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On Darwin's palaeontology in *The Origin of Species*

La paléontologie de Darwin dans L'Origine des espèces

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ABSTRACT

I investigate the role of palaeontology within Darwin's works through an analysis of the two chapters of *The Origin of Species* most especially devoted to this science. Palaeontology may occupy several places within the structure of the argumentative logic of Darwinism, but these places have remained to some extent ancillary. Indeed, palaeontology could well document evolutionary *patterns*, showing the actual occurrence of evolution as a general "historical fact", but it was poorly adapted to demonstrate the main point of Darwinism: the actual evolutionary *process: natural selection* acting among *individuals*. I also show, in agreement with Gould, that Darwin had great confidence in the ultimate ability of palaeontology to support his theory, and that in interpreting palaeontological evidence, he expressed a vision of natural selection much wider and more eclectic than that which has generally been ascribed to him.

Mots clés :
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RÉSUMÉ

La paléontologie de Darwin dans *L'Origine des espèces*. On met en question la position de la paléontologie dans l'œuvre darwinienne, au travers de l'analyse des deux chapitres de *L'Origine des espèces* où cette science est particulièrement envisagée. Compte tenu de la logique argumentative propre au darwinisme, la paléontologie a pu occuper plusieurs places au sein de cet argumentaire, mais ces places sont demeurées quelque peu subordonnées. En effet, la paléontologie pouvait bien renseigner sur les *patterns* évolutifs, en documentant l'évolution en tant que « fait historique » général, mais elle était peu armée pour appuyer l'essentiel ou « noyau dur » de l'argumentation darwinienne, c'est-à-dire le *process* ou mécanisme fondamental de la transformation évolutive : la *sélection naturelle* s'exerçant entre les organismes *individuels*. On montre par ailleurs, en accord avec Gould, que Darwin a manifesté une grande confiance quant à l'aptitude future de la paléontologie à appuyer sa théorie et qu'il a exprimé à son propos une vision du mécanisme sélectif bien plus large et éclectique que celle que l'on lui a généralement attribué.

« En fin de compte, Darwin était de son époque, même s'il la transcende de bien des façons. Il doit à son génie propre d'avoir pu autant accomplir et synthétiser. Un siècle et demi plus tard nous en profitons encore et essayons de comprendre toutes les leçons qu'il avait à nous enseigner ». (K. Padian 2004)

1. Introduction

The relationship between palaeontology and Darwin's works is complex. It has been approached recently (2005)

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by Herbert, within the framework of an exhaustive survey of Darwin as a geologist [1]. Nevertheless, the specific importance of palaeontology for Darwin's works cannot be fully expressed with reference only to the field of geology. Indeed fossils are, first and foremost, the actual evidence of what living beings have been through geologic time, before they offered mere biostratigraphic records useful to the geologist. Accordingly, they convey a special meaning regarding the Darwinian issue of "*Descent with modification*", an expression that Darwin would ultimately replace with *Evolution*, a more popular and straightforward term. In other words, fossils could have been, for Darwin, a key argument favouring evolution, understood as the actual fact of a general transformation of living beings through the protracted history of planet Earth.

Reading *The Origin of Species* [2] suggests, in my view, that this possibility of a pre-eminent situation for palaeontology within the Darwinian argument has remained somewhat restricted and almost completely unfulfilled.

Two kinds of explanations can be offered retrospectively to account for what has been, perhaps, an unfinished encounter between palaeontology and Darwin. On one hand, there have been causes internal to palaeontology itself, linked not only to the state of the art of this science in Darwin's time, but also to the current interpretations (fixism, catastrophism,...) of the causes of change in the history of life. On the other hand, there have been causes external to palaeontology but internal to Darwin's Darwinism, in other words to the logical structure of the argument framing Darwinism itself.

My point of view will be developed in three phases. First of all the general logic of the Darwinian argument will be reviewed and I will discuss the place(s) palaeontology could have had (and effectively did have) within this argument. Then the analysis of a key Darwinian text will allow me to emphasise the quality of the argumentation, the analytical sharpness, scientific probity and, above all, innovative thinking of Darwin regarding the palaeontology of his time. Finally, the contrast between the palaeontological data available to Darwin and our current knowledge will permit some brief conclusions about the mutual influences of palaeontology and the Darwinian works.

Professional history of science would require an analysis of all of Darwin's works to assess in full the issue of his relationship with palaeontology, but it is obviously impossible to do so within the framework of a short essay. Accordingly, I will concentrate on the analysis of a key text: chapters ten and eleven of the sixth edition of the Origin (1872), "On the imperfection of the geological record" (344–378) and "On the geological succession of organic beings" (379–412), respectively [2].

