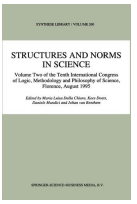

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THE "PARAMOUNT POWER OF SELECTION": FROM DARWIN TO KAUFFMAN

1. INTRODUCTION: "EXPLANATORY POWER" AND "POWER" OF NATURAL SELECTION

For approximately two decades now, the Darwinian interpretation of evolution has now been challenged in many ways. Modern criticisms make it difficult, even for the staunchest Darwinians, not to take a distance from Darwin's bold phrases on the "power" of natural selection. Let me remind you of some famous declarations of Darwin on the subject:

> "It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life".[1]
>
> "What limit can be put to this power, acting during long ages and rigidly scrutinising the whole constitution, structure and habits of each creature,—favouring the good and rejecting the bad? I can see no limit to this power, in slowly and beautifully adapting each form to the most complex relations of life. The theory of natural selection, even if we looked no further than this, seems to me to be in itself probable".[2]
>
> "The long-continued accumulation of beneficial variations will infallibly have led to structures as diversified, as beautifully adapted for various purposes and as excellently co-ordinated, as we see in the animals and plants around us. Hence I have spoken of selection as the paramount power, whether applied by man to the formation of domestic breeds, or by nature to the production of species".[3]

[1] Charles Darwin, *On the Origin of Species*, London: Murray, 1859, (Facsimile: Cambridge: Harvard University Press, 1964), p. 84.

[2] *Ibid.*, p. 469.

[3] Charles Darwin, *The Variation of Animals and Plants Under Domestication*, 2nd ed., 1875, quoted in *The Works of Charles Darwin*, New York, AMS Press, vol. 8, p. 426; see also p. 236.

M.L. Dalla Chiara et al. (eds.), Structures and Norms in Science, 265–282.

The purpose of this paper is to provide some landmarks in order to better assess the implications of assertions, old and new, about the "power" of natural selection.

One important distinction must be made from the outset. There are in fact two possible meanings for the expression "power of selection", but only one can be found in Darwin himself. The "power of selection" has been often understood, particularly in contemporary literature, as "the explanatory power" of the principle of natural selection, or in other words the answer to the question: —what classes of phenomena does it account for?[4] In that sense, extinction, divergence, or patterns of classification, as far as they can be presented as consequences of natural selection, belong to its explanatory power. However, Darwin himself did not speak of the "power" of selection in that sense. Rather, he habitually restricted it to the explanation of only one class of phenomena, the adaptive modification of species. It is only in this precise context that he qualified selection as a "paramount power", or simply (in *The Origin of Species*) as a "power", or else as an "agent". In Darwin's spontaneous philosophical vocabulary, the *power* of selection, either artificial or natural, consisted in the immediate result of its *action*. In other explanatory contexts, he preferred to say that natural selection "entails", "leads to", "explains"[5], "induces" or even "causes"[6], for instance, extinction, divergence or affinities.

We will see that this distinction between two senses of "power" is more important than it looks at first sight. In particular, it can shed light on contemporary challenges to Darwinism. Most criticisms addressed to the Darwinian paradigm in recent times, especially in the context of macroevolutionary debates, have dealt with the explanatory power, or theoretical responsibility[7], of natural selection, or its claim to account for many classes of facts other than adaptive modification. Moreover, as strange as it may appear, attacks against what Darwin what called the "paramount power of selection" —its

[4] In a similar sense, Jonathan Hodge speaks of the "responsibility" of the principle of natural selection ("Natural Selection as a Causal, Empirical, and Probabilistic Theory", in *The Probabilistic Revolution*, 1987, L. Krüger, G. Gigerenzer, M.S. Morgan, Eds., Vol. 2., Cambridge, M.I.T. Press, pp. 233–270).

[5] "Whether natural selection has really thus *acted* in nature, *in modifying and adapting* the various forms of life to their several conditions and stations, must be judged of by the general tenour and balance of evidence given in the following chapters. But we already see how it *entails* extinction... Natural selection, also *leads to* divergence of character..." (Charles Darwin, On the Origin of Species, London: Murray, 1859 [Facsimile: Cambridge: Harvard University Press, 1964], pp. 127–128. Emphasis added). "Natural selection, as has just been remarked, *leads to* divergence of character ant to much extinction of the less improved and intermediate forms of life. On these principles, I believe, the nature of the affinities of all organic beings may be *explained*". (*Ibid.*, p. 128. Emphasis added.)

[6] "We shall then see how Natural Selection almost inevitably *causes* much extinction of the less improved forms of life, and *induces* what I have called Divergence of Character". (*Ibid.*, p. 5. Emphasis added.)

[7] On this term, see above, n. 4.

ability to modify and adapt species—, have been much rarer in contemporary literature. Attacks of this latter sort were in fact commoner in the early history of Darwinism, when, for example, Lamarckian or mutationist theories of evolution contested natural selection as a sufficient or even conceivable explanation for the genesis of adaptations. However, a strong exception in recent literature can be found in the work of Stuart Kauffman. In his recent book on *The Origins of Order*[8], the problem of the "power" (and correlatively the "limits") of selection is explicitly central from the beginning to the end.

