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CRITICAL NOTICE

Between the Seventeenth and Twenty-First Centuries

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What Darwin Got Wrong, by JERRY FODOR and MASSIMO PIATELLI-PALMARINI, NEW YORK, FARRAR, STRAUS AND GIROUX-MACMILLAN, 2010, 288 pp. $ 12.47.

INTRODUCTION

Evolutionary biology is one of the most vibrant and exciting areas of current science, attracting more and more people from different disciplines such as physics, computer science, philosophy, psychology and so on. However, far from being attracted to it, Jerry Fodor and Massimo Piattelli-Palmarini (hereafter FPP) have launched a fierce attack on current evolutionary theory in their book *What Darwin Got Wrong* (2010). Parts of this challenging critique have been answered by several frontline biologists and philosophers of biology [Block and Kitcher (2010), Coyne (2010), Diéguez (2011), Díez and Lorenzano (2013), Futuyma (2010), Godfrey-Smith (2010), Pigliucci (2010), Richards (2010), Rosenberg (2013), Sober (2010)]. Here, we will focus on two different issues dealt with in FPP's book: the concept of adaptation and the supposed conflict between an external and an internal view of evolution. Thus, we will divide this paper into two parts. In the first part, we will discuss the notion of adaptation postulated by FPP and its striking resemblance to pre-Darwinian positions. The second part will focus on the explanatory dimensions of evolutionary theory.

I. ADAPTATION AND NATURAL ECONOMY

As stated above, FPP's book has sparked a great many comments. But, despite this, one issue seems to have gone unnoticed by most of its reviewers: the approach to the phenomenon of adaptation. The current view of biology maintains that Charles Darwin's work was a naturalist's account of adapta-

tion, which had received supernatural explanations hitherto. In fact, John Maynard-Smith even said "adaptation is the most obvious and all-pervasive feature of living things, and one that any theory of evolution must explain" [Maynard-Smith (1989), p. 4]. The adaptation phenomenon, apparently an exquisite fine-tuning between environment and living beings, was among the *explanandas* which the Theory of Evolution by natural selection endeavors to explain from the start.

However, FPP have a radically different view of it. Thus they consider:

> You don't after all need an adaptationist account of evolution in order to explain the fact that phenotypes are so often appropriate to ecologies (…) It is just a tautology that (if it isn't dead) a creature's phenotype is appropriate for its survival in the ecology that it inhabits [Fodor and Piatelli-Palmarini (2010), p. 142].

And a few pages later:

> (…) you don't need the theory of evolution to explain why a creature's phenotype is well adapted to its environment (i. e. to the world); that follows simply from the fact that there are creatures with that phenotype. All creatures that are neither extinct nor imaginary are ipso facto adapted to the world [ibid., p. 145].

From FPP's perspective, adaptation need not be explained because fine-tuning between organisms and their environment is something "natural", even "logical". We do not need a *theory* to explain it. Apparently, FPP are so baffled by evolutionary theory – initiated by Charles Darwin – because their view of adaptation, as we will try to show, leads them to the pre-Darwinian epoch. Historiography [Ruse (1986), Ayala (2004)] has emphasized adaptation was a phenomenon recognized by authors before Darwin, but it was he who formulated a naturalist's explanation. Nevertheless, according to Gustavo Caponi's work [(2011)], we will show that pre-Darwinian adaptationism is barely sustainable, and is quite similar to the position maintained by FPP.