2. The situation of palaeontology within the logic of Darwinian argumentation

I follow herewith the analysis of Darwinian argumentation proposed by Gayon from 1997 to 2009 [3–5]. According to this view two well-known fundamental statements form the framework of the Darwinian argument.

The first is "*Descent with modification*", which emphasises the material-historical reality of evolution and which would approximately match the study of the actual evolutionary history of life, or what is currently understood as the study of *evolutionary patterns*.

The second one is *natural selection*, which constitutes a general mechanism (or *evolutionary process*) actually causing the evolutionary transformations and offering a rational and natural explanation of them within an explicit scientific framework (methodological materialism).

2.1. The situation of palaeontology in the study of evolutionary patterns

Descent with modification postulates with more or less precision the relatedness or kinship among all living beings and, *in fine*, their common rooting in a remote and primeval form of life. Starting from this, a succession of diversifying splits and progressive complexifications (and extinctions) would lead to the biodiversity currently observed. This general scheme, called "the theory of the reality of evolution" by Løvtrup [6] is not exclusive to Darwin. It can be found, with more or less clarity, among many "forerunners of Darwin" as Glass (1959) called them [7], and notably in Lamarck, according to Laurent [8], One might also claim that the theory is already present during the XVIIIth century [9,10], subject to all the nuances which Roger [11] argues that the passing of time since the enlightenment currently imposes on interpretations of texts from that period.

Nevertheless, Darwin (1859) offers a much more precise view of specific transformations or transmutations than his forerunners [2]. His concept of descent with modification becomes precise enough to be clearly analysed, even if he never formalised it himself. Among its characteristics, as formally expressed recently [5] let us only recall the paramount importance of changes at the level of the individual (i.e. within species) and their gradual outcome. It follows that supraspecific taxa and their relative hierarchical rankings would be arbitrary and that they would represent, at best, mere schemata of the results, rather than true units of evolution. On the other hand, according to Padian (2004) the "gradual" pattern of evolutionary change, much emphasised by Darwin, could as well be understood not as a continuous "anamorphosis", but literally as a series of small discrete steps, as along a graduated test-tube, a stair, or the graduations from one grade to another in school [12].

The Darwinian view of *descent with modification* is illustrated by the famous drawing on p. 117 in chapter four of the *Origin*, a scheme used and commented on by Darwin in various chapters to illustrate very different things (see below).

The Darwinian argument related to palaeontology mainly illustrates the *compatibility* of the palaeontological record with this particular pattern or scheme, *but the scheme itself is not at all derived from this record*.

2.2. The situation of palaeontology in the study of evolutionary process

Darwin builds up his explanatory mechanism of evolutionary transformation from the consideration of data, or empirical facts, stemming from a limited series of well-documented biological domains (potential reproductive rates of organisms, limitation of resources in a given environment, heritability and variability of individual features) and from the analogy with an "experimental" model (artificial selection). Together, they allow Darwin to infer his "mere hypothesis" of natural selection.

The hypothesis of natural selection is thus based on a critical synthesis and generalisation stemming from limited but precise empirical data. This inference is at once an induction, because it generalises from limited data, and a deduction, because it follows a logical causal pathway (if... then...), is formally coherent and "inescapable".

With the hypothesis of natural selection thus formulated according to "Newtonian" principles and in agreement with the epistemological prescriptions of Herschel and Whewell [5], Darwin thinks he has the efficient cause (*vera causa*) of evolutionary change, in other words the very mechanism itself (or *process*) underlying each and every historical development of life (the *evolutionary pattern*).

The next step, according to the epistemological constraints followed by Darwin, would be to "test" the functional and explanatory values of the hypothesis of natural selection. This "test" cannot take the form of an experiment since the only possible and relevant experimental test in this domain would be artificial selection, which already assumes the hypothesis' premises. It is thus necessary to rely on other kind of tests, not experimental ones, but ones which will *show* the explanatory power of natural selection in *fields other* than the ones from which it has stemmed. The more the hypothesis can explain numerous empirical data in those supplementary and independent fields, the more its explanatory value will increase and generalise, and at the same time its plausibility will rise. More than a formal demonstration of the hypothesis, the method used by Darwin to progressively enhance his hypothesis towards the status of a theory is that of "additive consiliency", in accordance with the epistemological model that Darwin had committed himself to follow and illustrate.

