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LAMARCK AND DARWIN: DOGMA, HISTORY AND SCIENCE

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ABSTRACT

The text discusses three relevant aspects of biological evolution: the Darwinian and Lamarckian dogmas, historical aspects and some relevant questions on the contemporary molecular genetics.

Key words : biological evolution, historical aspects, molecular genetics.

RESUMO

O texto discute três aspectos relevantes sobre a evolução biológica: os dogmas Darwinianos e Lamarckianos, aspectos históricos e algumas questões relevantes sobre a genética molecular contemporânea.

Palavras–chave : evolução biológica, aspectos históricos, genética molecular.

DOGMA: DARWINISM *VERSUS* LAMARCKISM

We are all familiar with the Dogmas of biological evolution: There is the Darwinian Dogma of "random variation and natural selection", which is still largely adhered- to, particularly by the ecologists of "The Old World", and there is the discarded, Lamarckian Dogma of the inheritance of phenotypic modification of organs as the direct effects of use and disuse. The customary examples cited are the Darwin- Finches of the Galapagos Islands with more or less curved beaks, and hence, more or less successful alimentation and reproduction (Darwin, 1859), and the giraffes with ever longer necks, because they try to reach ever higher branches when feeding (Lamarck, 1809).

Both theories with - of course - more refined arguments and evidence, were taught worldwide up to the 1920-ties, when, as a consequence of social revolutions and two world wars, the world of *Homo sapiens* broke up into the *Capitalist*-dominated and the *Communist*-dominated countries with their respective regions of influence (colonies, etc). In the Sowiet Union, Lamarckism was indoctrinated, because a better society should improve the social behaviour of humans, and in the Western World (the Americas, Australia and western Europe) Darwinism remained as the exclusive theory of evolution, and spread into every-day life: growth via competition and selection, survival of the fittest, guaranteeing successfull business, excellence in science, etc, etc. Eventually, "The Berlin Wall" fell (1989) and the communist dictatorship of the Sowiet Union came to an end.

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Subsequently, dogmatic Darwinism conquered the world. The success of Darwinism was supported by contemporary science, mainly by classical genetics with successful selection of "mutants", i.e., inheritable genotypes with their respective phenotypes, and by the discovery of the DNA-chromosome structure (Watson & Crick, 1953), with the demonstration of random mutations. Thus, 20st-century molecular genetics resulted in the *Neo-Darwinian Central Dogma: Evolution as the result of random mutations and natural selection*. Lamarck and Lamarckism had died and Darwinism remained as the sole theory of evolution, as recently expressed by Richard Dawkins in "Newsweek" (Dec. 2005-Feb. 2006): "...natural selection, the engine of evolution first discovered by Charles Darwin"...."New variation is added to the gene pool by mutation , random mistakes that occasionally turn out to be superior".

HISTORICAL NOTES

As a matter of fact, scientific discussions on possible mechanisms of biological evolution reach back to the Classical Greek epoch some 2400 years ago.

Aristoteles (384 - 322 BC) presented the theory that *Homo sapiens* and the higher animals were the result of a continuous evolution from the inorganic, mineral world via plants to plant-like animals (the reef fauna!) to the higher animals. As regards the higher animals, he based his views on embryological criteria (Mason, 1961) and of comparative anatomy. Thus, he refers to the high similaritiy of anatomy between apes and *Homo* as an argument for evolutionary relationship. He maintained that the particular features of organs were the result of their function. Using the example of human teeth, he explains that the sharp front teeths developed because they are continuously used for cutting, and the shape of the molars because they are used for chewing. But then, he writes: "it is said, that this does not occur for a purpose, but happens in this way by chance, also in case of the other organs which appear to fulfill a purpose. Now, those organisms, in which everything is formed as if it were for a purpose, would survive, because everything fitted as if for a particular function, those, however, for which this was not the case, would get extinct" (Nestle, 1953; Walker, 2005).

Here they are, the two theories neatly separated: evolution of the specific shape of organs as the result of intensive use, or else, natural selection of random variants. I cannot deny my considerable surprize when I came across this passage in Aristoteles' text (Nestle, 1953), and I imagine that the same happened to Lamarck and Darwin, because both refer to Aristoteles in their work.

