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SPECIAL FEATURE: DARWINIAN CORE AND POST-DARWINIAN EXTENSIONS

Darwin, and the role of theories in evolutionary thinking

Darwin y el papel de las teorías en el pensamiento evolutivo

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ABSTRACT

The section “Special Features” is dedicated to share with its readers thematic works about natural history, ecology and evolution. In this introduction we focus on the role that theories play in the construction of evolutionary thinking. First, we briefly show the importance of Lamarck’s work in the context of pre-Darwinian theories about organic evolution. Then, the main components of the Darwinian theoretical core and its postDarwinian extensions are thoroughly discussed. Finally the essays following this introduction in the present issue are summarized.

Key words: Darwin, evolutionary thinking, theories.

RESUMEN

La sección “Temas especiales” está dedicada a compartir con sus lectores trabajos temáticos sobre historia natural, ecología y evolución. En esta introducción nos centraremos en el papel que juegan las teorías en la construcción del pensamiento evolutivo. En primer lugar, se mostrará brevemente la importancia de la obra de Lamarck en el contexto de las teorías predarwinianas sobre evolución orgánica. Luego se discutirán en detalle los principales componentes del núcleo teórico del darwinismo así como sus extensiones postdarwinianas. Finalmente se resumen los ensayos que siguen a la presente introducción.

Palabras clave: Darwin, pensamiento evolutivo, teorías.

PRESENTATION

One year ago Revista Chilena de Historia Natural celebrated the 200th Darwin anniversary introducing this “Special Features” section, addressed to share with its readers thematic works about natural history, ecology and evolution (Camus 2009). There, Camus (2009) referred to the 200 year of the publication of “Philosophie Zoologique” by Jean Baptiste Lamarck (1809) as to one of the “forgotten anniversaries” in Darwin’s year. The contribution of Lamarck’s work to the consolidation of pre-Darwinian and Darwinian evolutionary thinking, is related, among other, with the development of a natural system of classification based on the comparison of structural attributes (i.e. nervous system), shared by discrete groups of organisms gradually increasing in complexity from “lower” to “upper” forms, but also with his less known reflections about the origin and evolution of Man, closing the first volume of his

“Philosophie...” (Lamarck 1809, in Packard 1901): “If man were distinguished from the animals by his structure alone, it would be easy to show that the structural characters which place him, with its varieties, in a family by himself, are all the product of former changes in his actions, and in the habits which he has adopted and which have become special to the individuals of his species. Indeed, if any race whatever of Quadrumana, especially the most perfect, should lose, by the necessity of circumstances or from any other cause, the habit of climbing trees, and of seizing the branches with the feet, as with the hands, to cling to them; and if the individuals of this race, during a series of generations, should be obliged to use their feet only in walking, and should cease to use their hands and feet, there is no doubt (...) that these Quadrumana would be finally transformed into Bimana (Man), and that the thumbs of their feet would cease to be shorter than the fingers, their feet only being of use for walking.”

After considering a series of more sophisticated attributes evidencing the gradual "supremacy" reached by those "more perfect" *Quadrumana*, Lamarck (1809) concludes (in Packard 1901): "Such would be the reflections which might be made if man, considered here as the preeminent race in question, were distinguished from the animals only by his physical characters, and if his origin were not different from theirs".

The contribution of Lamarck to evolutionary thinking was practically neglected in the frame of the 100th anniversary of the publication of the "Origin...", with the introduction of the caricature of the Lamarck's explanation for the giraffe's neck in the textbooks and mass literature dedicated to explain Darwin's work to the broad public, mainly in the U.S.A. Before that, anglosaxon literature was far more polite with the French heritage in evolutionary thinking, as is evidenced by the British zoologist Alpheus S. Packard (1901): "The rise and rehabilitation of the Lamarckian theory of organic evolution, so that it has become a rival of Darwinism; the prevalence of these views (...) especially in France, where its author is justly regarded as the real founder of organic evolution, has invested his name with a new interest". Certainly not ever since Darwin, the celebration of the 200th anniversary of the birth of modern evolutionary thinking continues. The topics treated in this Special Feature were first presented at the 51st Annual Meeting of the Society of Biology of Chile in the Symposium "Current problems in Evolutionary Biology and Genetics: The role of theories" (Manríquez 2008¹), being later sent to *Revista Chilena de Historia Natural* as formal contributions. The main aim of the meeting was to explore and discuss the role that Darwinian theories have played and continue to play in the construction of evolutionary thinking. Conscious that it is practically impossible to reach that aim in one, or indeed in many meetings, the presentations were focused on some post-Darwinian extensions (macromutations, neutralism, evo-

devo, biocultural studies), as well as on the relationship between them and the core of Darwinian theories (i.e. the question of the need of a new evolutionary paradigm).