These preliminary remarks justify the direction of my argument. The first step will be to clarify Darwin's assertions about the power of selection. I will examine this notion in relation with other philosophical categories used by Darwin for characterizing the status of Natural Selection. I will then turn to contemporary evolutionary biology. I will first provide a recent example of the independence of the meanings I have previously distinguished for the "power" of natural selection. I will then consider two clear cases in which more or less genuine Darwinians have tried to face the difficulties raised by Darwin's argument on the "paramount power" of selection in modifying and adapting species. One will be taken from classical population genetics. The other will concern Kauffman's theoretical reflections on self-organisation and selection.

2. DARWIN AND THE "POWER" OF SELECTION

2.1. *Natural Selection as Hypothesis, Theory and Power*

Darwin had relatively clear ideas about the philosophical status of natural selection. These ideas were not explicitly formulated in *The Origin of Species*, but in *The Variation of Animals and Plants under Domestication* (1868). There, he used three important words for qualifying the status of natural selection: "hypothesis", "theory", and "power". Let us begin with "hypothesis" and "theory". This distinction is made in the introduction of *The Variation*:

> "In scientific investigations, it is permitted to invent any *hypothesis*, and if it explains various large and independent classes of facts it rises to the rank of a *well-grounded theory.* (...)
> The *principle* of natural selection may be looked upon as a *mere hypothesis*, but *rendered in some degree probable* by what we positively know of the variability of organic beings in a state of nature, —by what we positively know of the struggle for existence, and the consequent and almost inevitable preservation of favourable variations, —and from the analogical formation of domestic races.
> *Now this hypothesis may be tested*, and this seems to me the only fair and legitimate manner of considering the whole question, —*by trying*

[8]Stuart A. Kauffman, *The Origins of Order: Self-Organization and Selection*, New York and Oxford, Oxford University Press, 1993.

> *whether it explains several large and independent classes of facts*, such as the geological succession of organic beings, their distribution in past and present times, and their mutual affinities and homologies. If the principle of natural selection *does explain* these and other large bodies of facts, it ought to be received" (emphasis added)[9].

These sentences make the structure of the argument of *The Origin of Species* explicit. Considering natural selection first as "a mere hypothesis", Darwin says that it is "rendered (...) probable" by certain classes of empirical data. This assertion refers to the first five chapters of The Origin, where natural selection appears to be a conclusion drawn from a set of highly probable universal premises (about the rate of reproduction of organisms, about the limitations of resources, and about variation and heredity). Note also the allusion to "the analogical formation of domestic races". Here, Darwin does not refer to a premise leading to the natural selection hypothesis, but to an experimental analogical model, the main function of which is to convince the reader of the efficacy of selection in modifying species. I will return later to this aspect, which is important for the interpretation of selection as a "power".

As for the "well-grounded theory", it is a clear reference to the second half of *The Origin* (chapters 7 to 12 in the 1st edition), where natural selection plays the role of a principle in the old Newtonian sense, that is to say a proposition able to unify and explain various classes of independent facts. Thus, for instance, Darwin invokes natural selection for the explanation of animal instincts, extinction, divergence, geographical distribution of species, affinities and homologies. Hence a second strategy of justification of natural selection, through consequences of the hypothesis.

To sum up, we find in Darwin two levels of justification for natural selection. The "mere hypothesis" is concerned with direct evidence for the existence of natural selection, and with the concepts required for thinking coherently about it. The "well-grounded theory" is a reconstruction of the whole theoretical structure of natural history: in this grand theory, natural selection functions as a remote principle for many classes of facts. As noted by many historians and philosophers, the whole argument is in good agreement with the traditional strategy of confirmation of hypotheses in physical sciences since Newton, or, in other words, the ideal of the *vera causa*[10]

[9]Charles Darwin, *The Variation of Animals and Plants Under Domestication*, 2nd ed., 1875, quoted in *The Works of Charles Darwin*, New York, AMS Press, 1972, vol. 7, p. 9.

[10]David Hull, *Darwin and his Critics*, Cambridge, Massachusetts, Harvard University Press, 1973; V.C. Kavaloski, *The* vera causa *principle: a historico-philosophical study of a metatheoretical concept from Newton through Darwin*. University of Chicago, Ph.dissertation, 1974; Michael Ruse, "Darwin's debt to philosophy: an examination of the influence of the philosophical ideas of John F.W. Herschel and William Whewell on the development of Charles Darwin's theory of evolution", *Studies in History and Philosophy of Science*, 6: 159–181; M.J.S. Hodge, "Natural Selection as a Causal, Empirical, and Probabilistic Theory", in L. Krüger, G. Gigerenzer and M.S. Morgan (eds.), *The Probabilistic Revolution*, Cambridge, Massachusetts: The MIT Press, 1987, vol. 2, pp. 233-270.

Let us now come to the third concept Darwin utilized for characterizing the status of natural selection —selection as a "power", or, as said in *The Variation...*, a "paramount power". I have already given the key quotation. Here it is again:

> "The long-continued accumulation of beneficial variations will infallibly have led to structures as diversified, as beautifully adapted for various purposes and as excellently co-ordinated, as we see in the animals and plants around us. Hence I have spoken of selection as the paramount power, whether applied by man to the formation of domestic breeds, or by nature to the production of species"[11].