The fields, or independent domains, in which natural selection will show its explanatory power, are numerous and varied. One thinks especially of the origins of morphological adaptations, instincts, geographical distributions, stratigraphic succession of fossil forms, data on divergences, extinctions, comparative anatomy (homologies) and embryology (recapitulation), and lastly of systematics (the structure of classification). Chapters 8 to 15 of *the Origin* effectively illustrate (rather than demonstrate) the explanatory power of natural selection in those various domains in such a way that the "mere hypothesis" of departure is effectively raised to the rank of a theory.

Among all the domains where natural selection shows its explanatory power, only one, strictly speaking, formally covers palaeontology: that of the stratigraphic succession of fossil forms. Nevertheless, from a wider point of view, it is clear that palaeontology also interacts with many other domains where natural selection is involved, such as distributions, divergences, extinctions, homologies, and systematics. Actually, the various fields where natural selection shows its explanatory power are *not really independent* one from another, and paleontology forms an effective link among many of them.

Those considerations show that either directly or indirectly, palaeontological data are important to the Darwinian argument about *process*. They play their role in the *final phase* of that argument, which justifies the hypothesis. By extension, the palaeontological data contribute to the hypothesis' explanatory value, helping to raise it to the rank of theory. On the other hand, they are lacking in the "upstream" corpus from which the hypothesis is derived. This in turn introduces two kinds of considerations.

First, it appears that the "hard core" of Darwinian evolutionism is the proposition that a *general and efficient mechanism* (natural selection) forms a true *explanans*, which is able to account for a large *explanandum*. The *explanandum* consists of data which are independent and partly contingent (because of its historical background), but which requires a common explanation. In short, in Darwin's mind, the explanatory mechanism of evolution (the *process* of natural selection) takes precedence over the "fact" or historical reality of evolution (*pattern*). Darwin's general tree-like scheme (p. 117) is a theoretical bet stemming from his analysis of the process, rather than a synthesis of empirical observations.

Second, it appears that upstream of the *explanans*, that is of natural selection and its immediate empirical roots, there should exist for Darwin a gigantic and more or less implicit *explanandum* that may contain palaeontological data. Among the pre-Darwinian transformisms (theories of transformations), it was the *hypothesis of species transformations itself* that could offer an *explanans* of many data brought forward by natural history, including facts of homology, structure of systematics, and embryology. Within Darwinian logic, the "fact" of evolution seems to be acknowledged at once and the *explanans* thus has to "jump" up a step. From the "fact" of evolution (now a *pattern*) it jumps to the analysis of its mechanism (*process*). Briefly, in Darwin's mind it is indeed the process that takes precedence over the historical pattern, in contrast to some pre-Darwinian transformisms (see below).

If one sets the palaeontological data in this intellectual framework, it is clear enough that they amount to a large *explanandum* that may be found at several levels of reasoning, rather than of the Darwinian *explanans*, the heart of the theory. Because of this, palaeontology could at best play a secondary, even ancillary role in the Darwinian structure. Nevertheless this role is not negligible, and it expresses itself at several levels.

First, Darwin's need to build up the "mere hypothesis" stems from the previous consideration of a host of empirical data (*explanandum*) demanding explanation.

As we have seen, this consideration is implicit, and it antedates the discovery of selection. This is the first level of reasoning at which numerous palaeontological data could appear. Exactly the same facts and data could be found again at a second level, this time downstream from the explanatory reasoning. There could well exist some circularity here. The very same facts (palaeontological and others) that are taken to generate questions about the mechanism of evolution are also used as "evidence" for the hypothesis about that mechanism. They are at once upstream and downstream from the Darwinian reasoning about the process of evolution.

In between, the hypothesis of natural selection will obviously have explained them, within the framework of descent with modification.

All that may explain an entire English-speaking tradition that claims that evolution was really not "thinkable" before Darwin because there was no real explanatory mechanism available before him. This point of view strongly contrasts with the actual occurrence of several "continental" pre-Darwinian theories of species transformations. They generally insisted on the validity of empirical data (facts of homology and development, structure of systematics...) forming a first hand *explanandum*, the *explanans* being, as we saw, the very fact of the historical/evolutionary pattern itself. This view could well match Lamarck's transformism, according to Laurent (1987) [8]. In turn, the occurrence of the historical evolutionary pattern would itself need an *explanans* at a second level. The explanans would be the mechanism of evolutionary transformation itself. This process was generally recognised before Darwin (and by Darwin himself) as the "Lamarckian" heredity of acquired characters.

With this in mind, it is interesting to consider, more than one century apart, the situation of evolutionism with that of continental drift. In both cases one faced for a long time a gigantic *explanandum* fed by numerous, varied and inescapable empirical facts of natural history, but which were more or less undervalued or rejected as long as a satisfactory *mechanistic explanans* (natural selection on one hand, plate tectonics on the other hand) was not available.