THE DARWINIAN CORE AND ITS POST-DARWINIAN EXTENSIONS IN EVOLUTIONARY THINKING

"A theory is a good theory if it satisfies two requirements: It must accurately describe a large class of observations on the basis of a model that contains only a few arbitrary elements, and it must make definite predictions about the results of future observations" (Hawking 1996).

The cell theory of structure and function of living beings, the chromosomal theory of heredity, and the theory of organic evolution constitute the conceptual framework of current biological sciences. Although all of them satisfy Hawking's requirements to be considered as "good" theories, perhaps the most comprehensive and general is the theory of evolution. Following the classical definition of Kuhn (1977), from Darwin times the theory of evolution has represented a paradigmatic change in the way the members of the scientific community study the origin and diversity of life on Earth, making it possible to test hypotheses about the causality of evolution as a factual process. Its comprehensive character is reflected in the specific theories proposed by Charles Darwin understanding evolution as a process of descent with modification from a common ancestor (Darwin 1859, 1871), by means of natural selection (Darwin 1859) and sexual selection (Darwin 1871).

After Gould (2002) these Darwinian theories are on its own the "syllogistic core" over which the post-Darwinian evolutionary thinking has been constructed and should be thereafter constructed. Thus, these two nomological corpuses, namely the Darwinian and the post-Darwinian represent, respectively, the structural basis and the extensions of current evolutionary theory. According to this interpretation, the principle of natural selection is deduced from the syllogism, if A = superfecundity; B = variation, and C = heredity, and being A, B, and C true,

¹ MANRÍQUEZ G (2008) Simposio problemas actuales en genética y evolución: El lugar de las teorías. Actas LI Reunión Anual de la Sociedad de Biología de Chile (Coordinador, G Manríquez). Biological Research 41 (Sup. A) R-25.

then natural selection will occur. The empirical evidences given by Darwin itself for A, and B in the “Origin...” (Darwin, 1859), and for A, B, and C by the founders of the synthetic theory of evolution and therein, show unambiguously that natural selection is an evolutionary factor. However, the principle of natural selection does not allow inferring per se the agency of selection, neither to know its effects. Moreover, this principle does not allow by itself to understand the pattern of phenotypic variation observed in the fossil record or in ecological contexts. These three issues were solved by Darwin considering that selection operates on individuals competing for limited ecological resources, that the main effect of selection acting in natural populations are adaptations, and that natural selection can be extrapolated as the main cause of evolutionary change occurring at all scales and levels, including geological (Gould 2002).

Neodarwinism, neutralism, punctuated equilibrium, and more recently, the evo-devo and biocultural approaches are, among many other, representatives of the post-Darwinian extensions of the Darwinian theoretical core, in the sense that all them are characterized by a critical revision of the extrapolation of natural selection to levels not related with microevolutionary processes, including human societies. These post-Darwinian extensions are also characterized by an emphasis on the populational nature of Darwinian original proposals. It seems therefore reasonable to consider that being constitutive parts of the same theory, there would be no contradiction between both corpuses but a sort of genealogical continuity accompanied by historically determined transformations through permanent revisions. Following Gould (2002), it is a revisited interpretation of the Hull's (1988) concept of theories as “conceptual lineages”.

Undoubtedly, the Darwinian populational approach, as well as the extensions of post-Darwinian evolutionary thinking have influenced the way we understand evolutionary processes working at different levels of structural complexity. The deep analogies found between molecular and organismic levels of evolution as expected according to the classical directional, disruptive and purifying selective patterns (Díaz-Arenas &

Lehman 2009), the gene-culture coevolution hypothesis stating that cultural values have evolved, are adaptive and influence the social and physical environments under which genetic selection operates (Chiao & Blizinsky 2010, Pinker 2010), the use of populational thinking to construct a realistic and testable theory of culture (Richerson & Boyde 2005), the comparative analysis of human languages as phylogenies (Pagel 2009, Whitfield 2009), are just a few examples of the above mentioned influence. Finally, in the frame of post-Darwinian extensions the historical continuity of the Darwinian core is accompanied by a shared content which, according to Gould (2002): “(...) should be expressed as a minimal list of the few defining attributes of the theory's central logic- in other words, only the absolutely essential statements, absent which the theory would either collapse into fallacy or operate so differently that the mechanism would have to be granted another name”.