This text states that selection is the major force orienting change in species. What is the relation between this thesis and the "hypothesis" vs. "theory" distinction? The "paramount power" thesis bears on a special aspect of the theory: the explanation of adaptive change. Darwin's claim is that selection, if not the sole force orienting evolutionary change, is able to overcome any other force (such as: random variation, correlation of organs, or the effect of use and disuse). Although this thesis was absolutely crucial for Darwin, it must not be confounded with the representation of selection as unifying the whole field of the natural history of life. Modification of species is one thing; extinction, geographical distribution of species, divergence and diversity (as reflected in classification) are other things. The "paramount power" thesis is concerned only with adaptive modification of species.

At this point, it can be useful to represent the relations between "hypothesis", "theory" and "power" in a diagram. In most of its features, this diagram is classical. Please note that adaptations appear as a consequence of the hypothesis of natural selection. In a certain sense, this way of speaking is consistent with Darwin's own declarations. This can be seen easily for instance in the quotation above: "The long-continued accumulation of beneficial variations will infallibly have led to structures... as beautifully adapted as...". But, as we will see shortly, in other respects this presentation, as far as one does not take into account the "power" aspect of selection, is misleading. Indeed, the "paramount power" thesis might well be already there in the very formulation of the hypothesis.

[11] Charles Darwin, *The Variation of Animals and Plants Under Domestication*, 2nd ed., 1875, quoted in *The Works of Charles Darwin*, New York, AMS Press, vol. 8, p. 426; see also p. 236. In *The Origin of Species*, there is a similar sentence, but it concerns only the case of artificial selection: "Over all these causes of change I am convinced that the accumulative action of Selection, whether applied methodically and more quickly, or unconsciously and more slowly, but more efficiently, is by far the predominant Power" (1st ed., 1859 [Facsimile: Cambridge: Harvard University Press, 1964], p. 43).

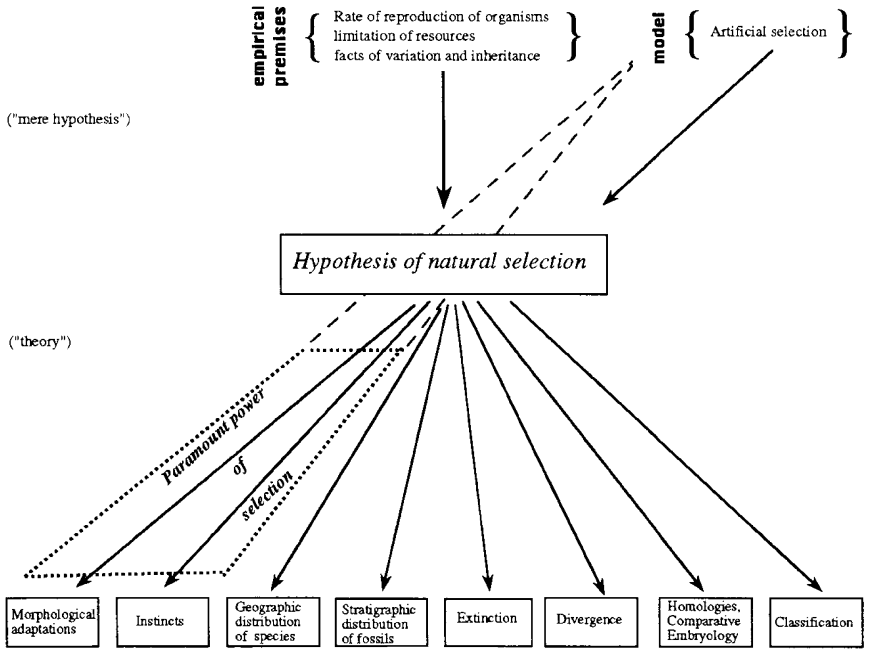

Fig. 1.

2.2. *Further observations on the "power" of selection in Darwin's discourse*

We must now answer two further questions. First, why is selection said to be a *paramount* power for the modification of species? Second, what is the function of Darwin's use of the word "power" in the general economy of his big "argument"?

Why is selection a *paramount* power for the adaptive modification of species? The argument consisted in an examination of the relation between variation and selection. Darwin admitted his complete ignorance of the laws of variation, but he believed that variation obeyed some laws, which were the precondition for any event of selection. Thus, he never said that selection could produce any arbitrary thing. He admitted for instance that there are strong correlation constraints restricting the range of possible variation. Other factors involved in the production of variation were, for example: direct or indirect action of changing conditions of life, use and disuse, reversion[12]. What he claimed was that, if there is variation of some sort among the members of species, then

[12]See *On the Origin of Species*, ch. I & V; *The Variation of Animals and Plants Under Domestication*, ch. XXII–XXVI.

this causal factor of change will necessarily be in a subordinate position in comparison with selection. Whatever may be the origin of variations, selection will both use them and overcome them:

> "I have spoken of selection as the paramount power, yet its action absolutely depends on what we in our ignorance call spontaneous or accidental variability. (...) The variations of each creature are determined by fixed and immutable laws; but these laws bear no relation to the living structure which is slowly built up through the power of selection, whether this be natural or artificial selection. (...) Although variability is indispensably necessary, yet, when we look at some highly complex and excellently adapted organisms, variability sinks to a quite subordinate position in comparison with selection"[13].

