
HOW DEEP IS THE CONFLICT BETWEEN SELF-ORGANIZATION AND NATURAL SELECTION?

EUGENIO ANDRADE

This paper is meant to fully endorse, while complementing some views expressed by Linde (2010) in her paper entitled "Natural selection and self-organization: A deep dichotomy in the study of organic form." The conflict between self-organization (SO) and natural selection (NS) goes back to eighteenth century physics that was based on the Newtonian formulation of inertia¹, according to which the intrinsic state of matter is that of being inactive or inert, so that it can only be set in motion by external forces. I wish to examine how Lamarck and Darwin dealt with this Newtonian claim about the inherent passivity of matter that became a deep-rooted presumption that still today prevents people from accepting self-organization. The former will be considered as one of the precursors of self-organization and internalist approaches, and the latter as the very icon of evolutionary biology, the proponent of natural selection that justifies the externalist views.

LAMARCKISM: THE INTERNALIST STANCE AND THE ANTICIPATION OF SELF-ORGANIZATION

The intrinsic passivity of matter was unsuccessfully challenged by German natural philosophers and French naturalists throughout the eighteenth century, who adhered to explanations based on vital principles not amenable to mechanical explanations and beyond empirical testing. At the onset of the nineteenth century, Lamarck, like Buffon a few decades before, under the influence of the mechanic conception of nature proposed to understand life solely in material terms. Lamarck (1802) suggested that isolated particles of matter are indeed passive or Newtonian, but pointed out that this principle does not apply to organized living matter that posses a dynamical principle that he wrongly identified with the fluid of heat and electricity. Fluids were then considered as material

Department of Biology, Universidad Nacional de Colombia. / leandrade@unal.edu.co

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subtle substances that filled the space available between the atomic particles of hard matter and were held responsible for transmitting movement to them. Lamarck (1802) believed that a solid theory of life transformation must be based on an explanation of spontaneous generation or the phenomenon of symmetry breaking of an inorganic world that generated and is still generating the simplest living organisms (Fox Keller 2003). Thus, as the living world emerged and is still emerging, it self-organizes and tends to display a growing heterogeneity and asymmetry by the combined action of mechanical Newtonian forces and the *vital force* of heat and electricity that must not be confused with supernatural substances (Burkhardt 1995: 151-157). Regrettably, the search for these organizing principles was doomed to fail since Lamarck's chemistry had already been refuted by Lavoisier and his physics was soon after overthrown by Thompson's mechanical explanation of heat. That is the reason why self-organization approaches have been held responsible of being based on supernatural forces.

Nonetheless, Lamarck's unbending commitment for a physical explanation of spontaneous generation makes him a precursor of SO. Organisms were, this way, conceived as self organizing material systems and, even more, as sentient beings endowed with inner feelings and impulses that allow them to respond to external environmental influences. In consequence, Lamarck was labeled as a monist materialist by Haeckel (in Lamarck 1986), in recognition for his rejection of an external force that organizes matter in order to produce life. Lamarck's spontaneous generation was a process induced by the incorporation of the subtle material fluid of heat. The existence of material fluids of light, heat and electricity were widely accepted by chemists before Lavoisier. Lamarck's epistemic standpoint has not been truly appreciated, since he challenged the Cartesian matter/mind dichotomy and outlined instead a monist materialistic ontology in which matter has two faces or expressions, an external one that reveals inorganic mechanical properties and an internal one that functions as the site of life or organized matter, while preserving the continuity between them. This distinction between internal and external aspects within matter can be tracked back to Venel (1753) in his ardent defense of chemical interactions or affinities as distinct from Newtonian mechanical forces. Lamarck (1802, 1809) laid down the foundations of a new science, biology, as he recognized that life emerged and is still emerging from the spontaneous organization of matter, consequently, life, though wholly material cannot be reduced to indivisible particles.

Lamarck overcame the Newtonian preconception at a wrong time, when it was not possible to develop an alternative view, and thus he had to conciliate in some points with Newtonian determinism. Lamarck also proposed a series of parallel transformations arising from several events

of spontaneous generation that in accordance to a *plan of nature* tend to increase organization from insensitive to sensitive and finally to intelligent animals (Lamarck [1809] 1986: 126-128). Given that Newtonian matter behaves deterministically it was not surprising that under similar physical conditions spontaneous generation should bring forth similar forms, nonetheless, whereas simpler or lower living beings are shaped by environmental physical forces, animals in which growing organizations includes nervous systems and brain are shaped by habit, but always in full conformity with physical laws. In other words, as the inner organization increases, organisms are ever more capable to counteract external influences, so that the body is shaped by internal accommodations of its parts as induced by habits and use and disuse, one more justification for internalism.

The attempt to cautiously move away from Newtonian philosophy of nature justifies the historical myth that sees him as the precursor of biology and evolutionary theory, but also holds him responsible, against his own projects, for reviving an old fashioned vitalist explanation based on non-physical substances.

DARWINISM: THE PREVALENCE OF NATURAL SELECTION AS AN EXTERNAL FORMATIVE FORCE

With the rise of Darwinism, natural selection was conceived as the external force that shapes life, a way to avoid the need to recur to unknown organizing principles, whose physical nature could not yet be demonstrated, even if Lamarck had endeavored to do so. Darwin made a great step towards the naturalization of life, not yet completed since the physical grounding of NS was not explicitly shown at that time.

The reason for Darwin's externalist preference has to be examined, since Darwin believed for instance, that life had originated by a spontaneous generation once or very few times in a distant past. For him the underlying framework of the origin of life was SO.

It is often said that all the conditions for the first production of a living organism are now present, which could have been present. But if (and oh! what a big if!) we could conceive in some warm little pond, with all sorts of ammonia and phosphoric salts, light, heat, electricity, etc., present, that a protein compound was chemically formed ready to undergo still more complex changes, at the present day such matter would be instantly devoured or absorbed, which would not have been the case before living creatures were formed (Darwin 1859).

Besides, he established some analogies between development and evolution, as if the organizing system would pass from flexibility to rigidity; a

point that I will discuss below, since it is an interesting view that has consequences for biology today.

From birth onwards a series of structural modifications are incorporated into the germ and at a certain time when the organization is still flexible (childhood) such modifications became fixed as if they had been added onto old individuals during thousands of centuries (Darwin 1838: 84; Richards 1992: 117-118).

Even more, Darwin stood close to accept recapitulation or the doctrine that states that organisms in their ontogeny go through stages resembling or representing successive stages in the evolution of their remote ancestors (Richards 1992, Darwin 1838, 1838-1844 and 1859), and attempted to provide an embryological account of evolutionary variations.