3. The analysis by Darwin of the palaeontological data of his time: A clear-sighted and innovative mind

It is generally accepted that Darwinism *sensu stricto*, beginning with Darwin himself, is based on one evolutionary process only: natural selection working at the level of the individuals within species. This interindividual and intraspecifc selection represents the "orthodoxy" of Darwinian evolutionary mechanics and also of its historical and intellectual offspring, the Synthetic theory of evolution (1930-present) [13,14].

A careful reading of the two chapters that Darwin devotes in *The Origin* to the geological and palaeontological aspects of his theory suggests a wider and more open view of his theory. Thus, it is not surprising that some evolutionary palaeontologists deeply influenced by Darwinian texts, Stephen Jay Gould being at the forefront (Gould 1980, 2002), did not hesitate to grant Darwin himself a clearly more open and eclectic view of natural selection than that which became the ruling "orthodoxy" of the synthesis [14–16]. This could explain why some Darwinian palaeontologists (rather than Darwinian biologists) did express reluctance towards what they resented as a narrowing and hardening of "Darwinism" within the mature phase of the classical synthesis of the years 1960–1970.

Darwin opens his chapter ten on the geological and palaeontological data connected to his theory with a discussion of the significance of the lack of intermediate forms between species in the present world and those in the fossil record (344–346). His argument tends to show that this lack is precisely a logical consequence of the process of natural selection. He discusses acutely the nature of intermediate forms, showing how seeking intermediates between two extant (or synchronous) species does not at all convey the logic of his theory, hence rejecting in advance sophisms such as "man derives from the ape".

"In the first place it should always be born in mind what sort of intermediate forms must, on the theory, have formerly existed. I have found it difficult, when looking at any two species, to avoid picturing to myself forms *directly* intermediate between them. But this is a wholly false view; we should always look for forms intermediate between each species and a common but unknown progenitor; and the progenitor will generally have differed in some respects from all its modified descendants" (345). Let us notice that Darwin implicitly but clearly states here the need to introduce at least *three* taxa to consider a phylogeny. If, instead of "*a* common but unknown progenitor" (which may be down deep and not exclusive to the two species under consideration) he had specified: "their last unknown common ancestor" (i.e. the proximate and exclusive common ancestor), Darwin would have opened the realm of cladistics!

Darwin then explores more specifically geological considerations of lasting interest (347–352) on the dynamics of denudation by erosion of the continents and deposition of sedimentary formations. This was aimed at familiarising the reader of his time with the actual duration of geological time pertinent to his theory of speciation. He notes especially the unknown duration of the local episodes when neither deposition nor erosion occurred, creating gaps or unconformities in the sedimentary records, and he links those various circumstances to subsidence, or rates of deposition and erosion. He devotes six pages (352–358) to "the poorness of palaeontological collections", an important topic in which he reviews lucidly the causes and consequences of sampling bias linked to the very nature of the fossil record. Those biases are varied and linked to numerous biotic (ethology, ecology, biomineralisation...) and abiotic (environment, geography, altitude, taphonomy, geological period...) factors altogether explaining the partial (i.e. incomplete *and* biased) pattern of the record. This sub-chapter forms almost a continuous *lamento* on the incompleteness and poor quality of the fossil record. Nevertheless, Darwin shows that the available data, in spite of their poor quality,

are perfectly compatible with his theory of descent with modification. He also shows a great confidence in the palaeontological discoveries to come, noticing (372) that since the first edition of the *Origin*, twelve years before, significant progress had accumulated, and all of it favoured his views, notably the discovery of *Archaeopteryx* in 1861 (370). The next sub-chapters are devoted to the absence of numerous intermediate varieties in any single formation (359–368) and to the sudden appearance of whole groups of allied species (368–372). Generally speaking, Darwin tends to link the deposition of richly fossiliferous beds to subsidences. Yet he suggests that speciation events are more frequent during times of emersions (which are not favourable to the deposition of rich fossiliferous beds and prone to the erosion of fossiliferous beds already deposited). Thus, he concludes that speciation events will be especially poorly sampled in the fossil record. This hypothesis may seem to us somewhat *ad hoc*, but Darwin comes back to it several times (366, 392, etc.).