Thus, for Darwin, provided that there is variation, selection will necessarily modify species and increase their adaptation. Hence the bold declaration of the concluding chapter of *The Origin*, already quoted: "I can see no limit to this power..."[14]

Let us come to our second question: what is the function of Darwin's systematic characterization of natural selection as a "power" in the context of adaptive modification? Many historians and philosophers have pointed out the archaic character of Darwin's statements on natural selection as an "agent" or "power". Assuredly, there is some truth in this remark. However the interesting point, again, is that it is only when he speaks of modification and adaptation of species that Darwin uses such a vocabulary. Why does he not merely say that natural selection explains, or entails, or causes adaptive modification, just as it explains, entails, or causes extinction, divergence and affinities[15]? The reason for this is that, for Darwin, adaptive modification is a little more than a consequence of natural selection, even if an immediate consequence. Actually, Darwin tends to incorporate adaptive modification in the very formulation of the hypothesis of natural selection. Let us consider again this hypothesis. As classically presented[16], the hypothesis comes as the conclusion of an argument of the following sort:

1. In every species, all organisms tend to increase in geometrical ratio.
2. Many more individuals are born than can possibly survive.
   Hence:
3. Individuals compete for survival and reproduction.
4. For a number of characters, there is heritable variation.
   Hence:
5. (hypothesis of natural selection)

[13]Charles Darwin, *The Variation...*, *loc. cit.*, vol. 8, p. 236.

[14]See above n. 2.

[15]For quotations, see above n. 5 & 6.

[16]See for instance Julian Huxley, *Evolution: the Modern Synthesis*, London, Allen & Unwin, 1942, chap. I, § I.

Now what is the precise content of this hypothesis? In fact one finds two versions of it in Darwin's text. Let us call them the weak and the strong version. The weak or sober version is the following:

> "Each slight variation, if useful, is preserved"[17].

And here is an example of the stronger version:

> "Every slight modification, which in any way favoured the individuals of any of the species, by better adapting them to their altered conditions, would tend to be preserved"[18].

Most often, Darwin introduces the second version shortly after the first one[19]. In his own vocabulary, the first version describes the "process" of natural selection[20], the second one describes its "action" (adaptive modification). Darwin would never say that extinction, divergence or affinities describe the way selection "acts" in nature. And whenever Darwin evokes the "power" of selection, it is always in relation with its immediate action consisting in "modifying and adapting". Of course, this power becomes the greater as selection accumulates successive variations. But this is only a question of degree. Furthermore, one must observe the parallel with artificial selection: both natural and artificial selection are described in terms of their "power" and "action": both "modify" and "adapt"[21], and both are "predominant" (or "paramount") in that respect[22]. This confirms that Darwin's reflections on the "power" of selection definitively bear upon an intrinsic philosophical feature of the "hypothesis" of natural selection.

I will not pursue this terminological enquiry further. What I have tried to show is this: one should not confuse the explanatory capacity of the hypothesis of natural selection with what Darwin calls the "power" of natural selection. Of course, in a sense, adaptations can be viewed as "explained" by natural selection. But in the deductive hierarchy of Darwin's argument, adaptations do not stand on the same level as extinction, divergence, affinities and other explananda. For this reason, the classical diagram on which I commented earlier is not satisfactory. Under the light of artificial selection (the analogical model), the "power" of selection thesis percolates through the "hypothesis" *and* the "theory" of natural selection. But it does not diffuse in all regions of the theory. Hence the unusual "triangle" I have introduced in my diagram.

If we now turn to various challenges and criticisms addressed to Darwinism in the course of 20th Century evolutionary biology, this analysis has interesting consequences. One can indeed conceive of two very different kinds of criticism. One kind consists in denying that natural selection explains a vast

[17] Charles Darwin, *On the Origin of Species*, London: Murray, 1859, (Facsimile: Cambridge: Harvard University Press, 1964), chap. III, p. 61.

[18] *Ibid.*, chap. IV, p. 82.

[19] See for instance *Ibid.*, chap. III, p. 61; chap. IV, pp. 81–82, & 127.

[20] E.g. *Ibid.*, chap. IV, p. 102.

[21] *Ibid.*, chap. III, p. 61.

[22] See above n. 12.

array of "independent classes of facts" other than adaptations —such as: extinction, divergence, geographical distribution of species, fossil gaps, laws of comparative embryology, phylogenetic patterns, etc. This kind of criticism has been particularly intense in the field of macroevolutionary studies for the past two decades, but attacks coming from morphologists or embryologists would also fit this schema. A very different kind of criticism comes from those who have challenged Darwin's conviction that natural selection has the power of increasing adaptation. This kind of criticism implies a challenge to what Darwin named the proper "power" of selection — or its immediate and apparently self-evident "action". The following section will be mainly devoted to the question of possible intrinsic limits to the adaptive power of selection.

