

Jerry Fodor and Massimo Piattelli-Palmarini

What Darwin Got Wrong.

New York: Farrar, Straus and Giroux 2010.

288 pages

US\$26.00 (cloth ISBN 978-0-374-28879-2)

The authors (FPP) aim ‘to show that Darwin’s theory of natural selection (NS) is fatally flawed’ (xiv). Their relentless deconstruction of the Darwinian paradigm will delight those who distrust Darwinist explanations of evolution by NS and exasperate those who revere Darwin and believe that it is only through appeal to NS that we can hope to understand how the adaptations of the many forms of life evolved.

FPP’s attack on Darwinian theory unfolds in two parts. In ‘The Biological Argument’ FPP elaborate the interactive genetic structures of genomes that determine ‘endogenous’ constraints on the development of phenotypes. FPP endeavor to show that what Darwin did not know about genetics vitiates his account of evolution by NS. They suggest attributing whatever ‘directing’ and ‘perfecting’ of adaptations occurs in evolution to non-random genetic variation rather than to NS. In the second part, ‘The Conceptual Situation’, FPP attack the very conception of selection *for* traits, concluding that Darwin’s mechanism of adaptation by natural selection cannot be used to explain the adaptive fit between organisms and their environments.

FPP argue that putatively random variations are highly constrained by internal structures of the evolving organisms. But it is not the origins of variations that are constrained by genetic structure, only how the variations function. Since there is no evidence that mutations of DNA *occur* non-randomly with respect to their influence on phenotypes, FPP can only point to changes in genetic structure which are not triggered by mutations. In cases of ‘genetic assimilation’ an environmental factor, such as temperature change, may interact directly with genomes. But that such a change in genomes would result in adaptation *to that very environmental change* is highly unlikely. FPP’s suggestion that ‘laws of form’ govern the organization of processes by which organisms *develop* is also of little help in understanding the historic *evolutionary* origins of the genetic resources of genomes.

FPP rightly emphasize that the complexly organized adaptive traits of organisms must build on a history of previous constructions, something to which Darwin and Darwinians have paid insufficient attention. While this changes the picture of evolutionary history, it need not change the role of NS. What is principally wrong in Darwin’s ‘gradualist’ conception of evolution by NS is not a question of the speed of emergence of new species but rather Darwin’s construal of the origin of species as consisting in *accumulations* of ‘small’ phenotypic changes. Darwin was presumably thinking of the evolution of major phenotypic differences among species rather than speciation by reproductive isolation, which often does not involve otherwise adaptively significant phenotypic change.

FPP quote a ‘sad (in hindsight) passage’ expressing Darwin’s commitment to the continuity of evolution: ‘If it could be demonstrated that any complex organ existed which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down’ (195). Is there any plausible counterexample to a *complex organ*—such as the human eye or heart—being formed in a relatively continuous sequence of modifications? Genetic continuity across widely separated branches of the Tree of Life seems to support rather than undermine Darwin’s continuity thesis. For example, FPP cite the commonality of essential genetic structures involved in the development human eyes with those of the eyes of sea urchins and fruit flies, as well as other vertebrates.

Darwin’s genius was to recognize a pattern of historic change, the dynamic of NS, which is distinctive of life forms, yet which involves the same kinds of physical causal processes that operate in nonliving physical nature. The difficult problem this poses for Darwinian theory is how to mesh the multifarious proximate efficient causes that constitute a process of NS with the ‘evolutionary cause’, the Darwinian selection dynamic. Unable to conceive of how NS processes can organize the innumerable causal processes in the development, survival, reproduction and death of organisms, FPP reject Darwinian theory of NS as illusory, arguing that no general pattern of *adaptive* selection exists. (An interesting analogy might be drawn between the role of Darwinian NS in explaining evolutionary change and that of the Marxian materialist dialectic of economic class competition in explaining the dynamics of human history.)

FPP correctly point out that a description of a NS process as a change in gene frequencies says nothing about the causal mechanisms actually giving rise to the diversity of phenotypes. This follows from the recognition that NS is not conceived in neo-Darwinian theory as a *physical kind* of process. Darwin’s reference to NS as a ‘mechanism’ for phenotypic change misleadingly suggests a kind of general efficient cause. The physical efficient causation involved in a process of NS occurs in the development of the phenotype and in causal interactions of organisms with environmental factors. NS has been construed as a causal mechanism, as a kind of Newtonian force that drives evolution. A better analogy is to view NS as ‘acceleration’ of genotype change that is causally dependent on the ‘forces’ arising from interactions between phenotypes and selected environmental variables. As acceleration a is a function of the net force applied to a body with mass m (according to Newton’s law, $a = F/m$), so change in gene frequency is a function of external environmental ‘forces’ and phenotypic properties of organisms (crudely analogous to mass.)

The elemental structure of a selection process is clear in Manfred Eigen’s model for the evolution of naked RNA replicators. Rates of changes of proto-genotype frequencies are expressed by an explicit function representing the interactions of birth (replication) rates, death (dissolution) rates, and environmental nucleotide resources. The selective organizing function of the processes of replication and dissolution of the RNA molecules depends on differential replication success of the ‘phenotypes’ of the different molecular sequences, which in turn depends on the differential ‘adaptations’ for stability of the molecules and competition for nucleotide resources. In this hypothetical example

of a primitive process of NS, the sense of selection of fitter phenotypes (= genotypes here) *for* elemental adaptive capacities for reproductive success involves none of the conceptual problems FPP see in examples of Darwinian accounts of selection for phenotypic properties of vastly more complex organisms.

