sequence (and the corresponding DNA sequence), but is dependent on the context in which the protein is synthesized (see Newman and Bhat 2007b for a review of this topic).

And neither is it true at higher levels of organization. *Samonella* flagellum can exhibit two different morphologies, wavy and curly; yet these two morphologies are not explained by differences in composition: the two morphs are composed of the same protein, flagellin. The wavy and curly forms of the flagellum are thus not encoded in genes (see Goodwin 1996, chapter 6, to see examples at higher levels of organization).

Of course, genes are important to morphogenesis in specifying many of the necessary substances, but they are not sufficient to explain form. Nijhout (1990) provides a useful way for thinking of the role of genes in development:

> The most generally useful hypothesis about the function of genes is the following: Genes are passive sources of materials upon which a cell can draw, and are part of an evolved mechanism that allows organisms, their tissues and their cells to be independent of their environment by providing the means of synthesizing, importing, or structuring the substances (not just gene products, but all substances) required for metabolism, growth and differentiation (p. 444).

The foregoing examples concern one-to-many relationships. Examples in support of the other alternative, the many-to-one relationship, also exist. In these cases, differences at the lower level do not generate differences at the higher level, also negating the idea of morphogenesis as a crystallization process.

Forgacs and Newman (2005) provide a very interesting example from the inanimate world. Pseudomorphs are minerals in which the molecular constituents that determined their structure have been replaced by others over time, leaving the original structure intact. So the "same" structure can be composed of different substances.

In a simple non-morphological trait, coloration, the relation between genes and phenotype is less than direct. In three species of the genus *Drosophila*, differences in the melanin pigmentation pattern were correlated with expression pattern of the gene *yellow* (yellow protein is required to produce black melanin). However, differences in coloration in other two species of the same genus were unrelated to expression of this candidate gene, but rather with the gene *ebony*, which is involved in the production of yellowish pigment and reduces the production of black melanin. These results also showed that there are other genes implicated in the pigmentation pattern (Wittkopp, et al. 2010)

Similar melanic patterns may involve different genes, and the same genes can be involved in different patterns. There is no specific gene coding for a specific color but several gene products are components of a complex dynamical process from which the phenotype emerges.

3.1.2. OTHER CONSIDERATIONS

The idea that the DNA contains the essence of life led to the organization of billion dollar projects for gene sequencing, like the Human Genome Project (Delisi 1988, cited in Webster and Goodwin 1996, p. 83).

If DNA sequence explains morphological diversity, as suggested, it would be expected that different organisms contain different DNA sequences and that more complex organisms have a larger number of genes, so that a larger number of proteins could construct a more elaborate morphology. In consequence, comparisons between genomes of different species would show both that more distant species have more divergent genomes than close related species and that simple organisms possess fewer genes than complex organisms.

One of the first surprises of the molecular revolution was the discovery that an enormous percentage of the DNA—as much as 95 per cent—did not code for proteins[16]. These sequences were originally called 'junk DNA', since it was thought that these non-coding sequences had no role in explaining morphological diversification.

The first comparisons between human and chimpanzee proteins showed that amino acid sequences were often essentially identical, for example, a comparison of 2 633 amino acid sites from 12 relevant proteins, showed a difference of only 0.007 per cent (King and Wilson 1975, table 1). Thus, it seemed that morphological difference could not be explained by differences at the molecular level:

> We suggest that evolutionary changes in anatomy and way of life are more often based on changes in the mechanisms controlling the expression of genes than on sequence changes in proteins. We therefore propose that regulatory mutations account for the major biological differences between humans and chimpanzees (King and Wilson 1975, p.107).

Comparison at the DNA level between humans and mice showed that 99 per cent of the 30 000 protein-coding genes estimated for these two species are homologous (Waterston, et al. 2002), reinforcing the conclusion suggested by King and Wilson (1975).

In reference to the relation between genome size and morphological complexity, the results were astonishing. The number of genes of the human genome was estimated in 31 000, a modest number in comparison with previous estimates (around 140 000 genes). Human genome remained the genome with higher number of genes, but humans were just 5 000 genes ahead of the genome of the tiny plant *Arabidopsis thaliana* (Hahn and Wray 2002).

These results did not support the idea that form is encoded in the DNA sequence. The discoveries suggested, instead, that the organization of the genome is more complex that it was previously supposed. The explanatory basis was changing from the structural genes to the control of their expression. It now appeared that much of the non-coding genetic material, so-called 'junk DNA' could be devoted to regulating the expression of other genes during development and, therefore, turn out to be a major player in evolution.