Darwin considered also the existence of directed variations by modification of habits through use and disuse, wondered whether instincts were learnt, and postulated the influence of organisms' actions on heredity in his theory of pan-genes (Darwin 1883). Moreover, Darwin described living organisms as capable of reacting to external circumstances and as endowed with some degree of intelligence as explained in extenso in chapters 3 and 4 of the *Descent of Man and Selection in Relation to Sex* (Darwin 1874).

The fact that the unity of type is explained by common ancestry, it does not rule out *per se* the existence of physical laws that rule morphogenesis and so account for the resemblance of embryos². According to Darwin NS explained the fixation of departures from the *Bauplan*, but he also considered that the *Bauplan* itself represented a functional adaptation present in the common ancestor that was selected in a remote past, argument that demarked his turn away from structural internalism and into externalist functionalism. This turn had no objection and was welcome since it left unharmed the Newtonian perspective. Following Gould (2002: 116-125) and Depew and Weber (1995: 113-139), the main reason why Darwin preferred the externalist explanation that conditioned the mainstream acceptance of NS, and the neglect of SO, lies in his commitment to Newtonian theological and mechanical preconceptions.

Newtonian mechanical and natural theology preconceptions exerted an important influence on Darwin, who did not intend deliberately to overcome these received views that addressed two related concepts: design and adaptation. Assuming that matter is passive, the emergence of an organic form required in all instances an external divine force, as defended by Newton (1706) in his optical queries and later by Paley in his *Natural Theology* (1802). Darwin's investigations led him to propose that species were not created in a remote past in the state we find them today, but instead he thought that their emergence and adaptation was the result

of secondary causes like the ones that control the birth and death of the organisms.

Authors of the highest eminence seem to be fully satisfied with the view that each species has been independently created. To my mind it accords better with what we know of the laws impressed on matter by the Creator, that the production and extinction of the past and present inhabitants of the world should have been due to *secondary causes*, like those determining the birth and death of the individual (Darwin 1859: 402).

Therefore, the formulation of NS as a secondary cause or the immediate mechanical cause, was a way to deal in good terms with natural theology and at the same time to advance in his search for a rational explanation of evolution.

Since Darwin, we turn to a single, singular force, natural selection, which we might well capitalize as though it were the new deity. Random variation, selection-sifting. Without it, we reason, there would be nothing but incoherent disorder (Kauffman 1995).

Were there no external organizing force, no form at all would be expected, since nineteenth century physics did not provide any hint on how order could be originated from randomness. Darwin presented natural selection as a law having the same status as gravity and Newtonian laws. How could a law inspired in Malthusian economy be raised up to the level of a Newtonian Law? Following Depew and Weber (1995), Adam Smith had shown with great elegance that the laws of economy are utterly compatible with the Newtonian view of nature. Darwin adhered to Smith's externalist "invisible hand" argument that equilibrates supply and demand and fixes the prices in the market where individuals strive to maximize individual benefit.

Although NS was advanced under the ignorance of the inner structure of organisms, before the cellular theory and the chemical enzymatic theory of living processes were widely diffused and accepted—not considering the Mendelian laws of heredity and genetics—it served to solve the problem originated in the lack of a physically grounded account of evolution. The law of NS, regardless of how bloody and cruel it may be, leads to improvements, adaptations, equilibrium and harmony within the productions of nature.

In the nineteenth century, it was accepted that natural laws reflect the order that God impressed into matter, an idea that was not challenged by Darwin, in spite of public opinion that NS overthrew natural theology. On the contrary, God as a law-giver, was still the only justification of natural laws. What happened was that against the doctrine of design inspired in

Paley's theology, Darwin argued in favor of evolution by NS in order to account for theological inspired ideas of design and adaptation. Darwin did not kill God; he only discharged Him of the business of designing every single species separately at one particular moment back in time. NS became the supreme law of evolution that overthrew Paley's intelligent design based theologies, while it left unchallenged the less known Kingsley's theological views that were based on the idea of the universality of natural laws, being NS one of them.

For Darwin, an externalist standpoint was justified by extrapolating to nature what he had learnt through artificial selection in domestic animals.

I came to the conclusion that selection was the principle of change from the study of domesticated productions; and then, reading Malthus, I saw at once how to apply this principle (Darwin, 1859 letter to ARW).

However, Ruse (1975) has suggested that it was rather the other way around, Darwin re-examined his conception of artificial crosses after discovering NS, in spite of the above claim. Therefore, the validation of the externalist approach based on the practice of directed crosses takes us back again to Darwin's commitment to Newtonian and natural theology assumptions. Below I will show that to focus on artificial selection in domestic (plastic) animals led him to over emphasize NS and to overlook that in wild (rigid) animals structural constraints play a fundamental role. In consequence, NS alleged unlimited powers to shape organized matter, without considering its intrinsic dynamics and plasticity, were widely debated by neo-Lamarckians and by defenders of orthogenesis. The higher the weight given to NS, the lesser the weight given to the problem of the origin of evolutionary variations and the emergence of organized systems.

If our architect succeeded in rearing a noble edifice, using the rough wedge-shaped fragments for the arches, the longer stones for the lintels, and so forth, we should admire his skill even in a higher degree than if he had used stones shaped for the purpose. So it is with selection, whether applied by man or by nature; for though variability is indispensably necessary, yet, when we look at some highly complex and excellently adapted organism, *variability sinks to a quite subordinate position in importance in comparison with selection*, in the same manner as the shape of each fragment used by our supposed architect is unimportant in comparison with his skill (Darwin [1883] 1894: 236).

In consequence, habit as a causal agency of variations became second in importance to NS. However, it must be recalled that Darwin devoted three chapters (1, 2 and 5) in the *Origin of Species* to the search for the laws of variation, and that in *Variations of Animals and Plants Under Domestication*

five chapters (from XXII to XXVI) dealt with this matter. I want to remark the importance that Darwin gave to this problem whose complexity he acknowledged. The point is that if variations can be influenced by environmental factors and by organisms' reaction to these factors it was, thus, inevitably associated to the physical constitution and internal organization of the organisms, a research program not open to investigation at that time.