3. LIMITS TO THE EXPLANATORY POWER OF NATURAL SELECTION AND LIMITS TO THE "POWER" OF SELECTION: TWO DIFFERENT ISSUES

I now turn to contemporary evolutionary biology. In previous papers[23], I have claimed that the questions about the identity of Darwinism, past and present, could be clarified by admitting what I called a "decoupling conjecture". This conjecture consists in saying that there have been various regimes of Darwinian discourse, corresponding to the three philosophical roles assigned to natural selection in Darwin's own writings: those of "hypothesis", "theory", and "power". In the present section, I will use the two latter categories in order to distinguish two very different kinds of challenges to Darwinian schemes in recent evolutionary debates. It is one thing to deny that natural selection entails various large classes of facts other than adaptation, such as extinction and divergence. It is another thing to question the very idea that natural selection is able to improve organisms by better adapting them. The first kind of criticism aims at what Darwin called the "well-grounded theory" of natural selection (its explanatory capacity), the second one is concerned with what he named the "power" of selection. I do not want here to give an exhaustive account of these two kinds of criticisms, but to illustrate them by means of clear-cut cases.

3.1. *Challenging the "theory" of natural selection (its explanatory capacity)*

Recent macroevolutionary debates provide extensive evidence of criticisms of the grand Darwinian argument. One can think here, of course, of the con-

[23] Jean Gayon, "What does "Darwinism" mean?", *Ludus vitalis*, 2 (1994), pp. 105–118; "La biologie darwinienne de l'évolution est-elle réductionniste?", *Revue philosophique de Louvain*, 93 (1995), pp. 111–139; "Neo-Darwinism", in *Concepts, Theories and Rationality in the Biological Sciences — The Second Pittsburgh-Konstanz Colloquium in the Philosophy of Science*, ed. by Gereon Wolters and James G. Lennox in coll. with Peter McLaughlin, Universitätsverlag Konstanz/University of Pittsburgh, 1995, pp. 1–25.

troversy over punctuated equilibria, but this case is a rather complex one. I will therefore analyze a much simpler case, that of David Raup's reflections on extinction of species, in his recent book on the subject[24]. Raup challenges the classical Darwinian interpretation of extinction. In the classical Darwinian view, perfectly explicit in Darwin's Origin of Species, extinction is interpreted as a consequence of natural selection. As natural selection transforms species, some of them happen to be fitter in the competition with other species. The less favored forms decrease in number and finally go extinct[25]. This is the argument that permits Darwin to say that "the extinction of species... almost inevitably follows on the principle of natural selection"[26]. Raup does not deny that species go extinct in this way. But he says that a considerable number of extinctions, particularly mass extinctions, might well have been caused by non-biotic factors, of major physical changes affecting the earth, such as big climatic changes, impacts of comets, etc. Species which happened not to be equipped for such brutal perturbation in the physical environment went extinct for reasons which were independent of their relative success in the ecological theater.

Now the issue is: is this attitude non-Darwinian, and in what sense? In the conclusion of his book, Raup himself raises the question whether his interpretation of extinction challenges "Darwin's natural selection". He clearly answers "no", specifying that natural selection remains the only possible explanation for adaptations. But he adds that natural selection alone could not have produced mass extinction events, and the diversification of living beings which probably followed. Thus, Raup does not contest Darwin's idea of natural selection as the "paramount power" or cause of modification of species; but he denies that selection provides a sufficient explanation for at least one major class of facts other than adaptations. Thus, if there is any significant departure from Darwinism here, it is at the level of what Darwin named the "well-grounded theory of natural selection".

I have chosen Raup for the simplicity of the example. Raup does not question either the hypothesis of natural selection nor its power in modifying the adaptive features of organisms. His argument bears on natural selection as a sufficient principle for a general theory of the history of life. And even in this perspective, only one traditional Darwinian deduction is contested, that concerning extinction.

From this example, it is relatively easy to locate various other challenges arising within the field of macroevolutionary studies. Divergence of species and patterns of classification, for instance, have been major targets for criticism, particularly by the defenders of punctuated equilibria. More generally, serious doubts have been raised about the possibility of explaining patterns of

[24]David Raup, *Extinction. Bad Genes or Bad Luck?*, New York, Norton and Co., 1991.

[25]Charles Darwin, *On the Origin of Species*, London: Murray, 1859, (Facsimile: Cambridge: Harvard University Press, 1964), pp. 109–111.

[26]*Ibid.*, p. 475.

distribution in higher taxa or large scale ecological phenomena, solely in the language of natural selection. These various kinds of criticisms can be easily visualized on the diagram above. They boil down to suppressing one or the other of the "boxes" in the lower part.

3.2. *Challenging the (adaptive) power of selection*

I now come to the last part of my analysis. It will bear mainly on Stuart Kauffman's recent reflections on self-organization and selection. Reading Kauffman's recent book on *The Origins of Order*, I have been struck by his explicit concentration on the question of the "power" of selection. The first part of the book is indeed explicitly devoted to the examination of "the power and limits of selection when acting on complex systems exhibiting spontaneous order"[27]. However, before analysing the precise meaning of such adeclaration, let us briefly examine some previous circumstances in which evolutionary biology faced the question of the power of selection.