Two Views of Natural Economy

Up until the mid-nineteenth century, the study of living beings was dominated by naturalists and theologians (and even men who were both). While naturalists mostly devoted their time to collecting and classifying animals, *theories* were put forward by theologians. However, these theories were actually "the theory of divine origin of all biological elements", with God as the creator of biodiversity. Thus, from the works of theologians such as John Ray (*The Wisdom of God Manifested in the Works of Creation*, 1692), William Derham (*Physico-Theology*, 1713), William Paley (*Natural Theology*, 1809), William Kirby (*On the Power, Wisdom and Goodness of God, as Manifested in the Creation of Animals, and in Their History, Habits and Instincts*, 1837), or Charles Bell (*The Hand: Its Mechanism and Vital*

Endowments as Evincing Design, 1837), the hand of God shaped both the characteristics and behavior of all living beings. All of them formed part of the *natural economy* devised by God, "The wisest disposition of natural beings, established by the supreme creator, whereby such beings tend to common aims and possess reciprocal functions" [Biberg ([1749] 1972), pp. 57-58]. Before Darwin, the natural economy view understood organisms to be static beings, whose purpose was not to survive and reproduce, but to be necessary components of the ecosystem as a whole. Therefore, nothing could be created or destroyed in the natural economy. All beings, thanks to the features bestowed upon them by God and placed at the service of other organisms had their place and role in nature.

The idea of natural economy was accepted and adopted by naturalists of that time. So Linnaeus tells us through his student Christophorus Gedner:

> In every plant, in every insect, we will observe some particular skill which we could not find in others bodies. And, after having compared between them, we find that it was not done by chance, but focused to an accurate and determinate aim, by a determinate cause, which serves both the propagation of plants or animals, to their conservation or to the function of those beings with they are related. We confirm how plants preserve themselves against elements harshness and against animals' attacks; how every animal enjoy their means of defense, thanks to which they can protect themselves from the attacks of others; such *nothing which has been created can be destroyed* [Gedner ([1752] 1972), pp. 161-165] (emphasis added).

And Buffon states:

> In order to beings were succeed by another, it is necessary for them to kill each other; in order to animals nourished themselves and survive, it is necessary for them to destroy vegetal and other animals; *and as before and after destruction the amount of life remains equal*, it seems that might make no difference to Nature the fact that this or that species were destroyed more or less. However, as a treasurer mother, in the bosom of abundance, she has set the boundaries to waste and has prevented the apparently squandered: She gives only to a few animals the instinct to nourishes of flesh, she even reduce those voracious and carnivorous species to a small number of individuals, while she multiplied abundantly the species and individuals who nourishes of plants; and she seems to have lavished vegetal species, and have shared out in each one the number and fecundity [Buffon ([1753] 2007), p. 572] (emphasis added).

This "natural balance" cannot be broken because each individual plays a role in the natural economy. That is the reason why authors like Paley, traditionally viewed as the epitome of theological adaptive explanation, extensively focused more on the description of the functional correlation of parts than on the "ecological appropriateness" [cf. Caponi (2011), pp. 11-14]. The relationship between function and environment was not considered an issue worthy

of study. For all these pre-Darwinian authors it seemed evident, as it is for FPP, that organisms were adapted to their environment. No further investigation was required but the focus was, like the first part of FPP's book, on the "internal parts" of organisms.

Nevertheless, Darwin brought a new vision of the natural economy. Reading the work of Thomas Malthus, as is well known, was crucial at this step. Malthus set out, contrary to the enlightened idea of social progress, that the reason for poverty was an excessive reproductive capacity of individuals in relation to the available resources. More precisely, populations grew geometrically while food production increased arithmetically. This limitation of resources led to the "struggle for existence" among them. Darwin realized that this reasoning could be applied to all living beings: if resources are limited and not all born individuals can survive, then, those individuals whose traits enable them to survive better than others in a given environment will have more chances of passing these traits on to subsequent generations.