3.2. THE GENETIC PROGRAMME VERSION 2.0

Composition does not specify form, so it is necessary to postulate some mechanism by means of which cells are arranged in determinate forms. A reformulation of the genetic programme idea which takes this new factor into account is the theory of 'positional information' developed by L. Wolpert [17] (1969, 1971). According to this author, the embryo is divided into a series of regions in which a coordinate system is set up. The coordinates provide information which is interpreted by a cell to determine its fate. The coordinate system is generated by a system of chemical gradients, the chemicals themselves being referred to as 'morphogens'. Each dimension of the space is defined by a specific substance. Positions are specified by the identity and quantity of the chemicals.

The most distinctive feature of the model is that while the morphogens are used to set up the coordinate system, their pattern does not reflect the final result (they have no causative power in the generation of form). The fate of each cell resides exclusively in the genome. This can be described in terms of the schematic example proposed by Wolpert, "the French flag model."

Imagine a one-dimensional row of cells. These are totipotent cells that can become red, white or blue. How is possible to generate the specific pattern of the French flag? A chemical gradient (just one because we have one dimension) is generated along the cellular row by diffusion, with a continuous range of values from one extreme to the other one. The color exhibited by the cells (and the resulting pattern) is determined by the genome, which is organized so that it responds to values along the continuous gradient in a discontinuous (i.e., threshold-sensing) fashion. For example, cells become red at a concentration equal to two units, white at concentrations equal or higher than one unit and lower than two units, and blue at a concentration lower than one unit

According to Wolpert's original formulation, positional information is universal; it is the same in all organisms and in different regions of the same organism. Differences between organisms are due to different interpretations (genomes) of the same universal coordinate system. Thus, if we want to generate a red-white-red pattern, cells should be programmed to generate red at concentrations equal to two units or lower than one unit, and white at concentrations equal or higher than one unit and lower than two units.

The new pattern cannot be due to a difference in the chemical gradient (e.g., a concentration described by a parabola where the two extremes present the same concentration). Here, the same array of cells would generate the two patterns.

The model of positional information becomes very complex if we want to repeat the same feature several times along the gradient, e.g., to generate a row of alternate red and white spots. This happens since to repeat the same feature in different places it is required that a complex schema of concentrations and cellular responses should be set up.

The pattern formation problem can be simplified enormously if it is assumed that the gradient, rather that imparting "information," determines the formation of the pattern in a more direct manner. In the case of repeated structures—a common feature in organisms—Turing's reaction-diffusion mechanism can generate a series of spots of morphogen concentration, so only one threshold value is needed to generate the pattern (Turing 1952). The usefulness of this model in development structures has been extensively demonstrated (Meinhardt and Gierer 2000; Forgacs and Newman 2005; Newman 2010; Newman 1994; Sick, et al. 2006; Newman and Bhat 2007a; Kondo and Miura 2010).

Assuming that the chemical gradient can determine the pattern means that the physico-chemical laws governing the process influence the generation of form, depriving the genome of its assumed supremacy. The "positional information" model, in contrast, puts most of the burden for arranging cells in a specific manner on the genome, safeguarding the supremacy of genes in the explanation of form [18].

3.3. THE GENETIC PROGRAMME VERSION 3.0

The existence of regulatory genes associated with large phenotypic changes was proposed by Goldschmidt (1940) during the early years of the Modern Synthesis. The idea was strongly rejected by evolutionary biologists as large mutations deprived natural selection of its power to mould the organisms (this was called ′saltationism′). Mutations must be "copious", "small in scope" and "undirected" (Gould 1982).

In the 1980s, a new class of developmental regulatory genes [19] was discovered; they were called the *Hox* genes. These genes are involved in the formation of body plans, specifically, the formation of anterior-posterior body axis and segment formation. These genes are defined by the presence of a sequence, the homeobox, which code for a protein domain, the homeodomain. The homeodomain is the region of the protein that binds to the DNA molecule.

This discovery gave new impetus to consider the existence of a genetic programme for development, now contained in the regulatory sequences of these genes.

Under the expectation that different body plans were constructed by different regulatory programmes, distant species should have more divergent homeotic sequences than close related species. However, homeotic genes are astonishingly conserved across phyla (Lemons and McGinnis 2006), as are their functions. The conservation is such that they can be interchangeable between distant taxa: "Only a jaded biologist could not be astonished at the ability of the Pax-6 Hox gene from mice (which triggers eye formation) to induce in the fruit fly *Drosophila* the formation of fly eyes all over the body, even on the wings" (Coyne 2005, p. 1029).