Lamarck (1744 -1829) was professor of Zoology at the Museum of Natural History in Paris, and he was a member of the Naturalists Society of Moscau, of the Royal Academy of Science of Munich, among others, and just to highlight the globalization of Science some 150 years ago, it may be mentioned that George Cuvier (1769-1832), professor of comparative anatomy and a collegue of Lamarck, was a member of Scientific Societies and Academies of Stockholm, Copenhagen, Goettingen, Modena, Calcutta, among others.

Lamarck did for Zoology, what Linné (1707-1778) achieved for Botany: Lamarck (1809) created the classical systematics of the animal kingdom, as it is still largely valid today on the highest levels of classification (Phyla, Classes, Orders). It is in relation to the basic sub-division of the animal kingdom that Lamarck refers to Aristoteles: Aristoteles separates the animal kingdom into two divisions: Animals *without* blood and Animals with blood, while he, Lamarck, separates animals *without* backbones (*Invertebrates*) from animals *with* backbones (*Vertebrates*). Incentivated by the discussions between the scientists at his time as regards possible biological evolution, and based on his profound knowledge of comparative anatomy, morphology and behaviour, he defends a coherent theory of animal evolution, which he summarized as follows (Lamarck, 1809):

"I looked upon it as certain that, firstly, the movement within the animals - a movement which is progressively accelerated with the increasing complexity of the organization and secondly, the influence of the environment, insofar as animals are exposed to it in spreading throughout all habitable places, were the two general causes which have brought the various animals to the state in which we now see them". Translated into modern biological terms: The response of animals with an ever more complex physiology ("movement within the animals") to their specific environments ("spreading throughout all inhabitable places") results in the actual phenotype ("state in which we now see them"). Lamarck formulates two basic laws:

1. "In every animal which has not passed the limit of its development, a more frequent and continuous use of any organ gradually strenghtens, develops and enlarges that organ, and gives it a power proportional to the length of time it has been so used; while the permanent disuse of any organ imperceptively diminishes its functional capacity until it finally disappears".

2. "All the aquisitions wrought by nature on individuals through the influence of the environment in which their race has long been placed, and hence, through the influence of the predominant use of any organ, all these are preserved by reproduction of the new individuals which arise, provided that the acquired modifications are common to both sexes, or at least to the individuals which produce the young" (Lamarck, 1809).

In other words: physiological and behavioural ("use and disuse of organs") response of individuals to specific environments during their ontogenesis ("animal which has not passed the limit of its development") leads to inheritable acquisition or loss of organs and faculties "provided the race has long been placed in the respective environment". Thus, evolutionary change is a slow, long-term process, and heredity enters the scene via the condition that the "individuals which produce the young" must be affected by the specific phenotypic characteristics, and this implies *selection*. Besides, both, Lamarck and Darwin refer to plant and animal breeding of domestic races as argument in favour of evolution, selection of hereditary traits in agriculture was no novelty 200 years ago. Thus, while Lamarck certainly emphasizes "use and disuse", heredity and selection of animals with the respective phenotypic traits are implicit in his two laws. One source of later mis-representations is, that Lamarck himself did not clearly specify between periods of individual ontogeny and sequences of ontogenies in his first law: "proportional to the length of time of use" and "permanent disuse" refer to evolutionary periods, i.e. to sequences of ontogenies, while the individual physiological effects of use and disuse are restricted to the individual's period of development ("animal which has not passed the limit of its development").

Darwin (1809-1882) studied in Edinburgh and Cambridge, and in 1831 - being just 22 years old - he travelled on the sailing boat *Beagle* to South America on a scientific expedition. Later, he devoted his life to research and writing. "The Origin of Species" (Darwin, 1859) initiates with "An historical sketch", where Darwin introduces Lamarck as the (cit) "justly celebrated naturalist ... being the first man whose conclusions on the subject (= transformation of species) excited much attention", thus referring to Lamarck's work "Philosophie Zoologique "(1809). In a footnote in the same chapter, Darwin mentions Aristotoles, and presents an English translation of Aristoteles' example of the possible evolutionary transformation of teeths (*see the first paragraph of this topic*), and he adds (cit): "We here see the principle of natural selection shadowed forth....". In this "Historical Sketch" Darwin documents the situation of the biological sciences at his time, and the intense discussions for and against theories of evolution in Europe and the USA. He notes the remarkable coincidence, that his grandfather - (cit)