The glory of NS made Darwin the Newton of a "blade of grass" and shows that the scientific revolution was half completed. To assume that Darwin was indeed the Newton of biology is to accept that living forms can be explained solely by external forces, making unnecessary to open up the black box, though it was desirable to identify their atomic constitutive units. After the formulation of the cell theory by Virchow, Darwin modified his views and postulated that cells and every organic constitutive part reproduce his own, that is to say that the organism does not reproduce as a whole (Darwin 1883). This atomistic view was framed in a neo-Lamarckian standpoint that led to infer that organisms by means of changing habits in response to environmental challenges induce a physical change in the gemmules themselves. If inheritance rests on discrete particles, their modifications by environmental influences and use and disuse must require the action of physical forces. It is the hypothesis that after all, natural selection was not the only formative force.

Darwin's concern about to what extend the "provisional hypothesis of pangenesis" would challenge the status of NS has been downplayed as a historical curiosity that does not question the primacy of NS. Yet Darwin's concerns were serious indeed; otherwise one cannot understand the following quotation:

I hardly know why I am a little sorry, but my present work is leading me to believe rather more in the direct action of physical conditions—I presume I regret it, because it lessens the glory of Natural Selection... (Darwin 1862).

And later:

In my opinion, the greatest error which I have committed has been not allowing sufficient weight to the direct action of the environments, i.e., food, climate, &c., independently of Natural Selection... When I wrote the 'Origin,' and for some years afterwards, I could find little good evidence of the direct action of the environment; now there is a large body of evidence, and your case of the Saturnia is one of the most remarkable of which I have heard (Darwin 1876).

Darwin always upheld some of his internalist views, since he was never hundred percent satisfied with the explanatory power of NS and believed

that variations are produced as a consequence of the direct interaction between individual organisms and the environment.

NEO-DARWINISM OR THE CONSOLIDATION
OF THE EXTERNALIST STANCE

Despite of the fact that Darwin made a parallelism between individuals and species (Darwin 1838 in Richards 1992), considering they both have a birth, progress through time, produce new species and die, he introduced a distinction between individuals and species as populations, hence promoting the investigation of statistical parameters in order to describe populations. Nevertheless, the development of population thinking in biology had to wait the incorporation of Boltzmann and Maxwell's statistical mechanics into genetics by Fisher and Wright, a fact that conferred a mathematical formalism to evolutionary theory. Fisher showed that Newtonian physics fell short to model the evolution of life and proposed instead that there was an underlying isomorphism between Boltzmann's statistical mechanics in equilibrium thermodynamics and populations' genetic analysis.

Natural selection was, thus, empowered in spite of the fact that the analogies between the Boltzmann's gas diffusion and population genetics rest on a limited and reductive atomic view of life in which genes took the place of atomic constituents of living organisms. Fisher's claim about changes in gene frequency by NS did not imply that the box was opened, since their mode of functioning and the way they carry information had not been unraveled. For Fisher it is needed to start with an ample range of genetic variability within a population to let NS shape life in line of a growing adaptation to the external environmental restrictive conditions. Indeed, to sustain evolution on a collection of genes that recombine, mutate and disperse randomly in the population was a step forward, yet limited as long as the models were inspired in equilibrium thermodynamics.

The genetic revolution promoted the idea that form was encoded in genes so that in order to account for a specific living form one can disregard physical forces and be satisfied with a genetic explanation. Since nothing was said about the origin of the genetic program, externalist views like preformism survived in a new guise in genetics (Oyama, 2000:17-ff), claiming that SO was unnecessary. But it is a mistaken idea to argue that SO acts where genes do not, for it forgets that genes have a physical nature that encode proteins and facilitate their production as needed without having to produce them *de novo* in order to streamline SO in ontogeny.

Modern genetics rests on the notion of a Weissman's barrier, according to which the phenotype was determined by the information encoded in the genotype so that the modifications induced by the action of the

environment cannot affect the genes, a way of reasoning that further inspired the central dogma of molecular biology in the 1950s. The environment for neo-Darwinians provides the external selective pressures that provoke a shift in the genetic composition of the population. In consequence, organisms were stripped of their intrinsic autonomy associated to their inner dynamics and organization, and came to be imagined as determined by two opposing causes: from the bottom-up an external genetic program and from the top-down NS that operates from without (environment). Since 1970 onwards, the notion of genetic program was placed at the heart of biology by Monod, presenting it as a determinant factor of form that made SO unnecessary.

A truly physical explanation of NS had to wait the development of far from equilibrium thermodynamics and the study of SO, namely by Prigogine (1984) and Kauffman (1993). Even if a few decades before Prigogine, within neo-Darwinism, the idea of a global equilibrium state was questioned by Sewall Wright who advanced the idea of shifting balance between local equilibrium states, and later by Kimura for whom equilibrium is never reached since what prevails is genetic drift.

SELF-ORGANIZATION AND EPIGENETIC APPROACHES:
INTERNALISM VINDICATED

Self-organization is a process in which a huge energy flow-through makes organization possible without the need to depend on external instructions. Out of thermodynamic equilibrium, self-organizing systems gather and incorporate environmental information that stabilizes them between energy thresholds that at critical unstable points enable them to choose at least between two different alternative conformations. In living beings, stabilization requires the incorporation of genetic information that further induces new possible variations. Organized systems evolve by following stable paths, in which neutral mutations accumulate, leading to unstable bifurcating points that enable unpredictable choices between attainable stable states.

The dynamical properties of far from equilibrium systems were first announced by Maxwell (1870) in a letter to Galton, where he referred to dynamical trajectories that lead to bifurcating points, which one is to be followed, is a random choice.

There are certain cases in which a material system, when it comes to a phase in which the particular path which it is describing coincides with the envelope of all such paths may either continue in the particular path or take to the envelope (which in these cases is also a possible path) and which course it takes is not determined by the forces of the system (which are the same for both cases) but when the bifurcation of path occurs, the system, *ipso facto*, invokes

some determining principle which is extra physical (but not extra natural) to determine which of the two paths it is to follow. When it is on the enveloping path it may at any instant, at its own sweet will, without exerting any force or spending any energy, go off along that one of the particular paths which happens to coincide with the actual condition of the system at that instant (Maxwell [1870] 1990: 731).

In the case of living systems, they do not behave following Newtonian defined trajectories, nor prefixed orthogenetic routes of change. Living systems are inherently subordinated to path dependent constrained trajectories that enabled some directions of change by opening up at unpredictable bifurcating points. This Maxwellian approach that would boost the internalist stance is yet to be developed and integrated into biological evolutionary theories. In this vein, a major breakthrough was made by Prigogine (1984). Prigogine's research on non-equilibrium systems led him to formulate the idea of dissipative structures and so, after performing quantitative estimations of chemical reactions that put in evidence the existence of bifurcating trajectories with differing probabilities as anticipated by Maxwell. The importance of this approach is enormous because it not only challenges, but overthrows the Newtonian principle about the passivity of matter. Matter is active, and organizes in defined structures according to intrinsic and extrinsic factors. Finally, with Prigogine science unveiled the physical nature of organizing principles, without any need to hang on vital principles. Self-organizing systems do not violate the second law of thermodynamics since they require a constant input of matter and energy with low entropy, and they get rid of the internally generated entropy by dissipating heat to the environment. This allows them to produce ordered "dissipative structures" which maintain far from thermodynamic equilibrium systems, being life a clear example of these (Gershenson, et al. 2003).