There are at least two cases in which the modifying and adapting power of selection has been seriously questioned in post-Darwinian biology. The first case corresponds to a period running from approximately 1870 to 1920. In this period, the main challenge natural selection had to face was heredity. Was the Darwinian idea of modification through gradual accumulation of small individual differences compatible with existing theories and experimental evidence about heredity? Galton, who was the first to try to provide a quantitative description of hereditary phenomena, thought that this was not possible; the mutationists, and most of the early Mendelians, held similar views, saying that selection was unable to create or modify anything, and that it was limited to picking out big changes that had arisen from a sudden process of "mutation". It is only when it appeared that continuous variation could be accounted for by Mendelism that biologists again considered it plausible that natural selection could gradually modify and adapt species.

The other major case in which the power of selection came to be seriously questioned is the heroic period of theoretical population genetics. Population genetics consisted of a systematic exploration of the consequences of Mendelian genetics at the population level. Although a highly mathematized discipline, its fundamental concepts were all distinctively biological: the concepts of mutation, recombination, migration, selection, population size and structure — all refer to biological phenomena. The proper description and understanding of these phenomena belong to various laboratory and field disciplines, such as cytogenetics, biogeography, ecology, demography, ethology. However, in population genetics, these phenomena were described in the ho-

[27] Stuart A. Kauffman, *The Origins of Order: Self-Organization and Selection*, New York and Oxford, Oxford University Press, 1993, p. xv. In his preface, Kauffman says also that a major theme of his book is to "understand the extent to which selection can achieve systems able to adapt" (*Ibid.*, p. vii).

mogeneous language of their measurable effects on gene frequencies. Within the new framework, many qualitatively different factors of evolution were describable as forces — forces which determined commensurable effects in evolution. This methodology entailed a new vision of the hypothesis of natural selection. In this new methodological context, selection could no longer be seen as a principle with exceptional privileges. In fact, selection has no privilege whatsoever in the equations of population genetics; it is a force among others, and there is absolutely no a priori nor conceptual necessity that this force should be the major evolutionary factor. For instance, if the population is small, or if there is a high rate of mutation in comparison with the selective pressure, it is perfectly possible that a population be driven mainly by forces other than selection. Of course, as soon as one applies the models to particular situations, selection will stand as a good candidate for the status of a major or even predominant force. But this is precisely the point: theoretical population genetics made it possible to formalize the various conditions under which selection could or could not be a preponderant factor in biological evolution.

Both these stories are well known[28]. My purpose here was only to indicate that Darwin's ideas about the power of selection have been repeatedly and seriously discussed since the publication of *The Origin of Species*. What must be stressed from a philosophical point of view is the following point: the question of the modifying and adaptive power of selection has always been relative to a certain theoretical and experimental context; it has never been a self-evident issue. For more than a century, biologists have looked for limits to the power of selection: they have found them in theories of heredity and population structure. And these limits have been incorporated into the very theory of selection itself. This point had to be stressed before turning to Stuart Kauffman's examination of the power and limits of natural selection.

It is quite out of the question for me to set forth, or even summarize, the ideas developed by Stuart Kauffman in his book on *The Origins of Order*. It is a luxuriant work, endowed with a strong sense of paradox, which makes it somewhat difficult to decide whether the author has brought decisive arguments against the Darwinian view of evolution or whether he has genuinely deepened it and taken it a step forward[29]. I will do no more than classify some theses defended by Kauffman which have a direct bearing on the question of the "power" of selection.

Let us first point out the bold question addressed by Kauffman to the Darwinian interpretation of adaptive modification. Early in the book, Kauffman

[28]For a detailed historical account, see William B. Provine, *The Origins of Theoretical Population Genetics*, Chicago, Chicago University Press, 1971; Jean Gayon, *Darwin et l'après-Darwin: une histoire de* l'hypothèse *de sélection naturelle*, Paris, Kimé, 1992.

[29]David J. Depew and Bruce H. Weber provide interesting information and judgment on this point in their *Darwinism Evolving: Systems Dynamics and the Genealogy of Natural Selection*, Cambridge (MA) and London (England), Bradford & MIT Press, 1995, chap. 16.

evokes what he names "the unchallenged core of evolutionary theory", and makes a clear and orthodox reference to Darwin:

> "A curious, logically unnecessary, but powerfully influential feature of Darwin's thinking was that the variation within one species which paved the way for emergence of well-marked varieties constituting two species was of an indefinite range. The idea that variations could occur in virtually any direction, an idea which dominates Darwin's work despite attention to correlations among traits under selection, has had important consequences. It follows that selection could discriminate which new variants will be found in later generations. Here is one root of our current idea that selection is the sole source of order in the biological world"[30].

Kauffman's challenge to Darwinism flows from these declarations. He questions the very idea that living systems are able to adapt through the accumulation of advantageous variations. Even if there is variation and if individuals differ in fitness, it is not obvious that selection can achieve adaptive modification of organisms. "Darwin told us that adaptive evolution occurs by gradual accumulation of useful variants but failed to tell us what kinds of systems can evolve successfully by random variation and selection for fitter variants"[31]. This is a leitmotiv of the book. One can hardly imagine a more straightforward formulation of the question of the "power" of selection.