The assumption of the Malthusian principle (geometric growth of populations, but arithmetic growth of resources) and consequently the struggle for existence, redirected the interest in internal organ correlations to the struggle and conquest of an environment, which now took on a more important role. The world was no longer perceived to be a peaceful place where each individual took its natural place, but could rather be annihilated at any moment. Now, the ability to survive was no longer taken for granted. It was not "natural", "logical" or "common sense" but required an explanation. This is why adaptation would become a matter of empirical investigation and did not remain as a (marginal) theological consideration. This change is mirrored in the role played by living beings. Before Darwin, it was argued that living beings existed for each other. So it is not uncommon to find whole paragraphs describing the beauty of beings as an end in itself or for the enjoyment of others. From Paley's point of view, *beauty* was one of the main reasons for being. The colorful plumage of birds, the greenness of plants and so on, exist not because it gives them an attractive reproductive feature (i.e., for their own benefit), but these features are for the enjoyment of "others" (for instance, humans). Paley tells us:

> In plants, especially in the flowers of plants, the principle of beauty holds a still more considerable place in their composition; is still more confessed than in animals. Why, for one instance out of a thousand, does the corolla of the tulip, when advanced to its size and maturity, change its colour? The purposes, so far as we can see, of vegetable nutrition, might have been carried on as well by its continuing green (…) Is it not more probable, that this property, which is independent, as it should seem, of the wants and utilities of the plant, was calculated for beauty, intended for display? [Paley (1809), pp. 199-200].

Moreover, Kirby referring to some animal features at the service of others:

> The allwise Governor of the universe, when he gave to the sheep its covering, appears to have had in view not solely the protection of the animal form effects of cold, but more particularly the benefit of him whom he had enthroned at the head of his creation, by thus placing at his disposal a material so inestimable, for his use and comfort, as wool [Kirby (1835), pp. 63-64].

Darwin, by contrast, refers to the *universal struggle for life* occurring in nature. He emphasizes how insects and seeds are destroyed by songbirds, whose eggs are destroyed, in turn, by birds and beasts of prey [cf. Darwin (1859), p. 62]. He also points out how both the young and old continuously suffer destruction [cf. Darwin (1859), p. 66] particularly due to the amount of food available and the number of predators [cf. Darwin (1859), p. 68].

The lack of ecological studies available at that time would indicate that survival – adaptation to the environment – was something taken for granted: something natural. Ecological issues, those challenges or obstacles preventing the geometric increase of a species, were almost a mystery to mid-nineteenth-century naturalists. Darwin himself said, "What checks the natural tendency of each species to increase in number is most obscure (...). We know not exactly what the checks are in even one single instance. Nor will this surprise anyone who reflects how ignorant we are on this head" [Darwin (1859), p. 67]. Now survival, adaptation to the environment, is not taken for granted and, therefore, requires an explanation. Thus the study of organisms and their interaction with the environment became an essential part of evolutionary theory [cf. Collins (1986)]. In his work *On the Various Contrivances by Which British and Foreign Orchids are Fertilised by Insects* (1862) Darwin initiates the adaptationist view when he understands the apparently ornamental color of flowers is actually an adaptation that facilitates their fertilization.

The hypothetical harmony of nature and its admirable balance proved to be little more than a mirage. Prey and predators coexist because the former have managed to adapt to the latter, not because predators have helped them. Living organisms do not live to and for the others, as pre-Darwinian authors believed. For instance, in Yellowstone Park trees struggle against each other to reach enough light to photosynthesize (using a massive cellulose infrastructures) but such a high concentration of inflammable material causes huge fires and, consequently, brings about the death of hundreds of organisms [cf. Williams (1992), p. 482]. Therefore Darwin said that "If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection"[Darwin (1859), p. 201]. This appearance of harmony and stability is only a result of the struggle between individuals and it can and will be broken at any time.

II. The Dimensions of Evolutionary Theory

Although reluctant to postulate an alternative to current evolutionary theory[1], the first part of FPP's book is devoted to *showing* biological novelties, which seem to have been overlooked by Modern Synthesis or Darwinians (as FPP like to call them). Paraphrasing Dobzshansky's famous quote, they say: "Evo-devo tells us that it's the other way around: nothing in evolution makes sense except in the light of developmental evolution" [Fodor and Piattelli-Palmarini (2010), p. 30]. These novelties are essentially devoted to the internal processes of living beings, where organisms' development would be the essential part of evolution, changing the (supposed) simplistic neo-Darwinism view. The transition from fertilized egg to adult marks the limits within which the process of natural selection (NS) can act, constraining the variability on which NS could act.