ABOUT THIS SPECIAL FEATURE

The essays included in this Special Feature focus on theoretical issues concerning a developmental understanding of homology as a central concept in evolution, the appropriateness of some key concepts of the theory of neutral evolution, the discussion about the pertinence of a new post-Darwinian evolutionary paradigm, as well as a critical understanding of the difficulties that arose between Darwinian theories and social sciences in the 19th century.

Aboitiz (2010) shows how homology is a key issue in evolutionary biology, as it permits to trace the phylogenetic history of specific organs or components of the body. However, according to this author this concept is at the same time among the most controversial ones in this field, not the least because of the many different criteria used to identify homologous organs. In his article Aboitiz claims for a developmental understanding of homology and evolution in general, where the genetic regulation of the ontogenic process provides clues to the ancestry of different organs. More specifically, he discusses a highly controversial issue in comparative

neurobiology: the origin of the mammalian neocortex. Some authors rely on comparisons of neural connectivity between mammals and sister taxa to propose homology of this organ with specific non-mammalian brain components. On the other hand, other authors that are strongly based on developmental criteria, identify different non-mammalian structures as homologous to the neocortex. Aboitiz's proposal is that by identifying the genetic networks regulating the developmental mechanisms of different organs, a solution can be proposed that points to a conciliation of these radically different views of brain evolution.

Nespolo (2010), through a didactic review shows how biologists study adaptations at the population level, applied actual research examples to outline how the classic theory (termed as the "basic scheme") is useful to answer relevant questions in biology and how a less dogmatic paradigm (or a more versatile one) would be needed when dealing with the most recent and "extravagant" cases of gene, genotype, phenotype and environment interactions. In this review it is concluded that the basic scheme is useful and sufficient for testing relevant evolutionary hypotheses, in most cases. However, it is argued that something else is needed to explain the observed genetic variation that some species exhibit. Nespolo mentions the "extravagant" biology, which is represented by the recent discoveries in biological processes such as horizontal gene transfer, epigenetic inheritance, adaptive anticipatory conditioning, evolutionary capacitance and niche construction. It is clear that this "post-modern" biology need to be considered as widespread in nature, justifying an extended evolutionary synthesis.

Similarly Valenzuela (2010) states that in spite of the fact that the evolutionary theories include mutation, genetic drift and selection as the main factors of evolution, and that the theory of life based on autopoiesis includes also natural or phenotype drift, no evolutionary theory has proposed a quantitative proportion by which each factor contributes to evolution. So, according to Valenzuela's views, each theory has exaggerated the role of the factor it considers most important. After this author, this exaggeration has produced a bizarre

picture of the evolutionary process which deserves a theoretically based critic.

Finally, Manríquez (2010) analyzes the historical causes leading to a fragmented and not easy relationship between Darwinian theoretical corpus and social sciences in the academic world of Europe at the end of the 19th century. He also explores the background allowing the emergence of Darwinian theories on evolution of *Homo sapiens*, recognizing their relevance as tools of integrative thinking in social sciences. Manríquez (2010) then shows how the works of T.H. Huxley and A.R. Wallace positively stimulated Darwin to answer the question about the origin of man from a primate ancestor living in Africa, as well as to consider culture from an evolutionary perspective as a factor opposed to the negative action of natural selection on human societies. According to Manríquez (2010) this view is opposed to the classical interpretation of Darwin's work pervading social sciences during more than one century, according to which Darwin ideas contributed to an erroneous interpretation of the evolution of human societies due to the application of the principle of natural selection to social processes.

I would like to share with the readers my hope that the essays presented in this number will contribute to promote an open and critical discussion about the Darwinian legacy, its extensions, and their importance in the development of evolutionary thinking in our country, both in natural and social sciences.

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