Now, the perspective within which Kauffman raises this question is not indifferent: it is complexity. Whereas traditional evolutionary biology used to deal with particular traits, or limited groups of traits of organisms, Kauffman questions the power of selection from the point of view of organisms as complex systems, that is to say entities composed of many parts with many interactions between them. Hence the general question: is there anything in complex systems as such which could limit the adaptive and formative power of selection?

A word must be said about Kauffman's method. In most cases, it consists in speculating on formal properties of systems consisting of N parts, these N components having on the average K interconnections of some sort between them. Kauffman calls this the "NK model". By introducing a certain number of specific parameters, this basic idea can be applied to many biological, or non biological problems. In the case of evolution, it will lead, for instance, to the formulation of the following kind of question: —what will happen to a system of many genes with many epistatic relations between them, if submitted to a process of random mutation and selection? In particular, what will be the effect on the mutation-selection process of increasing the degree of complexity, by modifying both the number of parts and the average number of intercon-

[30] Stuart A. Kauffman, *The Origins of Order: Self-Organisation and Selection*, New York and Oxford, Oxford University Press, 1993, p. 6.

[31] *Ibid.*, p. 29. See also, p. v, xiv

nections? Similar questions can be raised about genetic regulatory networks, coevolving systems, and many other complex entities. In all these cases, the purpose is to evaluate the effects of increasing complexity on the evolvability and stability of the system, if exposed to some kind of mutation-selection process. In order to do this, Kauffman makes extensive use of computer calculation and simulation. In some cases, the computer is used for exploring numerical solutions to problems inaccessible to ordinary algebraic calculus. In other cases, the method consists in studying the dynamic properties of such and such a complex system by observing the behavior of an analogical system such as a Boolean network.

I do not want to go further into the detail about the methodology. I will concentrate on Kauffman's conclusions, focusing solely on the power of selection problem. These conclusions, although they are most often inextricably mingled with one another, fit into three different categories.

Kauffman's first assertion is that a number of the properties of complex systems arise as a function of their degree of intrinsic complexity, whatever the selective pressures are applied to them. These properties, which he calls "generic properties", cannot be viewed as the specific result of selection. In other words, they will arise in spite of selection, in virtue of "spontaneous sources of order". As a concrete example, Kauffman often cites the relation between the number of cell types and the number of genes in organisms. Most often however, the examples point to more formal self-organized properties. The general spirit of this first kind of limitation to the power of selection is that selection is not the "sole source of order". Complexity by itself restricts the field of possible solutions: in relation to the degree of complexity, there exist properties which will arise independently of, or in spite of, selection, even here selection is the proximate cause of change. This kind of limitation is in a certain sense exterior to the proper action of natural selection: just as selection cannot contradict the law of gravitation, selection must also coexist with regularities associated with complex organization. I am not sure that this comparison would resist a careful epistemological analysis, but there is no doubt that Kauffman has something like that in mind[32].

Beside this first kind of limitation, Kauffman explores another type, more closely related to the process of selection itself. A large part of the book on The Origins of Order tries hard to build models of selective evolution under the hypothesis that selection acts on a system of many genes with many interactions between them (epistasy in some models, regulatory loops in others). Using a generalized notion of fitness landscape, Kauffman tries to show that beyond a certain degree of complexity, there are serious limits to the ability of systems to evolve toward a higher fitness or even to maintain themselves at

[32]This first class of limits to the power of selection has been very carefully analyzed by Richard M. Burian and Robert C. Richardson, in "Form and order in evolutionary biology/ Stuart Kauffman's transformation of theoretical biology", *PSA*, 2 (1990), pp. 267–287. This article provides a deep analysis of the philosophical implications of Kauffman's enterprise.

a given level of fitness. Various kinds of "complexity catastrophes" can arise, as a function of the organizational constraints imposed on the system. Again, I will not enter here into the details of the models, but I would like to draw a parallel with classical theoretical population genetics. In the twenties and thirties, Fisher and Wright established that population structure imposed crucial limits on the capacity of selection to control the evolution of a Mendelian population. However their models were restricted to a very small number of loci, most often one. Kauffman's program is comparable in a certain sense: instead of looking for limits imposed by the population structure, he looks for them in the structure of the genome. And just as Wright believed that some kinds of population structure were more favorable than others to the action of natural selection, Kauffman tries to show that some kinds of connectivity within the genome are more favorable than others to the action of selection.

Finally, one finds in Kauffman a third category of proposals regarding the power of selection, which he calls "the bold hypothesis"[33]. The bold hypothesis does not place a limit on the power of natural selection; rather, it is a deepening of it. In fact, in a sense, Kauffman proposes more for the direct action of selection than Darwin did. The idea comes itself as an answer to the issue of the origin of adaptability:

> "We must ask that which Darwin did not broach: What kinds of integrated dynamical systems harbor the ability to adapt?"[34].

