CRITIQUE OF THE INTERNALISM/ EXTERNALISM APPROACH AS A WAY OF EXTENDING THE SYNTHETIC THEORY

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For around 150 years, Darwinism and the modern synthesis have endured as theoretical approaches in the field of evolutionary biology. Over this period, biologists have made unprecedented progress as regards to their concepts, methods and instruments. By way of example, when Darwin postulated his theory on the origin of species, it was not yet possible to see a chromosome, much less to see how it worked during the different stages of the cell division. Strikingly, the modern synthesis has generated a set of hypotheses that keep the core of Darwinian theory intact, as put forward in Marta Linde Medina's (2010) interesting target article.

A key concept in the theoretical structure of Darwinism and in the modern synthesis is that of 'natural selection,' which has yet to be scientifically defined in a clear-cut and verifiable manner. Thus, initially, natural selection was tautologically defined as the 'survival of the fittest,' and Mayr subsequently conceptualized it as 'differential reproductive success.' This shift entails much more than a mere semantic transformation. It also implies a conceptual shift from selection based on the organism's potential to a reproductive conception. In other words, what is 'selected' is the organism that leaves the most descendents or, to use current terms, the genes or sets of genes that pass on the most traits to future generations. This concept would be related to multicellular organisms that reproduce sexually, but would thus be inapplicable to organisms that reproduce asexually or by parasexual reproduction mechanisms. According to Dressino (2010), organisms that reproduce through these mechanisms are technically clones and do not present any genetic variation for natural selection to act upon. Another controversial aspect of natural selection is its metaphysical character, which Mayr (1998) himself asserts by stating

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This text comments the article "Natural selection and self-organization: A deep dichotomy in the study of organic form," by Marta Linde Medina, *Ludus Vitalis*, vol. XVIII, num. 34, 2010, pp. 25-56. Available at www.ludusvitalis.org/debates.

Ludus Vitalis, vol. XIX, num. 35, 2011, pp. 319-324.

that evolutionary explanations would not vary if 'God' were referred to instead of 'natural selection'. That is to say, if the causal factor were changed, the core structure of the theory would remain intact. On the other hand, Salthe (2010) conceptualizes natural selection as 'the physical principle of maximal energy gradient dispersion' (p. 227). This definition poses a thermodynamic approach to natural selection but it is very difficult to apply empirically.

In turn, Linde Medina proposes the internalism/externalism dichotomy as an argumental strategy through which to analyze the debate on the extension of the synthetic theory and the role of natural selection. Nevertheless, this controversy is becoming less significant as biology now relies on more integrated approaches, either deriving from or included in complexity theory. Thus, according to García-Azkonobieta (2005), the internalist perspective arises from material principles as a dynamic and systemic property that results from the interaction between simple units. On the other hand, according to the externalist approach, organization is the result of a historical selection process of functional adaptation to the environment, in which the organism is broken down into a series of features that can ultimately be considered as emerging manifestations of the genes they are made of. From this viewpoint, the autonomous character of organisms is weakened, since they are assumed to derive from an external organizing principle that brings about order. Therefore, the idea that the internalism/externalism debate itself might extend the synthetic theory is meaningless. Who would call into doubt that an organism is the resultant of self-organizing forces facing responses to environmental pressures? At present, the existence of a constant two-way exchange between organisms and their environment is widely recognized, thus bringing an end to the internalism/externalism controversy. Nevertheless, the dominance of the reductionist aspect of genetics avoids this interaction and, on the other hand, epigenetics seems to uncover the error of this approach. Therefore, the internalism/externalism dichotomy constitutes a methodological approach rather than an epistemological or philosophical one. In fact, the choice between an internalist (genetic, physiological, etc.) approach and an externalist (ecological, paleobiological, etc.) one is determined by the focus of the researcher when conceptually delimiting the system to be studied. In any case, an expansion of the synthetic theory could not be determined through these approaches.

The development of models based on the concept of modules is a reflection of this. In this sense, Schlosser (2002) proposes that, under certain conditions (which he does not specify), modules act as 'units of evolution'. He thus asserts that modules are more important in delimiting units of selection than either organisms or genes because they are less easily disrupted by recombination. However, Schlosser does not explain how a module can be selected or what definition of natural selection he is adhering to in order to justify this.

On the other hand, the modular perspective has also been applied to physiological adaptation—another important component of this theory, together with adaptation in its broadest sense—by means of a formal definition (Dressino 2005) and by a more general framework aimed at a modular theory of adaptation (Dressino and Lamas 2010). These authors have revealed the conceptual problems underlying traditional understandings of adaptation and the usefulness and biological sense of modular proposals relating to adaptation. In short, the scenario has moved from a strictly reductionist viewpoint (the traditional understanding of the gene) to an integrationist approach represented by modules.

The main problem of the synthetic theory is its reductionism, which is strongly based on the conceptual framework of "gene-centrism" (Dressino 2010) and the exclusive role of natural selection as a 'mechanism' or 'process.' It is evident that *mechanism* and *process* represent completely different ideas, but this is part of the conceptual polysemy proper to the synthetic theory in particular, and of biology in general (Folguera 2008). At any rate, regardless of whether natural selection is conceptualized as a mechanism or as a process, there is no doubt that it should be possible to enumerate or refer to its constituent elements. Yet this cannot be carried out since natural selection is, at best, a complex system very difficult to characterize.