The essence of SO is that systems' inner structure emerges without explicit instructions given by pressures or constraints from outside the system. There is nothing external that imposes its form. In other words, the constraints on form are internal to the system and result from the interactions between its constitutive components and between the organized whole and the external environment. The point is that external factors have a morphological influence only if they are selectively picked up by the developing organism. The external pressure due to scarcity of resources only defines the frequency distribution of realized morphologies, but it does not create them. The confusion about the creative role of NS comes from the fact that once an evolutionary trajectory is stabilized by NS, it fixes a path in which unpredictable situations may encounter a bifurcating point. But this goes in accord to its own dynamics and internal

organization depending on how the external factors are selectively picked up by the living organism.

Organisms are SO systems that determine moment by moment its way of interactions with the environment in the course of its ontogeny.

In other words, every ontogeny as an individual history of structural change is a structural drift that occurs with conservation of organization and adaptation. We say it again: conservation of *autopoiesis* and conservation of adaptation are necessary conditions for the existence of living beings; the ontogenic structural change of a living being in an environment always occurs as a structural drift congruent with the structural drift of the environment. This drift will appear to an observer as having been "selected" by the environment throughout the history of interactions of the living being, as long as it is alive (Maturana & Varela 1992).

Every single factor that contributes to development is an informational source; in consequence, genetic information requires an organized system that interprets it, in such a way that out of the same genome different forms may arise depending on the context of interactions. Evolutionary variations are modifications of ontogenies based on the organisms' ability to adjust metabolic, physiological, ontogenic, and behavioral parameters. In every adjustment information is gained, since it implies the adoption of one among the many possibilities within reach.

As mentioned above, defenders of SO side with epigenetists since development is a far from equilibrium process driven by high-energy flow through. Defenders of NS have opted for the genocentric view that makes all variations dependent on random DNA mutations and consequently evolution entirely dependent on the external pressure exerted by natural selection. Being so, we can now ask to what extent, is ontogeny a cuasiderministic process guided by a selectively fixed genetic program? Also, to what extent phenotypic adjustments provoked by environmental fluctuations have an effect on future evolution? The point is to conceive ontogeny from an internalist stance, so to speak, as a process in which the developing systems themselves selectively pick up and incorporate additional information from the environment. According to Oyama (2000), the developing embryo is a self-organizing system that uses genetic and environmental formative factors. In early stages of animal evolution, development was mostly guided by morphological determinants supplied by the external environment that acted upon primitive cellular aggregates (Ho and Sauerbrenn 1979, Goodwin 1994, Jablonka and Lamb 1995, Jablonka and Lamb 1998, Newman and Muller 2000). Along evolution the action of external environmental factors of development was taken over and reinforced by genetically specified proteins that impact on the resultant morphology. Genetic assimilation (Waddington 1957, 1961) hooked morphogenesis

to a genetic circuit that streamlined ontogenies making them partially free from, though still dependent on, external factors. That is why it is affirmed that genes arrive late in evolution to consolidate previous epigenetic processes (Newman and Muller 2000; Salazar-La Ciudad, et al. 2003; West-Eberhard 2003: 157). This idea can be illustrated by means of Waddington's epigenetic landscape model (Waddington 1957, 1961; see figure 1).

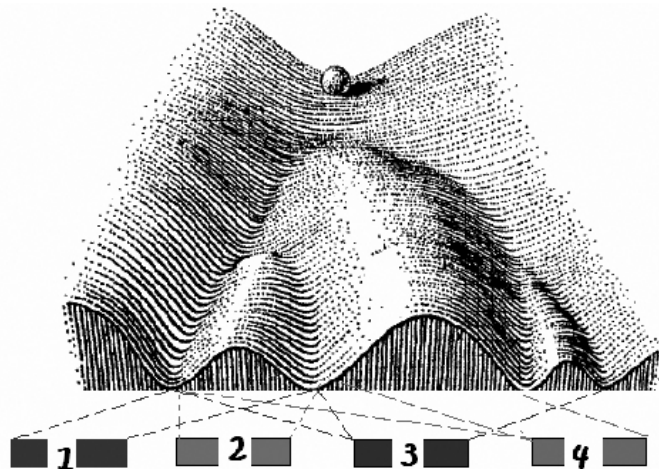


FIGURE 1

The epigenetic landscape stands for a dynamic interface between genes and environment, where developmental paths open up and are modified along development. The ball in the upper side stands for any undifferentiated system (cells, organism) that possesses many developmental possibilities. The deep valleys located between energy stability thresholds stand for stable developmental paths, whereas bifurcating points are unstable, since small fluctuations either, produced by the environment or by genetic mutations, push the system towards one way or the other (Waddington 1957, in Slack 2002).

As NS eliminates a branch of the tree of life, a set of unrealized possibilities becomes impossible, but potential will be enabled from the selected lineages. Despite the advances in thermodynamics and evolutionary developmental biology, the debate over the "passivity vs. activity" of matter is not completely over, since the cultural inertia bequeathed to us by Newton still lingers in the educated people who side between two seemingly irreconcilable camps, either NS or God, a war equally fed by both American Christian Creationists and ultra-Darwinians alike. The public diffusion of this conflict hides the common underlying principles shared by both camps, the acceptance of an external formative force, Divine for creation-

ists and naturalized for scientists, for even to NS defenders this could well be either a law intentionally impressed by God into nature (Dobzhansky 1973) or just natural, like an "blind watchmaker" that acts also from without (Dawkins 1986). Science and theology both need to do away their old Newtonian physics and metaphysics in favor of a monistic view.

The organic diversity becomes, however, reasonable and understandable if the Creator has created the living world not by caprice but by evolution propelled by natural selection. It is wrong to hold creation and evolution as mutually exclusive alternatives. I am a creationist *and* an evolutionist. Evolution is God's, or Nature's method of creation. Creation is not an event that happened in 4004 BC; it is a process that began some 10 billion years ago and is still under way (Dobzhansky 1973).