Kauffman's ultimate answer to this question is now well known. He supports the thesis that the most favorable situation is a regime intermediate between "ordered" and "chaotic". In other words, selection will be better able to improve the adaptation of organisms within a lineage as the system submitted to its action will be in this poised regime, "between solid and liquid". But what produces this miraculous state? Here comes the "bold hypothesis", repeated a number of times throughout the book. Let me quote a few passages stating the bold hypothesis in various ways:

> "[we are led] to the hypothesis that *the target which selection achieves* is complex systems poised in the complex regime on the boundary between order and chaos" (emphasis added)[35].
>
> "We examine the attractive hypothesis that networks poised at the edge of chaos can perform the most complex tasks. Furthermore, *we consider whether selection can achieve such poised systems*. If both answers are yes, as they begin to appear to be, then we may have succeeded in discovering the characteristic kind of complex systems which selection achieves in order to optimize both evolvability and fitness" (emphasis added).[36]

[33] For the characteristic formulas, see pp. xvi, 30, 175, 183, 209, 218, 221, 232, 280, 645.
[34] *Ibid.*, p. 209.
[35] *Ibid.*, p. 30.
[36] *Ibid.*, p. 175

> "Parallel-processing systems lying in this interface region between order and chaos may be those best able to adapt and evolve. Further, *natural selection may be the force which pulls complex adaptive systems into this boundary region.* If so, we begin to have a powerful tool with which to examine the collaborative interaction between self-organization and chaos" (emphasis added)[37].
> "Living systems exist in the solid regime near the edge of chaos, and *natural selection achieves and sustains such a poised state*" (emphasis added)[38].
> "We expect *that selection can mould the entities it acts on to improve the characters of the landscapes these entities explore...* In short, the capacity to evolve is itself subject to evolution and may have its lawful properties" (emphasis added)[39].

These quotations are puzzling. Here is an author who claims many times that there are strong limits, external and internal, to the power of selection. Nevertheless, the same author comes to support the view that, ultimately, selection has the power of "tuning" complex systems in such a way that they optimize the action of selection itself. In other words, selection is able to evolve adaptability itself. David Depew and Bruce Weber, In their recent book entitled *Darwinism Evolving*, say that in exploring such an idea, Stuart Kaufmann has indeed attempted to provide a theoretical basis for Dobzhansky's "intuitive vision of adaptations for adaptability"[40]. In that sense, the discourse about the limits of natural selection turns into an expansion, or better, a deepening of its power. Note that this is not Darwin's sense of the "power of selection" as I explained it above. Darwin's sens concerned the ability of selection to "adapt" and "form" the organisms within a lineage. Kauffman's question concerns the ability of selection to mold evolving systems so that they have the property of being subject to what Darwin called the power of selection[41].

Therefore, to summarize, on the one hand, Kauffman increases significantly the external and internal limits imposed to the power of selection in Darwin's sense; on the other hand, he increases this power, by extending it to the generation of properties such as "evolvability" and "adaptability".

4. CONCLUSION

What lessons can we draw from this story? I will formulate three.

First, I think I have made clear that historians and philosophers of biology should clearly distinguish questions related to the explanatory capacity of

[37] *Ibid.*, p. 218.
[38] *Ibid.*, p. 232
[39] *Ibid.*, p. 645.
[40] David J. Depew and Bruce H. Weber, *op. cit.*, p. 443.
[41] I am indebted to Richard M. Burian for this nice formulation.

natural selection and issues related to what Darwin called its "power". This distinction is particularly useful for anyone who wants to clarify contemporary criticisms of Darwinian evolutionary biology. It is one thing to contest the ability of natural selection to "entail" (and therefore explain) such and such a class of phenomena , it is another thing to question the intimate "action" of natural selection.

Second, one can be puzzled by the continuing importance of the question of the power of selection in the history of evolutionary biology. In the time of Darwin himself, his manner of speaking of natural selection with this kind of philosophical vocabulary was criticized as an archaism, and there was certainly some truth in this. However, in the course of time, this archaic philosophical vocabulary may have been useful. Darwin's confidence in the power of selection has indeed stimulated many people to seek for its limits. From biometry to population genetics, and today to the dynamics of complex systems, the "power of selection" issue has led to a repeated deepening of the concept of natural selection.

Finally, a philosopher cannot avoid asking about the strange use Darwin made of the term of "power". The distinction we find in Darwin's writings between the "power" and the consequences of natural selection can be captured as follows. In a sense, adaptation is one consequence of natural selection among others; in another sense, adaptation is the immediate result of the proper action of natural selection, and is a little more than a mere consequence, although it is indeed a consequence. This subtle distinction means that Darwin's notion of power is not merely epistemological. The explanatory capacity of natural selection is an epistomological issue: it is related to the deductive structure of a theory. But what Darwin called the power of natural selection requires one to think of it in terms of its action or causal efficacy in a defined material space. This is a material issue. Again, one must stress the fact that Darwin described both artificial and natural selection as a power. The model of artificial selection was indeed immensely important because it was the sole evidence Darwin had of the efficacy of a selective process. If Darwin had been interested only in the deductive structure of his "theory", he would not have needed to depend on this analogical model.

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