The sub-chapter on the absence of "Precambrian fossils" (372–378) and the sudden appearance of the rich Cambrian fauna is of great interest in retrospect, as here Darwin has to face the empirical data not favouring his theory and which he admits with probity (374) that he is unable to explain satisfactorily, although he tries to. Apart from *Eozoon,* which he discusses, almost no fossil data under the Cambrian strata were available in Darwin's time, although he notes that the occurrence of bituminous beds and phosphates in the strata suggest that plentiful life already existed. In spite of both the extreme unreliability of "absolute" (in millions years) dates available at the time, and the terrible constraints imposed by Sir W. Thomson's calculations (373), Darwin clearly perceived that the total duration of the "Precambrian" considerably exceeded that of the "Phanerozoic" (from the base of the Cambrian to the present time).

In these two chapters, Darwin gives especially clear and detailed comments on the famous drawing on p. 117 of the *Origin* (pp. 362–363 and still more pp. 396–398). One can find there, clearly expressed and organised, all the arguments linking "descent with modification" to the stratigraphic and systematic dimensions of palaeontology (note here that the very same scheme is used quite differently, i.e. at other integrative levels, in other parts of the *Origin*). A whole logic and tradition of post-Darwinian evolutionary palaeontology was directly and explicitly derived from the views expressed there, from the schemes used by some pedagogical vulgates of the "palaeontological proofs of evolution" to the sophisticated formalisations of the stratophenetic method by Gingerich, e.g. in 1987 [17].

I shall put forward below some excerpts from the two chapters of the *Origin* studied here which seem to illustrate especially well the "Darwinian orthodoxy" as applied to geology and palaeontology. I point out, later on, other excerpts where this "orthodoxy" seems to have been left behind and where Darwin's thoughts seem to open themselves to alternative or complementary avenues that may also prefigure some later trends and interpretations. (In the excerpts I have put some of Darwin's words or phrases in italics to emphasise them, I also added a few words in parentheses).

3.1. Geological and palaeontological documentation in agreement with the theory

In these passages there is an insistence on the discontinuity and incompleteness of the palaeontological record because of the very imperfect recording of time by the stratigraphic column. It follows that the "sudden" appearance (and disappearance) of species and higher systematic groupings can be regarded as "artefacts" and should not be taken at face value. This message was fundamentally retained by post-Darwinian evolutionary palaeontology, especially within the framework of the Synthetic theory (e.g. Ricqlès 1997) [13].

354: "The frequent and great changes in the mineralogical composition of consecutive formations, generally implying great changes in the geography of the surrounding lands, whence the sediments was derived, accord with the belief of *vast intervals of time having elapsed* between each formation".

355: "...sediment may be deposited to any thickness and extent over a shallow bottom, if it *continues slowly to subside*. In this latter case, as long as the rate of subsidence and the supply of sediment nearly balance each other, the sea will remain shallow and favourable for many and varied forms, and thus a rich fossiliferous formation, thick enough, when upraised, to resist a large amount of denudation, may be formed".

Nevertheless:

358: "During periods of elevation the area of the land and of the adjoining shoal parts of the sea will be increased, and new stations will often be formed: – all circumstances favourable, as previously explained, for the formation of new varieties and species; but during such periods *there will generally be a blank in the geological record*".

We may notice that it is usually thought today that marine regression phases will drastically reduce marine epicontinental shelves and the richness of the related ecosystems.

361: "It would seem that each separate formation, like the whole pile of formations in any country, has generally *been intermittent* in its accumulation. When we see, as it is so often the case, a formation composed of beds of widely different mineralogical composition, we may reasonably suspect that the process of deposition has been *more or less interrupted*".

380: "In members of the same class the average amount of change, during long and equal periods of time, may, perhaps, be nearly the same; but as the accumulation of enduring formations, rich in fossils, depends on great masses of sediment being deposited on subsiding areas, our formations have been almost necessarily accumulated *at wide and irregularly intermittent intervals of time*; consequently the amount of organic change exhibited by the fossils embedded in consecutive formations is not equal. Each formation, on this view, does not mark a new and complete act of creation, *but only an occasional scene, taken almost at hazard, in an ever slowly changing drama*".

380–381: "The process of modification must be slow, and will generally affect only a few species at the same time; for the *variability* of each *species* is independent of that of all others. Whether such variations or individual

differences as may arise will be accumulated through natural selection in a greater or less degree, thus causing a greater or less amount of permanent modification, will depend on many complex contingencies – on the variations being of a beneficial nature, on the freedom of intercrossing, on the slowly changing physical conditions of the country, on the immigration of new colonists, and on the nature of the other inhabitants with which the varying species come into competition". (we understand "varying species" as those species actually experiencing the evolutionary process). Note that already here reference is made to specific (not individual) characteristics of variability and to interspecific competition.