All appearances to the contrary, the only watchmaker in nature is the blind forces of physics, albeit deployed in very special way. A true watchmaker has foresight: he designs his cogs springs, and plans their interconnections, with a future purpose in his mind's eye. Natural selection, the blind, unconscious, automatic process which Darwin discovered, and which we now know is the explanation for the existence and apparently purposeful form of all life, has no purpose in mind. It has no mind and no mind's eye. It does not plan for the future. It has no vision, no foresight, no sight at all. If it can be said to play the role of watchmaker in nature, it is the *blind* watchmaker (Dawkins 1986).

EVOLUTIONARY CONSTRAINTS AND THE PRACTICE OF DIRECTED CROSSES

The main epistemic obstacle against SO is the same that prevents some researchers from accepting a positive role for structural constraints. In other words, the fact that the internal organization restricts or blocks a wide range of changes does not preclude that it may also enable some other directions of change. Once all the weight is given to NS, the Newtonian *a priori* about the passivity of matter passes unquestioned and as a result it is assumed that organisms as material systems vary at random and behave blindly. Such is the reason why ultra-Darwinians are the champions of absolute chance. This notion of chance as unbiased and blind exploration of all possible imaginable forms must be changed in favor of a historical and more down to earth vision of an undetermined world in which explorations take place among a set of structurally historically constrained alternatives, enabled at crucial moments in time. Restrictions surely block possible routes of change but they may also, under specific local environmental conditions, enable or open up lines of variability that insinuate future evolutionary paths. Gould pointed out that "constraint"

can also denote a causal positive aspect associated to allowed directions of changes.

The concept is commonly used in its negative sense and should instead be understood in a positive way as “causes in the direction of particular evolutionary changes” (Gould 2002: 1026).

Living organisms have a structural predisposition to vary in certain directions regardless of NS. Bifurcation points occur as contextualized individual's choices driven by SO. The point is, again, that NS, as an external action, requires the prior existence of SO, while NS favors phenotypes that are able to respond to changing conditions. To acknowledge that organisms execute intentional behaviors in matters related with the immediate conditions of life does not conflict with the idea of an open-ended and unpredictable evolution, in other words, evolutionary unpredictability is founded on the existence of creative responses at the individual level. Individual elections were clearly explained by Baldwin (1896) as he put forward a new factor in evolution, named “organic selection” or the capacity to somatically adjust to the varying environmental conditions. These phenotypic accommodations may be accomplished at different levels, metabolism, physiology, ontogeny or cell differentiation, behavior and learning (Gottlieb 2001). Moreover, organisms determine what is relevant, alter the external world as they interact with it, sense and interpret the physical signals that reach them from the outside world, transform the statistical pattern of environmental variation in the external world and modify their surviving strategies, so generating the conditions of their own selection (Levins and Lewontin 1985: 99-101). Natural selection is responsible for observed statistical regularity in a population, by favoring the organic and genetic constitution of plastic individuals that manage to modify their surviving strategies. Therefore, individual arbitrary elections are at the base of the evolutionary process, since survival is offered to individuals that manage to develop adequate strategies oriented to exploit the environment in their own benefit.

The analogy between artificial breeding (directed crosses) and natural selection has not been sufficiently discussed. The use of artificial selection on plastic and variable species like pigeons, reinforced Darwin's idea that selection acts as an external force and constitutes the truly formative principle of living organisms, since new races came into being thanks to the capricious and patient selection of breeders, as long as there is a large supply of variations, that for Darwin were related to individual reactions to changing conditions of life associated with the process of domestication (Darwin 1859). There are conspicuous differences between variations in tamed animal and in nature; domesticated animals are assumed to be

more plastic while wild ones less variable and more rigid (Darwin 1859). Directed breeding served to illustrate the power of artificial selection by the gradual accumulation of small favorable variations, and by extrapolation NS was assumed to play a similar role in wild conditions. Darwin said that the extrapolation of directed crossed or artificial selection to the workings of nature was only as a metaphor. To what extent he was right in so doing? How his views were affected by the recognition of not plastic, rigid and not variable species? How could he be sure that isotropic variations really occur?

Popov (2009) reminds that Danilevsky questioned Darwin's tenet that geese are variable but seems not to be variable because man breeds them only for one purpose, to eat them, and hence the idea that variations are the consequence of NS and not the cause. According to Danilevsky geese is a non-variable species due to its nature and not because it has not been submitted to selection. However, is variability the result of natural selection or its precondition? Artificial selection for variability has a limit since selected races reach a point in which they cannot vary anymore due to the correlations of parts. Besides, if artificially selected races are left to themselves and allowed to reproduce in the wild, a regression towards the original phenotype is observed. By contrast, wild animals that are more restricted to arbitrary change seem nonetheless to allow some biased directions of change, and even more selected species present wider spans of variations (or relaxation of the constraints).

Flegr (2008) points out that domesticated species are more variable and plastic because they are young in contrast to wild species that are old and then more constrained. In agreement with Hull (1978, 1980) species can be considered as real historical entities. Thence, Flegr (2008) divides the history of species in two periods: (1) a short one of plasticity and (2) a long one of frozen evolution. The period of plasticity can be subdivided into two. A first one (1a) that follows immediately after splitting of the population by a strong isolating barrier that entails decreases in genetic variability compensated by fixation of new alleles by drift. This is the birth of a species, a period in which different kinds of variants appear as a result of individual organisms' interactions with the environment. A second one (1b) in which population increases close to the limits of sustainability and then NS plays an effective role increasing fitness through gradual retention of favorable variants. Finally, the frozen plasticity period (2) is a long period in which species' response to selection pressures diminishes as they stabilize, and become vulnerable to environmental changes and eventually die.

At this point, I will show that Flegr's evolutionary species periods are a specific case of Salthe's (2010) generic changes of developmental systems as viewed from a physicalist thermodynamic perspective. Salthe's three

developmental stages of immaturity, maturity and senescence were inferred by estimating the energy throughput per unit of mass with time. This model illustrates that the second law of thermodynamics is responsible for the law-like character of self-organizing developmental systems that allows inferring general patterns of behavior characteristic of each phase (Salthe 1993, 1999, 2010).