FPP's statement is misleading because, were it true, if evolution makes no sense except in the light of developmental evolution then, by definition, none of the organisms lacking embryonic development would evolve. Development is a phenomenon arising from multicellularity, it is dependent on it and impossible without it. We can delve further into the contrast between an externalist theory and FPP's internalist one.

Let us suppose that evolution is a body of phenomena, which is relatively well explained from the externalist perspective. The classical externalist theory asserts that the origin and transformation of living things arise from the combined action of mutation and NS. This paradigm of biological change is so ingrained in Western culture that it is extraordinarily hard to envisage alternative approaches, which have come to light during the study of biological evolution. This simplistic view is taken by FPP [cf. Fodor and Piattelli-Palmarini (2010), p. 23] as the schematic representation of standard neo-Darwinism. Indeed, rather than ingrained we could use the term "branded" because it seems to be an insular, conclusive, all-encompassing theory. Some new approaches can be interpreted as accretions of the classical theory whereas others present themselves as alternatives, leaving no room for the former. To describe this lively intellectual battle, which has stirred up so much passion, we will employ the notion of the dimension of the body of phenomena comprising biological evolution. Let us suppose this evolutionary whole is explained or measured effectively by the classical externalist theory. When we use classical mechanics to describe the motion of a body as consequence of a system of forces, the dimensions of these bodies are fixed, so when we place a body (a volume to be more precise) in a space we need to know the exact coordinates (length, height and depth). Just one or two coordinates will not suffice; all are required to know where the body is located. Indeed, we require three dimensional coordinates to position or to locate the body. In the present case, the body in question is that forming evolution. Ac-

cording to classical theory, two dimensions are sufficient to explain any novelty in this evolutionary body. Do we need more dimensions to explain evolution? Thus though the architects of Modern Synthesis, promoted by Sewall Wright's work in particular [cf. Provine ([1971] 2001), Chap. 5], when the role played by chance –exemplified by genetic drift– became a third fixed and necessary dimension. The neutral theory of molecular evolution is a good example of the role played by chance in the evolution of genes. The combination of all three dimensions forms what we might call an extended externalist theory of evolution. The relevance of this theory lies not only in the role genetic drift plays in the evolution of genes, but also in the part played by chance in shaping the higher levels of the biological hierarchy through the evolution of individuals, populations, species or other taxonomic units. In other words, not only should we incorporate the neutral school's considerable achievements on the molecular scale, but also incorporate the points raised within the framework of these controversies by mutationists, saltationists, geneticists, paleontologists, developmental biologists ever since Darwin first voiced his ideas on NS. The thesis we endeavor to put forward here is that the dimension of chance has gained explanatory power. Thus, the current standard theory of evolution is what we refer to here as the extended externalist theory, whose three dimensions are: mutation, NS and chance. The latter encompasses phenomena resulting from accidental or random events, some of which are considered essential (e.g., symbiotic integration). Also, such developments could include the timely action of NS on these events. The eventuality of chance events in evolutionary history and their selection, or not, by NS, is a combination of the dimensions of NS and chance.

Note how we can consider mutation (also random) and chance orthogonally. This simply indicates that the dimension of mutation incorporates only those factors pertinent to biological evolution having a specific effect on genetic matter, rather than on the frequency of a particular new variant, or the likelihood of it arising. In this respect, we should mention that this dimension incorporates many of the internalist conceptions, for instance, the study of genome evolution shows that, through certain processes, genomes are likely to generate new variants, of all kinds. Indeed, among others, gene or genomic duplications and effects of transposable elements are clear examples of the immense importance this dimension must have in evolution. Many pro-internalist authors, followed by FPP, have trivialized externalist considerations basing their arguments on the effects of infrequent mutations, but the truth is that the dynamic nature of genomes creating new variants now forms an integral part of the modern externalist concept.