3.2. Some premonitions of "punctuated equilibria"?

The general model of "punctuated equilibria" proposed by Eldredge and Gould in 1972 was initially derived from the consideration of empirical data on Palaeozoic marine faunas [18]. In such data, there is an abrupt succession *in situ*, in the stratigraphic column, of slightly different forms replacing the preceding ones. This was linked to migrations and secondary recolonisations, by successions of more and more derived immigrants, of the areas formerly occupied by their immediately ancestral form, in connection with shelf evolution.

Although "Punctuated Equilibria" (PE) was initially offered, and widely resented, as an alternative to Darwinian gradualism, it is possible to find in Darwin himself almost identical expressions of similar considerations.

360: "We may safely infer that with marine animals of all kinds there has been *a large amount of migration* due to climatal and other changes; and when we see a species first appearing in any formation, the probability is that it only then *first immigrated into that area*".

This conveys the spatial component of the PE model.

364: "It is a more important consideration, leading to the same result, as lately insisted on by Dr. Falconer, namely, that the period during which each species underwent modification, though long as measured by years, was *probably short* in comparison with that during which it remained *without undergoing any change*".

This conveys the temporal component of the PE model.

367: "...the (new) varieties would at first be *local* or confined to one place, but if possessed of any decided advantage, or when further modified and improved, they would *slowly spread and supplant their parent-forms.* When such varieties *returned to their ancient homes*, as they would differ from their former state in a nearly uniform, though perhaps extremely slight degree, and as they would be found embedded in slightly different sub-stages of the same formation, they would, according to the principles followed by many palaeontologists, be ranked as *new and distinct species*".

This combines the components of the PE model.

369: "but, when this (*new)* adaptation had once been effected, and a few *species* had thus acquired a great advantage over other organisms*, a comparatively short time* would be necessary to produce many divergent forms, which would spread rapidly and widely, throughout the world".

This seems to suggest a supraspecific (or group) evolutionary dynamics.

409: "Although each species must have past through numerous transitional stages, it is probable that the periods, during which each underwent modification, though many and long as measured by years, *have been short* in comparison with the periods during which each remained in *an unchanged condition*. These causes, taken conjointly, will to a large extent explain why – though we do find many links – *we do not find interminable varieties, connecting together all extinct and existing forms by the finest graduated steps*".

Darwin seems to endorse here – and explain – the famous motto linked to PE: "stasis is data".

3.3. On the "Red Queen" and on inter- and supra-specific selection?

Generally speaking, one must admit that the systematic vocabulary used by Darwin in the two chapters under consideration is of careful and cautious neutrality. First, he puts forward the highly subjective character of the formal categories of systematics and of their boundaries (362–363), which gives practical flexibility to the meaning and value of words like species, sub-species and varieties as he uses them. Darwin praises and makes great use of informal systematic terms such as "forms" and "groups" and only a thorough critical analysis can bring the conviction, in some cases, that he means by them infra-specific categories, hence remaining within the "orthodoxy" of the evolutionary process. However, in several other parts it is not really possible to decide whether terms like "forms" or "groups" refer to infraspecific entities. Actually, the context would often strongly suggest, on the contrary, an interpretation of those words as pointing out supraspecific groupings of varying size and "rank", but always formed by actual genealogical kinship and possessing *ipso facto* what we would call now common (phylo) genetic charateristics. This concept would fairly well match the modern meaning of a clade. Also, as Padian pointed out in 2004, reading Darwin is a complex exercise and may be open to various interpretations [12].

381: "When many of the inhabitants of any area have become modified and improved, we can understand, on the principle of competition, and from the all-important relations of organism to organism in the struggle for life, that any form which did not become in some degree modified and improved, would be liable to extermination. Hence we see why *all the species* in the same region do at last, if we look to long enough intervals of time, *become modified, for otherwise they would become extinct*".

For me, this kind of interspecific competition (or race) is very akin to the "Red Queen hypothesis".

382: "*Groups of species,* that is genera and families, *follow the same general rules in their appearance and disappearance as do single species,* changing more or less quickly, and in a greater or lesser degree. A group, whence it has once disappeared, never reappears; that is, its existence, as long as it last, is continuous... *For all the species of the same group*, however long it may have lasted,

are the modified descendants one from the other, and all are *from a common progenitor*".

Because Darwin specifies "*all* the species. . ." his concept of "group" here seems to me extremely close to a monophyletic group in the cladistic sense (the common ancestor and all its descendents).

387: "Thus, as I believe, a number of new species descended from one species, that is a *new genus, comes to supplant an old genus,* belonging to the same family. But it must often have happened that a new species belonging to some *one group* has seized on the place occupied by a species belonging to a distinct group and thus have caused its extermination. If many allied forms be developed from the successful intruder, many will have to yield their place; *and it will generally be the allied forms, which will suffer from some inherited inferiority in common*".