This led to a new version of the developmental paradox: If different body plans are constructed by similar homeotic genes, how can we explain this morphological diversification?

The answer proposed was that this diversity is explained by changes in the switches that control gene regulation (Carroll 2008; Carroll 2005; Marshall and Valentine 2010; Davidson and Erwin 2006). That is, the coding sequence of transcription factor-specifying genes have been conserved but the promoters where their products bind have changed (not their sequences, but their location, that is, the downstream genes which have the corresponding promoter). Changes in the switches imply changes in the wiring of the genetic network, which could mediate the corresponding changes in body plans.

This focus on gene regulatory logic is part of a new and fast growing discipline known as evolutionary developmental biology or Evo-Devo (Arthur 2002; Gilbert, et al. 1996).

There is an alternative called the 'physicalist perspective' (Newman, et al. 2006; Newman and Müller 2010). Before we explore this alternate, I will comment to a relevant discovery in physics that took place during these hectic years in the pursuit of the 'book of life' in the DNA sequence and which has provided a solid physical background to the alternative.

4. A THEORY OF FORM BASED ON SELF-ORGANIZATION

4.1. RECOVERING THE 'INNER FORCE'

During the second half of the nineteenth century, the theory of evolution seemed to be in contradiction with the Second Law of Thermodynamics, This Second Law predicted that the universe should move towards a state of homogeneity where all free energy gradients will dissipate, while evolution contrarily implies an augmentation of complexity from the unicellular to the higher organisms.

Schrödinger (1944) showed that this was not a real problem since the prediction referred to close thermodynamically isolated systems, those that do not exchange matter or energy with their surroundings.

During the 1970s and 1980s, Prigogine and co-workers showed that the Second Law was not only compatible with evolution, but helped explain it.

In certain open systems [20] far from a thermodynamic equilibrium [21], there exists a threshold in a system's defining parameters at which the system is unstable. Above this threshold, a self-organizing process takes place and systems adopt a different configuration. The new structure causes the system to dissipate energy more efficiently by way of convection. Thus, the production of order is causally related to the Second Law of Thermodynamics. These self-ordering structures are called by Prigogine "dissipative structures" (1980).

Organisms are such systems. They are open systems far from equilibrium, which sustain complex structures by a constant exchange of energy and matter with the environment. This implies that organisms are active agents capable of can self-organize intrinsically without the intervention of an *external organizing principle*, to exhibit "order for free" (Kauffman 1993).

Finally, the inner force which has accompanied the alternative to the Darwinian model has been characterized. Self-organization is present in both the animate and inanimate realms and accusations of vitalism lose their sting.

The phenomenon of self-organization is so prevalent in nature that evolutionary biology can no longer avoid it (Meinhardt and Gierer 2000;

Solé and Goodwin 2000; Kondo and Miura 2010). The question is: How might self-organization and natural selection be related?

There are seven possible relationships between self-organization and evolutionary theory (Weber and Depew 1996; Swenson 2010). These positions can be ranged from those that assert that only one of these factors drives evolution—the extreme positions—passing through an intermediate point represented by those that accept the importance of both factors but not in equivalent degree (one a cause, the other a constraint), to those that assert that both factors are equally important to explain evolution.

But a close examination of the possibilities seems to lead to a conclusion. According to Batten, et al. (2008) "Self-organization proposes what natural selection disposes" that is, self-organization, not natural selection, is the creative factor in evolution.

4.2. THE DEEP DICHOTOMY

4.2.1. EXPLANATION OF FORM BY NATURAL SELECTION

The theory of natural selection is rooted in the physics of the nineteenth century (Depew and Weber 1996). The idea of living matter as a passive agent was imported from Newton's mechanics into biology. Thus the role of natural selection as a creative factor is inherently related to this idea. Any agency of living matter deprives natural selection of the capacity to be a creative factor in nature; to be the cause of biological order as proposed by Darwinism (the current paradigm). According to that concept, form (structure) has been forged during evolution by repeated episodes of sorting of the fittest, generation after generation. The result is the construction of machines designed to survive and reproduce. For this to occur, it is irrelevant as to whether natural selection has worked like an engineer or a tinkerer (Jacob 1977)

As matter cannot order by itself (in this view), it was proposed the existence of a genetic programme encoded in the hereditary material that governs development. This genetic programme is the *sine quan non* for generating ordered structures. The physical processes that take place during development are considered necessary for the formation of the organism, but it is assumed that the resulting structure is ultimately *generated* by genes, so the genome is sufficient to explain form.