Within neo-Darwinian models of selection, Fisherean genotype fitness is *defined* in terms of relative reproductive success, measured as the rate of change of frequency in a population context. But when the models are applied to explain adaptive evolution, the ‘fitness’ of a genotype is viewed as depending on salient differential functional effects of interactions of corresponding phenotypes on reproductive success, that is, in causal determination of birth and death rates (‘survival and reproduction’). The ‘fitness’ ascribed to a genotype, measured by relative change in frequency, should not be viewed as *physically causing* its reproduction rate. The interpretation of NS processes as generating adaptations requires that the effect of a complex of causal interactions within and on organisms ‘generate’ adaptations in terms of statistical summations of systematic differential changes in phenotype frequencies, which are causally correlated with changes in genotype frequencies.

The fundamental flaw that FPP ascribe to Darwinists is inferring from ‘*creatures are selected for their adaptive traits*’ to ‘*creatures with adaptive traits are selected*’ (xv). FPP argue that within a process of evolution ‘selection-for’ a trait cannot be distinguished from simply selection *of* a trait. They conclude that Darwinian theory ‘can offer no remotely plausible account of how filtering (of randomly generated phenotypes) by natural selection might work’ (16).

In FPP’s argument from ‘selection for’ we need to distinguish the sense of ‘select’ in ‘selection of creatures’ from ‘select’ in ‘selected for’. The simplest eliminative sense of ‘selection of whole organisms’ is their deaths. Selection of particular organisms refers to their individual survival and reproductive success, but selection of a *genotype* refers to the resulting difference in frequency of contrasting ‘competing’ genotypes in further generations. FPP employ a sense of ‘fitness’ of an organism as a kind of overall adaptedness which fosters confusion in understanding natural selection. This notion of fitness traces back to Darwin and is common in informal discussions of NS, but it has no definite sense. How could the different ways that an organism is ‘fit’ in exhibiting, say, hunting prowess, or resistance to disease, or ability to attract mates, be summed to yield its overall adaptedness? This notion of fitness has no coherent measure that could be used in modeling NS processes.

The difficult problem for Darwinian theory lies not in the *conception* of selection for a phenotypic trait but in how phenotypic characteristics came to be integrated into viable ‘adapted’ organisms, which are in an intuitive sense ‘well-designed’ to survive and reproduce in their environmental niches. Part of the answer is that the *evolved* genetic structures make possible the modularity of the bias in selection for competing genotypes, indexed to a particular genetic change that causally correlates with a particular adaptive phenotypic change, which in turn systematically affects the differential reproductive success of the corresponding genotypes.

FPP's analogy between natural selection explanations of adaptations and operant conditioning explanations of behavior misleads them into making a bizarre argument against Darwinism. They pose a problem: 'the distinction between traits that are selected-for and coextensive traits that free-ride upon them' requires counterfactual reasoning (113). The challenge of 'the intensionality of selection-for' (xviii), simply put, is whether a claim that gene *A* was selected for (in contrast to variant allele *B*) can be expressed in terms of physical causes without either invoking intentions, hence intensional language, or 'laws of selection' supporting counterfactual conditionals. FPP argue that 'selection for' cannot be characterized by logically extensive descriptions of physical causes—as if to determine the truth of the claim 'phenotypic property *P* was selected *for*' in a NS process, not merely selected, requires ascertaining 'intentions' of the selection process. Since there is no purposive agency with 'intentions' in Darwinian NS, it cannot survey possibilities in anticipating evolutionary change. Nor can a natural history of selection yield laws supporting counterfactuals (157). Thus a NS selection process cannot be described in terms of the purportedly intentional concept of 'selection for'.

FPP's account of how we determine adaptive effects of trait differences makes little sense in the examples they give. We determine the function of being white in the evolution of polar bears by noting that 'polar bears that are selected for matching their environment do win competitions with white polar bears in non-actual worlds where the environment is green' (118). Compare this with Richard Dawkin's answer to Bishop Montefiore's difficulty in understanding what neo-Darwinian explanation might explain why polar bears are white. 'If polar bears are dominant in the Arctic, there would seem to have been no need for them to evolve a white-colored form of camouflage.' Dawkins suggests a more plausible function: the adaptive benefit of concealment from their prey.

FPP's grand conclusion is that 'Darwin's theory of selection is *empty*' (16). NS always achieves its adaptive goals, as an unaimed arrow never misses. This is a radical extension of the classic critique by Gould and Lewontin of the 'adaptationist program'. Not only are there other important mechanisms involved in evolution and proposed Darwinian explanations of adaptations are often mistaken; it is wrong to suppose that Darwinian natural selection ever functions as a mechanism in evolution.

If FPP are right about what Darwinian theory of evolution gets wrong, what prospect remains for ascribing systematic meaning or coherence to the evolution of life? Lacking NS or any agency of Intelligent Design to generate the adapted forms of organisms, we are left with a view of life as one (wondrous or not) thing after another, with connections here and there, but no hint of any general systematic pattern in or of life's evolution. FPP largely fall short of their aim to demonstrate the failure of Darwinian theory of evolution, but they do point to the need to clarify what we do know and might hope to know about how Darwin's Tree of Life evolved.

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