Natural selection seems to act here on whole (supraspecific) groups because of their shared characteristics derived from their common ancestor.

388: "Moreover, when, by sudden immigration or by unusually rapid development, many species of a new group have taken possession of an era, many of the older (*local*) *species* will have been exterminated in a corresponding rapid manner; *and the forms* which thus yield their places *will commonly be allied, for they will partake of the same inferiority in common*".

Here, it is possible to understand a combination of "punctuated equilibria" and of group (supraspecific) selection.

392: "The old forms which are beaten and which yield their places to the new and victorious forms, *will generally be allied in groups, from inheriting some inferiority in common*; and therefore, as new and improved groups spread throughout the world, old groups disappear from the world; and the succession of forms everywhere tends to correspond both in their first appearance and final disappearance".

Here the general synchrony of faunal turnover worldwide seems to be linked by Darwin to the built-in general properties of large (supraspecific) groups.

410: "The dominant species belonging to *large and dominant groups* tend to leave many modified descendants, which form new sub-groups and groups. As these are formed, the *species of the less vigorous groups, from their inferiority inherited from a common progenitor,* tend to become extinct together, and to leave no modified offspring on the face of the earth. But the utter extinction of a *whole group of species* has sometimes been a slow process, from the survival of a few descendants, lingering in protected and isolated situations. When a group has once wholly disappeared, it does not reappear; for the link of generation has been broken".

Again, the concept of natural selection is clearly applied here to supraspecific groups understood as biological clades, rather than to mere convenient or traditional taxonomic groupings.

4. Concluding remarks

In the two chapters considered, Darwin often comes back to the idea that the palaeontological data, as he proposes to interpret them and in spite of the incompleteness of the fossil record, generally agree very well with his theory, justifying its value. He stresses eloquently the explanatory power of his theory in the concluding remarks (408–412) and goes as far as to claim that the data "are wholly inexplicable on any other view" (399). Nevertheless, it is probably not trivial to notice that, very often, this agreement is expressed by Darwin himself as illustrating "descent with modification" (396, 399, etc.) rather than demonstrating natural selection. In other words, the fossil record supports well the idea of the material reality of a general historical pattern of life change, continuously unfolding itself through time (phylogeny), rather than the mechanistic process (natural selection) of this evolution, the focal point of Darwinian theory. As often as possible, Darwinian rhetoric more or less subtly links the two aspects (patterns and process) of his theory. A forceful example of this appears at the end of chapter eleven, where Darwin writes (412) ". . .old forms having been supplanted by new and improved forms of life, the products of Variation and the Survival of the Fittest". Yet this rhetorical effort is just that, and can hardly hide the fact that the mechanism of natural selection among individuals is documented by the fossil record poorly, if at all.

This easily explains the fact that post-Darwinian evolutionary palaeontologists showed towards Darwin's theory a spectrum of positions as various and ambiguous as they were contradictory [13]. Although every evolutionary palaeontologist after Darwin acknowledged a concept of "descent with modification" of some sort and started research programs aimed at discovering the "palaeontological proofs of evolution" by unearthing the fossils' "missing links", many remained skeptical or even hostile to the Darwinian mechanism of natural selection. Hence, up to the 1940s, palaeontology remained pervaded by an extreme diversity of competing "explanatory" theories, in which natural selection often occupied at best an ancillary position.

It was only with the coming of the synthetic theory, and especially under the aegis of G.G. Simpson (e.g. Simpson 1944–1950) that paleontology at large generally embraced the Darwinian logic, as far as evolutionary processes are concerned [19]. This unitary situation, in turn, was contested by a new generation of palaeontologists, the unquestionable leader of which was Stephen Jay Gould (1941–2002). He proposed an "extension" of the Darwinian selectionist theory to a complete hierarchy of selective levels [15,16], in which the deterministic functional consequences of selection are balanced at every level, both by the constraints of structure and by the contingencies of history [14]. There is an interesting echo, there, of the way Darwin himself used his famous scheme of the Origin (117). Darwin used and commented this scheme differently in different chapters of the Origin, (116–125, 396–398, 420–422), and applied it, as a "fractal", to various levels of integration of the biological hierarchy. This is why it has been used and understood rather differently by his various followers.