Flegr's short plastic period immediately following isolation (1a) can be equated to Salthe's immature stage when internal stability is low because of high phenotypic plasticity due to susceptibility to external environmental factors, though the dynamic stability is high. This phase correlates to emerging or still young species. In this rapid phase species' internal constraints seem to play little, if any, role as was the case of domestic species. Selection indeed has a great formative power in plastic species as showed by directed crosses, but in nature usually this plastic periods of emergence are submitted to NS if we accept competition between groups of variants as postulated by Wallace (1858). Moreover the taming of animals is not to be seen as a manipulation of humans over wild animals, but as a mutual reciprocal interaction in which already social animals included us into their domain of experience, social network or niche, by adjusting their behavior and morphology to the conditions of life provided by humans. If it were only a matter of human control upon the wild animal, it could not be explained why the number of tamed species is too low with respect to the number of species that humans have come into contact. Sociability, it is argued to favor genetic diversity and phenotypic plasticity because it constitutes a more favorable condition for individuals, thus accounting for the higher plasticity of domestic animals. This phenotypic plasticity exploited by breeders emerged within the interactions between humans and the ancestors of present day domesticated species.

Flegr's plastic period of increasing population size (1b) can be equated with Salthe's mature developmental stage and would be applicable to relatively stable systems. As the population size increases, some genetic variability is lost by NS and genetic circuits of regulation might fall under the control of external factors and existing genes may be coopted for new functions (West-Eberhard 2003: 147-151). In this case, constraints may play a positive role allowing preferred directions of change upon which NS acts. This is the case of evolving wild species. Had Darwin given more importance to this phase of species history, the acceptance of NS would not have undermined the recognition of internal factors in evolution.

Flegr's frozen plasticity period (2) is equivalent to Salthe's senescent stage. As species fade away and decay, they become more constrained with phenotypes more dependent on genetic encoded information and less susceptible to phenotypically adjust to external circumstances. In this case, constraints play surely a negative role, such as the case of rigid wild

species close to extinction. Nevertheless, old species, when they emerged were more plastic and variable than the present day descendants that were retained by NS. Constraints play a positive role in stabilized mature species by enabling limited and biased directions of change, whereas for old species constraints play a negative role. Drastic environmental changes may push some species to extinction, while inducing phenotypic variability and plasticity in others that are still able to cope with the new challenges. The retention of juvenile traits by NS preserves plasticity and so accounts for neoteny as a mechanism that induces the generation of evolutionary innovations.

Peirce proposed, at the end of nineteenth century, that evolutionary variations are neither random nor directed, but instead generated by the organisms' tendency to adapt to a changing local environment. He opposed a gradualist view of change, arguing that drastic changes in the environment trigger rapid morphological modifications in plastic species (phenotypic plasticity). Thence, Peirce thought that natural selection required an internal election mechanism associated with the organism's activity under the pressure of selective conditions. This mode of evolution oriented to specific goals by means of external pressures and habit modification, reconciles not only chance and necessity (Peirce 1891), but also SO and NS, and the internalist and externalist stances.

Unconstrained young species are shaped by artificial selection in isolation. However, emerging new species in the wild are defined at the mother specie's mature stage according to the possibilities enabled by the constraints. New species occurs in large populations that split off giving birth to newly emerging small populations of variants. Dobzhansky and Ayala had claimed that NS favors the most variable species and preserves mechanisms that produce genetic variability, and today epigenesists argue that NS favors phenotypic plasticity of species, so that not all of the numerous variants that emerge at the bifurcating point are selected. Darwin stated that selected lineages tend to vary and diversify in order to allow for the establishment of new ecological relationships. Therefore, I argue that NS pulls the species to a point situated at the boundary between Fleg's periods "1a" and "1b" or between Salthe's immature and mature phases, that allows the exploitation of energy gradients, while SO pushes them to their frozen stage in case no new energy gradient is made available for exploitation.

OVERCOMING THE NEWTONIAN PRECONCEPTIONS

The conflict between NS and SO runs as deep as our rooted Newtonian preconceptions and beliefs. Even so, as Salthe (2010), Kauffman (1993), Linde (2010), Aranda Anzaldo (2009) and Andrade (2009) have suggested,

the times are ripe for a change. At the end of her thoughtful paper, Linde (2010) asks whether a new expanded synthesis is needed. The answer is yes, but will it be Darwinian? If the internalist perspective is included it cannot be, since neo-Darwinism has ruled out this option. I believe, however, that if we rescue and take seriously the neo-Lamarckian Darwin, there would be no problem in reaffirming its Darwinian character. Thus, it is more important to think that an expanded synthesis cannot be possible unless a new ontological framework that surpasses the Cartesian Newtonian *a priori* assumptions is accepted. First of all, it is urgent to give away the preconception about the passivity of matter in order to be more consistent with twentieth century physics. Once this obstacle is removed, living organisms should be thought as being alive and therefore as autonomous material organized systems that process information and are permanently adjusting to their environment by choosing between at least two attainable alternative conformations. Thus, living beings are not only alive but intelligent since their differences with humans as Darwin (1874) proposed is of quantity and intensity, not of kind. We lack a metaphysics that allows thinking in the continuity between “energy-matter” and life and intelligence.

In what follows, I will sketch such a framework, yet to be developed. To start with, it must be accepted the *a priori* existence of one reality in which two main domains, internal and external, can be distinguished without losing sight of the continuity between them. Reality is material in the sense that can be approached by scientific research and experiments. The internalist perspective focuses on the following characteristics: potentiality, chance, openness, spontaneity, propensities, incorporation of environmental information, far from equilibrium, self-organization. From its part, the classical externalist school concentrates on actualities, determinism, closure, law-like behavior, discreteness, stabilization, statistical average, equilibrium, natural selection (Andrade 2003, 2009; Garcia Azkonobieta 2005).

Each main domain, internal and external, assumes two main levels of representation: one that correlates to individual organisms and another to communities at the population level. In this way, four neighborhoods can be distinguished [internal (individual/population) and external (individual/population)]. Besides, in order to preserve an integrated view the boundaries in either direction internal/external and individual/population must be also included. Thence we finally get four faces with their two interfaces crossed in both directions that can support an underlying ontology that all together yields eight basic characteristics of one material reality (Andrade 2007).