"Erasmus Darwin in England, Geoffroy Sait-Hilaire in France and Goethe in Germany came to the same conclusions on the origin of species in the years 1794 - 1795" and thus, to some degree, anticipated the ideas of Lamarck. But here already, Darwin expresses his rejection of their "erroneous grounds of opinion" as regards the mechanisms of evolution (inheritance of characters originating via parental use or disuse of the respective organs). However, within the context of early 19th century science, concise separation between biological observations and scientific conceptualization was difficult, and also led to problematical statements by Darwin: In the Chapter on "Variation under Domestication" Darwin writes (cit): "Changed habits produce an inherited effect....With animals the increased use or disuse of parts has had a marked influence; thus I find in the domestic duck that the bones of the wing weigh less and the bones of the leg more, in proportion of the whole skeleton, than do the same bones in the wild duck: and this may be safely attributed to the domestic duck flying much less, and walking more, than its wild parents". Would Lamarck disagree? Two pages later, Darwin writes: "Any variation which is not inherited is unimportant for us"; and further "The laws governing inheritance are for the most part unknown" and this includes the origin of hereditary variation. Although Darwin does not refer to selection in the example of the ducks, he might have explained that the domestic ducks had stronger leg bones because the better walkers had a selective advantage, in other words, "use and disuse"enter as selective function. As a matter of fact, he leaves the "Lamarckian" versus "Darwinian" question open: In the last paragraph of "The Origin of Species", Darwin summarizes his basic theory of evolution (cit): "These laws, taken in the largest sense, being Growth and Reproduction; Inheritance which is almost implied by reproduction; Variability from the indirect and direct action of the conditions of life, and from use and disuse; a Ratio of Increase so high as to lead to the Struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of the less-improved forms".

It is interesting, that in this summary, "natural selection" is restricted to competition ("Struggle for Life"), while in the example of the ducks, and indeed, in large sections of "The Origin", Natural Selection refers mainly to improved morphology, physiology and behaviour. The likely reply to this comment is, that competition is won *because* of the improved phenotype. This may - or may not be the case. Suppose we keep an experimental culture of mice or insects under optimal conditions of maintenance and nutrition, keeping the population number constant by periodic random elimination of individuals: selection would be fully active via different growth rates of the respective types, in complete absence of competition for space or for resources. The fraction of the fastest reproducing genotypes would continuously increase. The analogous situation in natural systems woud be, that predation and disease keep populations at relatively low and constant densities.

Darwin's final - and largely intuitive - conclusion that competition is the only effective selection pressure in natural populations, as expressed in the last paragraph of "The Origin", eventually resulted in dogmatization, and as such, in a painful stagnation of theoretical biology. Would explicit consideration of todays molecular genetics in relation to possible mechanisms of evolution open up new questions, new answers and new aspects as regards the historical divergence between Lamarckian and Darwinian ideas?

SOME RELEVANT ASPECTS OF CONTEMPORARY MOLECULAR GENETICS

1. The Basic Questions: While obscure socio-political entanglements with science teaching may result in dogmatic stagnation, the obvious way out of it is progressive research, and todays problems of evolution must be tackled by molecular biology. The development from a single cell to a complex, multicellular organism, involves progressive cell-differenciation and cell-agglomeration to ever higher hierarchical levels of organization, be it ontogeny or phylogeny, and this process is programmed by the genome. Physically, there are two basic parameters: Structure = "order in space" and Function = "order in time", and any complex material system is the result of the obligatory linkage between these two parameters, as may be shown by a simple example: The material for the construction of a building is being deposited on the site, bricks, cement, sand, tiles, cables etc, does this allow anybody to predict the size, purpose or structure of the project, an apartment block, a series of one-family houses, a church, a palace, an industrial office block or what else? Only a concise construction plan, i.e., specified sequential activities, determine the final result. Even single, eucaryote cells are far more complex, both structurally and functionally, than a housing project, not to mention multi-cellular organisms with their hierarchical structure, where structural and functional causalities interact between different cells, tissues, organs and segments, linked by circulary and nervous systems. This shows that explicit specification of order in space and of order in time is required to understand any process of ontogeny and phylogeny.