It is supposed that biological order was not possible at all without the selectionist action. Natural selection is the ultimate organizing principle: form is the product of chance and sorting of genetic information. As such, it does not express any essential aspect of nature (a material law). Finality is just the result to the functional demands that the environment has imposed to organisms. Devoid of generative principles, evolutionary biology is an historical narrative, guided by contingent fluctuations. If the tape of life were to be replayed, things would be essentially different (Gould 1989).

Without generative principles, organisms are epiphenomena or the biological system's interpretation of genetic programmes; they are not real entities (Webster and Goodwin 1982; Webster and Goodwin 1996). Thus, Darwinism is a reductionist approach, concretely; it is what Sarkar calls 'genetic reductionism,' i.e., "genes can explain all phenotypic features of an organism" (Sarkar 1998, cited in Robert 2004).

4.2.2. EXPLANATION OF FORM BY SELF-ORGANIZATION

The alternative is rooted in the physics of complexity. When both mathematics and computing had been sufficiently developed to study the behavior of complex systems, it was possible to see that matter is capable of self-organization:

> This was a real lesson concerning the nature of matter: Complex systems tended to spontaneously simplify, giving rise to levels of organization and phenomena unanticipated by examination of the systems' fundamental units. But these emergent modes of behavior and organization were only evident when the systems were viewed at appropriated scales—they were not generated by the units acting like clockwork machines or programmed computers (Newman 2009, p. 126).

No modern physical scientists adhere to the old conception of all matter as passive, like a billiard ball, pulled and pushed by external forces (the crucial Newtonian-Darwinian assumption) (Goodwin 1994; Davies 1989; Solé and Goodwin 2000; Depew and Weber 1996).

Living matter is an active agent—excitable media (Goodwin 1994; Newman 2003a)—capable of self-organization, that is, to exhibit "order for free" (Kauffman 1993) by the interaction between different subcomponents, without the need of an external organizing factor (Halley and Winkler 2008). While genes and their products also have an essential role in this framework, they are not sufficient to explain biological organization.

Genes encode some of the systems' components, including those participating in self-organizing dynamics, and also specify molecules that, via natural selection, stabilize self-organized forms (i.e., forms already organized), but they do not generate these forms on their own (Forgacs and Newman 2005; Goodwin 1982; Goodwin 1994; Newman and Müller 2000; Newman 2010; Müller and Newman 2003; Newman 2002).

Form is the result of the laws that govern self-organization. Thus, organisms are coherent wholes reflecting the order immanent in the laws of nature. If the tape of life were to be replayed, things probably would be not essentially different, except in minor details. Life is not an exclusively historical phenomenon, isolated from the inanimate, but is part of the wave of creativity that expands through the universe from its origination in the Big Bang.

Biology would be a better science if these principles were acknowledged:

> Biology would begin to look a little more like physics in having a theory of organisms as dynamically robust entities that are natural kinds, not simply historical accidents that survived for a period of time. This would transform biology from a purely historical science to one with a logical, dynamic foundation... So rational taxonomy of biological forms could no more that reveal the logical order behind the major themes of the evolutionary drama as it has been played out so far (Goodwin 1994, p. 103).
>
> The twentieth century notion that genes represent a privileged level of explanation of the development and evolution of organismal traits is therefore a fantasy, and a distraction from the development of biology as a science (Newman 2003b).

Self-organizing systems usually exhibit emergent properties, properties characteristic of the system, not reducible to the characteristics of its subunits, properties which guide the behavior of the system as a whole (Gilbert and Sarkar 2000). This is a holistic approach to biology.

4.3. RECOVERING THE ORGANISM A LITTLE BIT: DYNAMICAL PATTERNING MODULES

Development is mediated by a set of gene products highly conserved between phyla. These molecules have been called the 'developmental-genetic toolkit' (Carroll, et al. 2005). The toolkit is composed of two types of gene products: 1) transcription factors: proteins that bind to the DNA molecule and regulate the expression of other genes, and 2) adhesion, extracellular and signaling pathways molecules, proteins and polysaccharides that mediate cell attachment and communication.