- (1) Internal individual zone, the realm of all present unconstrained possibilities, potentiality, chance, openness, spontaneity, tendency to diverge.
- (2) External individual zone, the realm of discrete individual actualized possibilities, closure, law like behavior, discrete actualizations of existing entities within concrete environmental boundaries and restrictions. For example, genes, organelles, cells, organisms etc.
- (3) Internal global zones, the realm of all real possibilities given the actual restrictions, propensities, constrained possibilities, informative potential given by the real possibilities enabled by historically gathered and constraining information. For example, DNA evolutionary recorded information.
- (4) Global external zone. It describes the frequency distribution or statistical regularities in a population of actualized potentialities in specific contextual restrictions. For example, the outcomes of NS.
- (5) The boundary from internal to external domains corresponds to unpredictable decisions about which of the constrained possibilities will be exteriorized and thus put to the external test of NS. Notice that these internally driven choices of one or a few among the many possible phenotypic adjustments depend on circumstantial environmental conditions, while being path dependent on evolutionary stored information. This is a process of "actualizing potentialities" characteristic of SO. For example, bifurcating points in development and evolution.
- (6) The boundary from external to internal zones will be best described as the gathering and permanent ongoing updating of environmental information and its incorporation into the internal record of organized living systems. That is the evolutionary process of "potentializing actualities". It expresses a feature of SO, since open systems self-organize by interaction with their environment, while at the population level it accords with NS in that it retains the genetic composition most fitted to the local environment.
- (7) The boundary from individual to population correlates to the emergence or aggregation of individuals into a higher level of organization. Emergence of higher order systems brings forth new unforeseen evolutionary possibilities.
- (8) The boundary from population to individual zones corresponds to the ultimate physical restriction to any natural process, as given by the second law of thermodynamics. Entropy is the most general law of evolution.

It must not be forgotten that the internal/external and individual/population boundaries are fuzzy for they are only aspects, faces or levels of

representation of one continuous organized whole, that nonetheless can best be grasped in a nested hierarchical systemic view in which units are contained within higher order units, since they are produced as entangled aggregates of such lower units. At every level of organization, the corresponding unit of interest is a higher order unit of a lower constitutive one and simultaneously a component of a higher level one. The recognition of these four domains and the corresponding interfaces configure a monistic materialistic framework for an ontology more suited for an expanded evolutionary synthesis, that would be Darwinian as long as it accords with his view of an unpredictable branching evolution that stems off from common ancestors. Yet this expanded synthesis will surely go beyond neo-Darwinism because it takes as fundamental the recognition of the internalist stance and SO, that is to say, the faces of reality named above as: (1) chance, (3) information potential, (5) individual choices at bifurcating points and (6) gathering and incorporation of environmental information.

The problem of deciding the weight that should be given to NS and SO can be solved by proposing two relations between them. First, SO is more general than NS, thence SO is a prior condition for the emergence of NS. Second, SO and NS are complementary. Once NS emerged, SO has to do with the emergence of organized systems and their variants and NS with the preservation of functionally selected variants in a local specific context. SO pushes the developmental systems through Salthe's phases immature (plastic), mature (positively constrained) until they reach senescence (negatively constrained) and inescapably break down and are subsumed by the lower levels of organization. In the interphase between the more vital juvenile and mature phase they reproduce and generate variants that are screened by NS. To summarize, NS pushes developmental systems towards the juvenile plastic regime where they maximize the exploitation of energy gradients thus dissipating entropy to the environment, whereas SO tends to increment internal entropy, so that the combined effect of both SO and NS leads to natural decay of all that once emerged and developed by SO and evolved by NS. To end up, NS screens a population of phenotypes modified by individual metabolic, physiological, ontogenetic and behavioral structurally constrained, yet random choices. Consequently, evolutionary theory cannot rely exclusively on the preservation by NS of functional structures that have proved to be successful, but also on the notion of organisms and species as self-organizing systems that emerge, vary, develop, ripe, reproduce, stabilize, decay and die.

NOTES

- 1 "Force is the causal principle of motion and rest and it is an external principle, which generates or destroys or in some way changes the motion impressed on any body. *Inertia* is the internal force of a body, so that its state cannot be easily changed by an externally applied force" (Newton en *De gravitate et aequipondio fluidorum*, cited by Koyré, 1965, p.189).
- 2 The highly constrained phylotypic stage due to physical forces allows divergences of considerable magnitude. Constraints do not exhaust evolutionary potential, but enable its actualization in certain preferred lines of variation.

REFERENCES

- Andrade, E. (2003), *Los demonios de Darwin. Semiótica y Termodinámica de la Evolución Biológica*. Bogotá, D.C. Colombia: UNIBIBLOS.
- Andrade, E. (2007), "A semiotic framework for evolutionary and developmental biology," *BioSystems* 90: 389-404.
- Andrade, E. (2009), *La ontogenia del pensamiento evolutivo*. Bogotá: Sello editorial, Universidad Nacional de Colombia.
- Aranda Anzaldo, A. (2009), "Darwin's two hundred years: is not time for a change?," *Ludus Vitalis* 15 (32): 87-99.
- Baldwin, J. M. (1896), "A new factor in evolution," *American Naturalist* 30: 441-451.
- Burkhardt, R. W. jr. (1995), *The Spirit of System. Lamarck and Evolutionary Biology*. Cambridge, Massachusetts: Harvard University Press.
- Darwin, C. (1838), *Notebook E, MS*, pp 83-84, in [Transmutation of species (1838-1839)] CUL-DAR124.- Transcribed by Kees Rookmaaker. (*Darwin Online*, <http://darwin-online.org.uk/>)
- Darwin, C. (1859), *The Origin of Species*. First edition. Chap. 13. London: J. Murray.
- Darwin, C. (1859), Letter 2449 — Darwin, C.R. to Wallace, A.R., 6 Apr 1859. www.darwinproject.ac.uk/entry-2449
- Darwin, (1862), Letter 3822 — Darwin C. R. to Hooker 24 [Nov 1862]. www.darwinproject.ac.uk/darwinletters/calendar/entry-3822.html
- Darwin, C. (1874), *The Descent of Man And Selection in Relation to Sex*. Chicago and New York: Rand, McNally & Company, Publishers.
- Darwin (1876), Letter to Moritz Wagner, Oct.13, in *Charles Darwin: Life and Letters*, edited by Francis Darwin, Murray, London, 1888, vol. III, p.159.
- Darwin, C. ([1883] 1894), *The Variation of Animals and Plants under Domestication*. Second edition revised. Fourth Thousand in Two volumes. Vol II with illustrations. New York D. Appleton and Company. 549 and 551 Broadway 1876.
- Dawkins, R. (1986), *The Blind Watchmaker*, Harlow: Longman.
- Depew, D.J. and B.H. Weber (1995), *Darwinism Evolving. System Dynamics and the Genealogy of Natural Selection*. Cambridge: A Bradford Book. The MIT Press.
- Dobzhansky, T. (1973), "Nothing in biology makes sense except in the light of evolution," *The American Biology Teacher*, March 1973 (35: 125-129).
- Flegr Jaroslav (2008), *Frozen Evolution. Or, that is not the way it is, Mr. Darwin*. Prague: Charles University in Prague, Faculty of Sciences.
- Fox Keller, E. (2003), *Making sense of life. Explaining biological development with Models, Metaphors and Machines*. Cambridge: Harvard University Press.