Although Darwin himself shows a great frustration in face of the palaeontological data of his time (and in the face of then current interpretations of those data), he nevertheless shows great confidence in the future of palaeontology

and its ultimate ability to illustrate and support his views. Indeed, the current knowledge of past biodiversity and of phylogeny of the living world along the geologic eras has made astounding progress. Many groups that are related but set apart in the extant world by apparently enormous gaps (such as the traditional vertebrate "Classes") are now linked along their proper relative degrees of relatedness by a host of "intermediate" fossil forms that would have delighted Darwin. Cladistic methods have now made possible the building of phylogenies allowing "classification to become genealogy", following his wish [12]. Finally, paleaontology is now making extensive progress towards describing Precambrian life, which posed only insoluble problems for Darwin. Many extraordinary Precambrian fossil remains have been discovered (such as the tiny triploblasts described by Chen et al. [20]), documenting a history more than three billion years old. All this vast "palaeontological message", now available and still expanding rapidly, illustrates and demonstrates "descent with modification" beyond any reasonable doubt. Does it also demonstrate that natural selection acting among individual organisms is necessarily the only material cause of all evolution?

As I have tried to show, it is doubtful that Darwin himself ever envisioned such a restricted view of the evolutionary process.

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References

[1] S. Herbert, Charles Darwin, Geologist, Cornell University Press, Ithaca, 2005.
[2] C. Darwin, The origin of species by means of natural selection or the preservation of favoured races in the struggle for life, 6th ed., J. Murray, London, 1872.
[3] J. Gayon, The paramount power of selection: From Darwin to Kauffman, in: M.L. Dalla Chiara, K. Doets, D. Mundici, J. van Bethem (Eds.), Structures and norms in science Vol II. Tenth international congress of Logic, methodology and philosophy of science, Kluwer, Dordrecht, (1997), pp. 265–282.
[4] J. Gayon, Darwinism's struggle for survival: Heredity and the hypothesis of natural selection, Cambridge University Press, Cambridge, 1998 .
[5] J. Gayon, Mort ou persistance du darwinisme ? Regard d'un épistémologue C. R. Palevol 8 (2–3) (2009) 321–340.
[6] S. Løvtrup, The four theories of evolution, Riv. Biol. 75 (1982), 53–66, 231–272, 385–409.
[7] B. Glass, Forerunners of Darwin, The John Hopkins Press, Baltimore, 1959.
[8] G. Laurent, Paléontologie et évolution en France 1800–1860, in : Comité Tr. Hist. et Scient, CTHS, EDT, Paris, 1987.
[9] E. Guyénot, Les sciences de la vie au XVII^e et XVIII^e siècles l'idée d'évolution, Albin Michel, Paris, 1957.
[10] P. Ostoya, Les théories de l'évolution, Payot, Paris, 1951.
[11] J. Roger, Les sciences de la vie dans la pensée française du XVIII^e siècle, Armand Colin, Paris, 1963.
[12] K. Padian, De Darwin au dinosaure : essais sur l'idée d'évolution, Odile Jacob, Paris, 2004.
[13] A. de Ricqlès, De la paléontologie évolutionniste à la paléontologie phylogénétique : avatars et permanence du darwinisme, in: P. Tort (Dir), Pour Darwin, PUF, Paris 1997, pp. 851–883.
[14] A. de Ricqlès, K. Padian, Quelques apports à la théorie de l'évolution, de la « synthèse orthodoxe » à la « super synthèse Evo-dévo » 1970–2009 : un point de vue, C.R. Palevol 8 (2–3) (2009) 341–364.
[15] S.J. Gould, Is a new and general theory of evolution emerging? Paleobiology. 6 (1980) 119–130.
[16] S. J. Gould, The structure of evolutionary Theory, Belknapp Press Harvard University, Cambridge, MA 2002, (trad. fr. M.Blanc, Gallimard, Paris 2006).
[17] P.D. Gingerich, Evolution and the fossil record: patterns, rates and processes, Can. J. Zool. 65 (1987) 1053–1060.
[18] N.G. Eldredge, S.J. Gould, Punctuated Equilibria. An alternative to phyletic gradualism, in: T.J.M. Schopf (Ed.), Models in Paleobiology, Freeman, San Francisco, 1972, pp. 82–115.
[19] G. G. Simpson, Tempo and modes of evolution, 1944, (Trad.fr. Rythmes et modalités de l'évolution par P. de Saint-Seine), Albin Michel, Paris, 1950.
[20] J.Y. Chen, D.J. Bottjer, P. Oliveri, S.Q.F. Gao, S. Ruffins, H. Chi, C.W. Li, E.H. Davidson, Small bilaterian fossils from 40 to 55 millions years before the Cambrian, Science 305 (9, 7) (2004) 218–221.