Darwinism, confirmed by classical genetics, was dominated by structural considerations: the duck's bones of the legs and wings determine its pattern of mobility; a particular mutation in the genotype causes a change of growth and differentiation: function is the result of structure. There is nothing wrong with this - this is the reason for the historical success of Darwinsm, but we ask, is this the whole story?

Lamarckism stresses the inverse causality: dynamic interaction between cells, organs and environment shapes the phenotype, which is eventually fixed in the genotype. Although there are inumerable examples of environmental effects on the physiology of animal and plant ontogeny, and hence, on adult anatomy and morphology (Lit. refs. see Walker, 2005), hereditary fixation of these induced phenotypes in particular genes was never shown. This is the convincing reason for the rejection of Lamarckism. But we ask: considering space-time interaction on the level of modern, molecular genetics, is this rejection justifyable?

2. Structure and Function of the Cell Nucleus: This is not an article on molecular genetics, but to bring the historical process to the present, a few aspects of todays state of affairs are briefly outlined.

The discovery of the genetic code as nucleotide sequence along the DNA double-helix of the chromosomes (Watson & Crick, 1953) was the decisive event that iniciated molecular genetics. The number of nucleotides per cell nucleus vary from several million in Bacteria to ca 3 billion (3 x 109) in *Homo sapiens* (Eigen & Schuster, 1979). The linear sequence of nucleotides in the chromosomal DNA determines the sequence of amino acids in proteins, that is, the *structure* of the DNA determines the *structure* of the basic building materials of the living cell. Thus, the shape and structure of the living cell seems to be the result of *spatial* determinants. Mutations in DNA result in changed organic structure and consequently, in variation of function and fitness.

A bewildering discovery was, that less than 5% of the DNA per nucleus was coding, the bulk of the chromosomes was consequently referred to as "junk DNA". In the course of time, functional aspects appeared: particular proteins are needed during particular phases of the cell cycle and of ontogenetic differentiation, particular genes must be transcribed into mRNA at different instants, and these must be transported out of the nucleus into the cytoplasm for translation into the respective proteins. Signal domains in DNA were identified, such as promotors which initiate transcription of specific genes upon particular stimulation by imported signal molecules etc. Scherrer

(1989) proposed that the three-dimensional structure of the genome with its "junk DNA" was essential for the guided transport of macromolecules into, through and out of the nucleus during DNA- directed growth control. Today there is no doubt that this model is fully realistic, and gene regulation, involving nuclear architecture, determining the time pattern of DNA- and RNA-dependent physiology is as well established as is the genetic code as such, as shown for example by Leers & Renkawitz (2005), and in an article on signal-dependent activation of gene transcription by nuclear receptors we read (Ju*et al.*, 2006,) : "Multiple enzymatic activities are required for transcriptional initiation". Enzymes are proteins and - as such - are coded for in the chromosomal DNA, that is, the genome codes for its own gene- regulatory mechanisms.The data in this article also show a functional link between the described mechanism of gene transcription and DNA-repair; complex machines need repair, and the cell nucleus is no exception, as is well known today.

Gene regulation determines the time pattern of ontogenesis and physiology: differential activation or silencing of genes results in different tissues, the number of mitoses in different tissues during ontogenesis determines the relative size of organs, of branching patterns in plants, of segmentation in animals etc. Thus, if we consider the different cells of an organism, we see that a "same" (original, gametic) genotype results in many different cell phenotypes within a given individual. This whole biochemical machinery is also influenced by environmental parameters, by temperature, pressure, diurnal rhythms, altitudes above sea level etc, which may result in diverse phenotypes. For instance, plants in high altitudes have relatively shorter stalks than the same plants in low lands, or a given species of micro-crustacea has different segmental patterns if raised in waters of different salinities (Abonyi, 1915) to mention two of the numerous classical examples. Furthermore, physiological activity may influence the dynamic pattern of gene regulation, and hence, have an influence on the phenotypes of the respective organisms: intensive use of wings or legs in the ducks may strengthen the respective bones, to return to Darwin's example. The inevitable conclusion is that similar genotypes may exhibit different phenotypes depending on the environmental and /or physiological conditions during ontogenetic development. Both, Darwin and Lamarck would agree.