- Garcia Azkonobieta, T. (2005), *Evolución, desarrollo y auto-organización. Un estudio de los principios filosóficos de la evo-devo*. Universidad del País Vasco. Euskal Herriko Unibertsitatea. Donostía, San Sebastián.
- Gershenson C. & F. Heylighen (2003), "", in Banzhaf, W, T. Christaller, P. Dittrich, J. T. Kim, and J. Ziegler (eds.), *Advances in Artificial Life*, 7th European Conference, ECAL 2003, (Springer, LNAI 2801.), p. 606-614.
- Gottlieb, G. (2001), "A developmental psychobiological systems view: early formulation and current status," in Oyama, S., Griffiths, P.E. & Gray, R. *Cycles of Contingency. Developmental Systems and Evolution*. Cambridge: A Bradford Book. The MIT Press.
- Gould, S. J. (2002), *The Structure of Evolutionary Theory*. Cambridge: The Belknap Press of Harvard University Press.
- Haeckel, E. (1986), Prologo a la *Filosofía zoológica* in Lamarck, J. B. [1809] (1986).
- Ho Mae Won. and Saunders, P. (1979), "Beyond neo-darwinism. An epigenetic approach to evolution," *Journal Theoretical Biology* 78: 573-591.
- Hull D. L. (1978), "A Matter of Individuality," *Philosophy of Science* 45: 335-360.
- Hull D. L. (1980), "Individuality and Selection," *Annual Review of Ecology and Systematics* 11: 311-312.
- Jablonka, E. and M. J. Lamb (1995), *Epigenetic Inheritance and Evolution. The Lamarckian Dimension*. Oxford: Oxford University Press.
- Jablonka, E. and M. J. Lamb (1998), "Epigenetic inheritance in evolution," *Journal of Evolutionary Biology* 11: 159-183.
- Kauffman, S. (1993), *The Origins of Order: Self-Organization and Selection in Evolution*. New York: Oxford University Press.
- Kauffman, S. (1995), *At Home in the Universe. The Search for the Laws of Self-Organization and Complexity*. New York Oxford: Oxford University Press.
- Koyré, A. (1966), *Newtonian Studies*. Harvard University Press. Cambridge, Massachusetts.
- Lamarck, J. B. ([1802] 2003), *Recherches sur l'Organisation des Corps Vivans*. Paris: Centre de Recherche en Histoire des sciences et des Techniques CRHST/CNRS. <http://www.lamarck.net>
- Lamarck, J. B. [1809] (1986), *Filosofía zoológica*. Presentación de Adriá Casinos. Editorial Alta Fulla.
- Linde, M. (2010), "Natural selection and self-organization: a deep dichotomy in the study of organic form," *Ludus Vitalis* 18 (34): 25-56.
- Maturana, H. and Varela, F. (1992), *The Tree of Knowledge. The Biological Roots of Human Understanding*. Boston: Shambala.
- Maxwell, J. C. ([1870] 1990), Letter to F. Galton 28 February 1870. En *The Scientific Letters and Papers of James Clerk Maxwell: 1874- 1879*. Volume 3. Edited by P.M. Harman. Cambridge University Press.
- Newman, S. A. and Müller, G. B. (2000), "Epigenetic mechanisms of character origination," *Journal of Experimental Zoology* 288: 304-317.
- Newton, I. (1706), In Clarke, S (1706), "A Demonstration of the Being and Attributes of God," London 1706, in: *The Works of Samuel Clarke*, London, 1738. Quoted by Dou SJ, A 1997: "Newton-Clarke, Hanson y la experiencia religiosa", *Memorias de la Real Academia de Ciencias, Serie de Ciencias Exactas*, tomo 31, Madrid.
- Oyama, S. (2000), *The Ontogeny of Information. Developmental Systems and Evolution*. 2nd revised ed. Durham: Duke University Press.

- Peirce, C. S. (1891), *The Architecture of Theories. La Arquitectura de las Teorías*. Spanish translation by Marinés Bayas (2004), p: 439. *The Monist* I (Enero 1891): 161-76. Also in *Collected Papers* 6. 7-34.
- Popov, I. (2009), "The problem of constraints on variation, from Darwin to the present," *Ludus Vitalis* 18 (32): 201-220.
- Prigogine, I. & Stengers, I. (1984), *Order Out of Chaos. Man's New Dialogue With Nature*. New York: Bantam Books.
- Richards, R. J. (1992), *The Meaning of Evolution. The Morphological Construction and Ideological Reconstruction of Darwin's Theory*. Chicago: University of Chicago Press.
- Ruse, M. (1975), "Charles Darwin and artificial selection," *Journal History of Ideas* 36: 339-350.
- Salazar-La Ciudad, I., Jernvall, J. and Newman, S. (2003), "Mechanisms of pattern formation in development and evolution," *Development* 130: 2027-2037.
- Salthe, S. N. (1993), *Development and Evolution. Complexity and Change in Biology*. Cambridge, Massachusetts. A Bradford Book. The MIT Press, pp. 9, 45 and 181-185.
- Salthe, S. N. (1999), "Energy, Development, and Semiosis," in Edwina Taborsky ed. *Semiosis, Evolution, Energy: Towards a Reconceptualization of the Sign*. Aachen: Shaker Verlag, pp. 245-261.
- Salthe, S. N. (2010), "Limits to Darwinism," *Ludus Vitalis* 18 (34): 227-235.
- Slack, J. (2002), "Conrad Hal Waddington the last Renaissance biologist?" *Nature Reviews Genetics* Vol. 3: 889-895.
- Venel, G. F. (1753), "Chymie", *Encyclopédie ou Dictionnaire raisonné des sciences, des arts et de métiers par une société de gens de lettres*. Diderot D. et d'Alembert J. eds. Paris, M.DCC.LIII p. 409, 410, 413
- Waddington, C. H. (1957), *The Strategy of the Genes*. London: Geo Allen & Unwin.
- Waddington, C.H. (1961), "Genetic assimilation," *Advances Genetics* 10: 257-293.
- Wallace, N. (1858), "On the tendency of varieties to depart indefinitely from the original type," in Barrett, P. 1977 (ed.) *The Collected Papers of Charles Darwin*, Vol.II. Chicago: The University of Chicago Press, pp: 10-18.
- West-Eberhardt, M. J. (2003), *Developmental Plasticity and Evolution*. Oxford University Press.