The non-transcription factor toolkit molecules mobilize physical processes of "mesoscale" (i.e., ~0.1 mm – 1 mm) "soft" (i.e., viscoelastic) excitable matter involved in the generation of form. These dynamical patterning modules (DPM) (the association of one or more non-transcription factor toolkit molecules and the respective physical processes they mobilize), acting individually or in concert are capable of generating a range of forms, which constitute *bauplans* and body parts. These morphological motifs represent a 'pattern language' for development and evolution (Newman and Bhat 2008; Newman and Bhat 2009a; Newman 2010).

Most of the non-transcription factor toolkit molecules were already present in the unicellular ancestors of the animals. Thus, the capacity to generate multicellular forms was inherently present in eukaryotic cells. Evolution always must work with pre-existing possibilities placed in new situations or under new constraints, the original meaning of 'epigenesis'—

'developing upon' (Salthe, pers. comm.). This would mean that metazoan body plans could be the result of self-organization, without the necessity of any major changes at the genetic level (Newman and Bhat 2009a; Newman, et al. 2006).

The consolidation or "canalization" (Waddington) of the self-organized forms by evolution under natural selection plausibly led to hierarchical genetic networks, which can be considered as a product of evolution, where forms already organized were stabilized by new or modified genetic circuitry. These programmes are not a precondition for living systems to organize in this view, but a highly derived condition. It is more reasonable that during these stages, cells exhibited "emergent" (i.e., self-organizing) genetic networks, with numerous feedback loops which mediate the interaction between cells, leading to pattern (Forgacs and Newman 2005).

These generic physical mechanisms, fundamental in the morphogenesis of body parts and organs in modern organisms (Newman and Bhat 2009a; Newman and Bhat 2008), reintroduce epigenesis, in a modern form, to development (Newman and Müller 2000; Forgacs and Newman 2005).

This physicalist vision has also been called Evo-Devo (Müller 2007). As suggested by Hall (2000), I think it is important to distinguish these opposing interpretations about the role of development in evolution (Linde Medina 2010).

4.4. DO WE NEED AN EXTENDED SYNTHESIS?

A recent book responding to this question contains contributions by a group of authors who come to various conclusions about the degree of conceptual change needed (Pigliucci and Müller 2010). According to the editors introduction, the core of the Darwinian paradigm remains intact. The only changes needed are the addition of new fields and concepts, absent in the Modern Synthesis formulated in 1930, without altering its basic principles: "the new ideas are 'not inconsistent' with the framework of the Modern Synthesis; this may very well be true—and most of us would gladly agree—but being consistent with the MS is not at all the same thing as being *a part of* the MS!" [emphasis in the original].

The figure 1 of the introduction reflects this position quite clearly. The scheme depicts the growing of Darwinism, where the core is formed by the fundaments of the Darwinian paradigm and new concepts have been added in subsequent layers. Evo-Devo is one of them. The placement of Evo-Devo to a layer of the Darwinian paradigm is possible if development is defined as a genetic controlled mechanism, the switch on and off of genes. This represents a gene centric perspective of development perfectly compatible with the standard framework (Carroll 2005; Davidson and Erwin 2006). It is assumed that these genetic regulatory networks are considered a *sine quan non* of body plans. In tune with the Darwinian tradition, the agency resides in the genome.

However there is other Evo-Devo version (the physicalist perspective) that represents a discordant piece (the chapter where the DPMs are introduced by Newman). Here the importance of self-organization in the generation of form is pointed out. Shifting part of the agency from genes to the self-organizing physical processes in morphogenesis, Newman asserts that the current framework is being stretched at risk of breaking.

The Darwinian evolutionary paradigm has prevented the development of a theory of morphogenesis. Stuart Newman's work represents a serious attempt to develop one. Until then, the possibility of a paradigm shift remains open.

ACKNOWLEDGEMENTS
I thank Stuart Newman, Stanley Salthe and Staffan Mueller-Wille for their useful comments. This work has been financed by the European Commission (Marie Curie postdoctoral fellowship PIOF-GA-2008-219676).

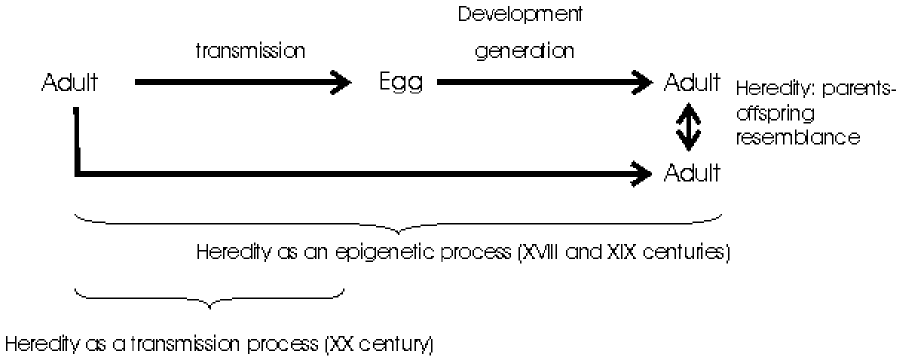

FIGURE 1
Heredity as a two stage process.