Several authors (Maturana and Varela 1984) have pointed out the ideological connotations of the expression 'natural selection', also implied in the statements of Mayr's discussed above. One way of eliminating the ideological nature of this concept would be to use the expression *natural drift*, as proposed by Maturana and Varela (1984) and Maturana and Mpodozis (2000). According to these authors, 'natural drift' is the result of invariance of autopoiesis (self-organization of living systems) as well as of adaptation. It then follows that natural drift would constitute the most appropriate hypothesis for a module-based biology that would be thus in line with complex systems, as was previously stated.

Building on the modular argument, Newman and Bhat (2008) put forward the concept of "dynamical patterning modules" (DPMs) consisting in products of the 'toolkit' genes that characterize mechanical and chemical processes of cellular aggregates such as cohesion, viscosity, elasticity, diffusion, etc. This theoretical approach represents a major breakthrough in the understanding of the physical and genetic determinants of multicellular systems' development and evolution. These authors claim that the body plans and organ forms generated by these DPMs have been stabilized and consolidated by natural selection and genetic drift. Proving this assertion empirically is very difficult, due to the following basic reasons.

First, DPMs include physical phenomena over which natural selection exerts no power whatsoever. Second, the concept of 'gene' itself is undergoing a deep crisis, according to the authors belonging to the 'Human Genome Project' consortium (Gerstein, et al. 2007; Gingeras 2007). In this regard, genes no longer represent particle units with a specific location on the DNA strand, but are instead conceptualized as modules or 'transcriptors.' Thus, the current understanding of genes involves a number of elements that are often far apart from one another in the DNA strand as well as molecules of diffuse origin such as small RNA (RNAs), non-coding RNA (ncRNAs), interfering RNA (siRNA), etc., which render the work of natural selection—or at least the classical conception of this—untenable. Furthermore, this understanding gives rise to another question, namely, which genic unit natural selection acts upon, taking into account the deep interconnection between genic modules.

Moreover, Linde Medina (2010) affirms that part of Evo-Devo is compatible with the Darwinian paradigm if development is defined as a mechanism, which is genetically controlled by switching on and off genes. This has been questioned by Salthe (2008) on the grounds that natural selection is a weak force during embryonic development. Nevertheless, in developmental biology growth and development are not usually conceptualized as being exclusively controlled by switching on and off genes. Besides, development is a process that responds to a complex dynamics that goes beyond the individual action of specific genes. In this sense, epigenetics has shown that the switching on and off of genes may be the result of methyl groups incorporated into certain positions on the DNA strand. As such, the author's assertion that Evo-Devo represents a gene-centric perspective compatible with the synthetic theory is questionable. Additionally, the problems posed by the modern synthesis are made more complex by the presence of numerous substances in the environment that act as endocrine disruptors that compromise the development and differential reproductive success of the exposed species, regardless of their genetic make-up (Gilbert and Epel 2009). The historical development of Evo-Devo thus clearly proves that it did not emerge as a line of research related to the modern synthesis. Furthermore, the efforts made so far to unite Evo-Devo and synthetic theory have not succeeded for the reasons discussed above.

In short, as was mentioned above, if the internalism/externalism dichotomy has to do with a methodological decision, then an extension based on this categorization would be impossible since, as has already been explained, it is up to the researcher to strategically decide or propose the methodology of their approach.

Moreover the main reason for the 'Altenberg 16' meeting of July 2008 was supposedly the paper written by Bossdorf and others on the role of epigenetics. However, this was just an excuse, since there were several research papers on epigenetics prior to that by Bossdorf, et al. (2008). As has been already explained, the problem is that we are still using a 150-year-old theory, the core of which remains largely unchanged. We continue to refer to concepts such as 'adaptation' and 'natural selection', though they no longer mean what they did in 1859. Which means that the literature uses the same terminology to refer to a wide range of different concepts.

At this point, it seems reasonable to raise some questions. Is it necessary to extend or resynthesize the synthetic theory? The brief discussion presented above leads me to reflect that the overwhelming amount of available empirical data justifies the need for either a resynthesis or the development of a new theory that would include, in an appropriate manner, the progress made in all fields. Further, why do we biologists insist on resorting to the concept of natural selection, even, for example, when carrying out experimental research from which natural selection should supposedly be absent? A plausible answer to this question has to do with something mentioned above, namely that we are facing a theoretical-conceptual vacuum, in which the lack of new and more suitable explanations leads us to resort to ancient ones. Even so, this is a controversial point since some concepts can effectively help us to explain numerous empirical problems, many of which are becoming important in certain fields. This is the case with, for example, directed mutagenesis (applied in oncology), horizontal gene transfer (a concept used in phylogenies), epigenetics as an explanation in cases of speciation and in medical oncology, and so forth. Nevertheless, it is likely that these issues are also influenced by factors related to the sociology of science and which lie far beyond the scope of this discussion.

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