3. Mutation and Selection in Gene-Regulation:

Naturally, genes coding for enzymes involved in gene regulation, and DNA-domains responding to specific gene-regulatory signals, are also suffering mutations, and as such, are subject to natural selection, as are the classical genes coding for structural proteins. But there is a very fundamental, physical difference between these two categories of mutations: gene regulation means phase order, i.e., pattern in time, and the *physical parameter of time is one-dimensional*. Structure, on the other hand, always involves space, and space is *three-dimensional*.

A mutation in the gene of a structural protein changes a defined point in the three-dimensional structure of this protein, and different proteins join to complexes of higher, hierachical order, such as hemoglobin for example, a tetramere composed of one pair each of two different hemoglobin monomeres. Whatever the mutations in the DNA that affect the sequence of amino acids in the respective protein, there is a one-to-one relation between the mutations in DNA and the changes in the respective protein. The pattern and complexity of the genetic code corresponds essentially to the pattern of protein complexity of the respective organisms. This direct spacial correlation explains the enormous success of classical genetics.

A mutation in the code of gene-regulatory enzymes and/or in DNA-signalling domains can have only two possible effects: enhancement or slow down of the functions directed by the respective molecules, slow down including zero function. Therefore, innumerable mutations and combinations thereof may lead to similar phenotypes, for instance to retardation of a particular phase during embryogenesis, resulting in increase or decrease of organs or of the number of body segments etc. In addition, environmental effects modify these genetically induced, dynamic patterns. Only modern molecular genetics combined with detailed physiological experimentation allows to disentangle the complex web of biochemical interactions of a gene-regulatory process.

Still, gene-regulatory systems are also subject to mutation and natural selection that optimize phenotypic fitness in particular environments. Species occupying highly and irregularly varying environments maintain their gene-regulatory, i.e., physiological flexibility and thus may exhibit a wide range of locally induced, yet reversible, morphological variation (= "somatic plasticity", *see* West-Eberhard, 2003); species occupying particular environments for very long periods accumulate mutations that optimize fitness in this particular environment and thus, are gradually fixing a particular phenotype, because selection for reversal is no longer active (Walker, 1983). These processes are practically inevitable, because of the one-dimensionality of time: innumerable mutations may have similar effects. The result is *genetic fixation of an environmentally induced phenotype via random mutation and natural selection*: Lamarck and Darwin in a single sentence.

4. Exon Shuffling - Open Questions: While this article is confined to DNA-random mutations and natural selection, biological mechanisms that certainly play their role in the process of evolution, it must be emphasized that todays molecular biology is no longer confined to this axiom.The "classical gene" as a defined DNA-sequence that codes for one particular protein no longer exists. "Genes" are variable physiological entities, composed of "exons", i.e. coding subunits which are separated by non-coding DNA-stretches, the introns. During embryogenesis different exons of a single gene - and/or exons joined from different genes- may compose the final codes of the particular proteins in the diverse tissues of the individual. In other words, tissue-specific genes are constructed during ontogenesis. Ontogenetic and phylogenetic genome analysis shows that both, within-gene and between-gene "exon shuffling" is a decisive mechanism of genome evolution, exon shuffling being directed by a highly complex process of gene regulation.

A specially relevant category of gene regulation is *epigenetics*. Within the evolutionary context it means that the parental genotype regulates specific gene functions in oocytes and/or zygotes, that is, non-DNA variations can be transmitted from parents to offspring (Jablonka & Lamb, 2002). *Epigenetic imprinting*, on the other hand, means that parental gene regulation changes the DNA-structure of the fertilized oocyte (Meroni *et al.*, 1996). Today, *epigenetics* is a wide field of research, both, in the context of medicine and of evolution, which resulted in the explicit rehabilitation of Lamarck and of his theories as a valid historical contribution to the development of the biological sciences.

To terminate this discussion we may conclude that - while contemporary Biology would not be possible without the historical scientific process including the essential contributions of both, Lamarck and Darwin - todays situation as regards the problem of biological evolution transcends the respective questions of the last two centuries.

While natural selection via the rates of reproduction and mortality is inevitable during the phylogenesis of whatever plant and animal species, the highly complex mechanisms of specific exon combination during gametogenesis and ontogenesis leaves the basic problems of evolution unresolved, namely the possible biochemical interactions between DNA-(random?) mutations and gene-regulatory functions that may result in viable, inheritable phenotypic variation, and - eventually - in taxonomic differentiation.

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