NOTES

1 The generation of form.
2 Its first meaning, as unfolding of the embryo during development.
3 Translation mine.
4 Today, hierarchy theory has taken up the non-reduciblity theme (Salthe 1993). Thanks to S. Salthe for the comment.
5 Lamarck's evolutionary theory was composed of two set of forces, one set to explain complexity and the other one to explain adaptations, small changes of form related with differences in environments. See Newman and Bhat (2009b) for new evidence supporting his evolutionary theory.
6 This is not an "unfortunate" term today. Recent work by Jablonka and Ginsburg show that it has a scientific basis. Thanks to S. A. Newman for this comment.
7 Unlike Lamarck's theory, Darwin's theory was only focused on explaining adaptations. In fact, the establishment of Darwinism as the paradigm in evolutionary biology interrupted the study of complexity (Salthe, pers. comm.).
8 Focusing on innate variations, it was possible to avoid the 'weak point' of Lamarck' theory.
9 This incongruence has been already stressed by Goodwin (1994, p. 24).
10 It has been pointed out elsewhere that Darwinism does not contemplate how form is generated. But this is not strictly true. Darwin wanted to explain the organization of living beings (form) and he already noted that for natural selection to work as a creative factor, the generation of variation had to present specific characteristics. Then, the generation of form and the idea of natural selection as a creative factor are closely related. Darwin elaborated some crucial assumptions about how form had to be generated. This passage of Gould's book (2002) explains this point quite clearly:

As the epitome of his own solution, Darwin admitted that his favored mechanism "made" nothing, but held that natural selection must be deemed "creative" (in any acceptable vernacular sense of the term) if its focal action of differential preservation and death could be construed as the primary cause for imparting direction to the process of evolutionary change. Darwin reasoned that natural selection can only play such a role if evolution obeys two crucial conditions: (1) if nothing about the provision of raw materials — that is, the sources of variation — imparts direction to evolutionary change; and (2) if change occurs by a long and insensible series of intermediary steps, each superintended by natural selection — so that "creativity" or "direction" can arise by the summation of increments.

Under these provisos, variation becomes raw material only — an isotropic sphere of potential about the modal form of a species. Natural selection, by superintending the differential preservation of a biased region from this sphere in each generation, and by summing up (over countless repetitions) the tiny changes thus produced in each episode, can manufacture substantial, directional change. What else but natural selection could be called "creative," or direction-giving, in such a process? As long as variation only supplies raw material; as long as change accretes in an insensibly gradual manner; and as long as the reproductive advantages of certain individuals provide the statistical source of change; then natural selection must be construed as the directional cause of evolutionary modification.

11 Darwin's pangenesis also influenced de Vries' ideas about heredity (see Gould, 2002).

12 This idea was proposed before the genetic coded was elucidated by Schrödinger (Schrödinger 1944).

13 Note that this introduced an epigenetic component that could rest to genes part of their agency, so according to the operon *lac* system, the cellular context is as important as the gene products for developing the organism. Monod safeguarded the supremacy of genes arguing that form is contained in genes; no other information is needed for reproducing an organism. The epigenetic component is just needed to actualized the form potentially contained in genes (Robert 2004).

14 The analogy between crystallization and morphogenesis was used, for example, by Schwann (cited in Russel, 1916): "the cell substance is either soluble in the cytoblastem and crystallises out only when the latter is saturated with it, or it is insoluble and crystallises as soon as it is formed, according to the aforementioned laws of the crystallization of imbibition-bodies... if one imagines cell-formation to take place in this way, one is led to think of the plastic force of the cell as identical with the force by means of which a crystal grows" (p. 185).

15 Monod, J (1972). *Chance and Necessity*. London, Collins.

16 Non-regulatory proteins.

17 In the description of Wolpert's model I rely on Saunders (1984).

18 See Smith et al. (2007) and Bolouri (2008).

19 Genes that code for proteins (transcription factors) that bind to the DNA molecule and regulate the expression of other genes.

20 Systems which exchange energy and matter with their environment .

21 When a strong gradient of energy exist between the system and its surroundings.

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