Now we can ask ourselves two more questions, considering the wide range of additional factors we have added, and which contemplate causes of organic evolution:

a) Do we need to consider further dimensions in our quest to understand the body of evolutionary phenomena?

b) Is NS really an explanatory dimension of biological evolution?

The first question considers the possible addition of one or more – as yet unspecified – dimensions to those described above in order to explain evolution. The second, regardless of whether new dimensions should be introduced, suggests NS might not constitute an explanatory dimension of organic evolution, which would lead us to eliminate the NS axis.

We should bear both these questions in mind when pondering new dimensions because many authors consider introducing new dimensions in an endeavor to exclude NS. Kauffman [(1993)] highlights the self-organizational ability of multi-element systems, including biological ones. Self-organization in biological systems would be responsible for generating significant evolutionary innovation, but would in no way be the exclusive product of the dimensions of an extended externalist theory. Kauffman's theory is based on the complex and regular behavior exhibited by interactive sets of elementary units (genes, cells, organisms, normally having binary individual responses, such as "on/active" or "off/inactive") when they receive signals from other units with which they communicate. This is his well-known NK model, where N is the number of units in the system and K the signals received by the unit. The massive quantity of real and complex behaviors that such models can generate is overwhelming, at least in theory, and some of them are similar to those shown by biological systems. Another theory related to the generation of complex behavior is the theory of self-organized criticality [Bak (1996)], albeit with a macroscopic basis and not rooted in the interactions and numbers of component units. The canonical example is the sand-pile model, which exhibits complex behavior, where periods of invariant sand-pile morphology (it is still a sand-pile despite size increase) are followed by intermittent sand cascades or avalanches. Avalanches, resulting from a domino effect in which one grain pushes others, and moves them, have only localised effects when the sand-pile slope is not too steep. However, when the slope becomes steep enough, reaching the threshold of the steady state, the behavior of any grain of sand can have wide-ranging effects: then we say it is in a critical state of emerging dynamics. Bak has applied this theory to account for punctuated equilibrium (saltationalism) in the evolution of species. The idea is that solely in this steady state can sudden changes (presumably genetic in nature) result in a leap to a new situation, or emergence of a new species. Neither theory, in their original formulation, refers to any selective dimension. Therefore, to accept such an alternative dimension, we should first assess to what extent all the phenomena explained by NS are also explained by this model, and more importantly, to what extent the new dimension can explain certain biological phenomena that NS cannot explain.

Closer to investigations of an empirical bent we have, once more, the internalist dimension of evolution emanating from mutationism and modern developmental biology. We should note, however, that the axes of mutation and of chance are formally incorporated by the extended externalist theory. We could allow a special dimension for development in biological evolution if, and only if, there is an evolutionary phenomenon that cannot be explained by the single or combined action of these three dimensions. For example, the inherent capacity organisms have to buffer mutations, or the Kauffman-like self-organizing ability of cell units involved in development in a way that is important to account for certain evolutionary patterns or phenomena. Take, for example, the canalization theory which states that development imposes restrictions that essentially buffer or channel the effects of mutational variability by evolutionarily well-established patterns of a limited number of morphological units [Gerhart and Kirschner (1997)]. Such patterns are contrary to the gradual effects of NS, which are eventually promoted after the emergence of individual mutations. These patterns have an intrinsic canalization capacity and thus do not change. The reader may be aware of certain similarities or resemblance between the theory of self-organization, criticality and the mutational canalization. Certainly we cannot be sure whether we are talking about one or more new dimensions. To make it easier to understand let us assume it is the same dimension, which is generally called the self-organizing dimension. The theory of complex systems forms the basis of this new dimension, but does not substitute the extended externalist theory, but rather forms an extension of the already extended theory. Given we now have proposals to synthesize life in the lab (although we should handle this concept with care), and considering the emergence of systemic theories of the macromolecular organization of organisms as well as the theory of complex systems, we might think we are approaching the realization of Goethe's dream: leaving the analytical dimension and entering a new one allowing synthetic recreation.

It would take too long to give examples and cite studies carried out in areas like ecology (ecosystem component species), animal behavior (individual components of species), or neuroscience (brain nerve cell components), in which the interaction between the corresponding component units can clearly generate complex patterns that might be explained only by resorting to self-organizing phenomena. Bell [(1997), p. xviii] states that the only worthy scientific objections to NS as the driving force of biological complexity today, are based on self-organization. Wagner [(2011), pp. 91-92], on the other hand, states that NS and self-organization are equally necessary to explain evolution, both being essential for innovation (self-organization) and for its preservation (NS). The new dimension, if verified not to be relegated to extended externalist theory, would be more fitting to explain the body of evolution as a whole and life in general. At this point, and at any other regarding the nature of scientific theories, we should apply the principle of Occam's ra-

zor. Indeed, there is no need to add new dimensions if we have sufficient explanatory power with the existing ones; or if we can show that the new dimensions be reduced to a minimal set of irreducible orthogonal dimensions.

III. Conclusion

The vision portrayed by FPP of current evolutionary theory does not correspond to the knowledge and work of biologists today. The authors' approach to the phenomenon of adaptation, as we have shown, is closer to the pre-Darwinian than the current view where adaptation requires an explanation. Furthermore, biologists – *malgré* FPP's belief – are aware of recent findings in developmental biology and other areas (genomics, molecular biology, etc.). Far from the apocalyptic picture painted by FPP, discoveries and debates have sparked further research. Whether or not we should incorporate new dimensions to evolutionary theory is a decision that depends on many things. But what is clear is that the degree of confirmation at the empirical level of evolutionary theory (and especially population genetics, its cornerstone) has become the litmus test of any evolutionary hypothesis [cf. Lynch (2007), p. 8598]. Thus, by no means can we state – as declared in uninformed circles or those prone to certain ideological or religious beliefs – that Darwinism or neo-Darwinism has come to an end. Rather, what we do have is a theory that is continually embraced by a larger more explanatory one, like an onion with multiple layers.

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Notes

[1] "… we don't know what the mechanism of evolution is. As far as we can make out, nobody knows exactly how phenotypes evolve" [Fodor and Piattelli-Palmarini (2010), p. 153].

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RESUMEN

En este artículo analizamos dos diferentes aspectos del libro de Jerry Fodor y Massimo Piattelli-Palmarini *What Darwin Got Wrong*. En primer lugar planteamos el anacronismo de su concepto de adaptación el cual se encuentra más en consonancia con las posturas de los autores pre-Darwinianos que con la usada por los biólogos actualmente. En la segunda parte, abordamos el supuesto conflicto planteado por los autores entre una visión internista y otra externista de la evolución, tratando las diferentes dimensiones de la teoría evolutiva de forma integradora.

PALABRAS CLAVE: *adaptación, pre-Darwiniano, teoría externista, dimensiones evolutivas.*

ABSTRACT

In this paper we analyze two topics discussed in Jerry Fodor and Massimo Piattelli-Palmarini's book *What Darwin Got Wrong*. Firstly, we defend the stance that their concept of adaptation is anachronistic, and is more closely related with pre-Darwinian ideas than with current concepts held by biologists. Secondly, we discuss the supposed conflict they claim exists between an externalist and an internalist vision of evolution. To do so, we deal the different dimensions of evolutionary theory in a comprehensive way.

KEYWORDS: *Adaptation, Pre-Darwinian, Externalist Theory, Evolutionary Dimensions*