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BIOLOGICAL EVOLUTION: FACTS AND THEORIES

A Critical Appraisal 150 Years
After
"The Origin of Species"

With an Address of Cardinal Levada

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HISTORY OF EVOLUTION THEORIES

Jean Gayon

1. Introduction

In this paper, I examine the question of the “continuity” of Darwinism as a theoretical tradition on a large historical scale. For nearly one-and-a-half centuries, evolutionary biologists have been haunted by the question of whether their conceptions are or are not “Darwinian”. This persistent positioning of new scientific developments in reference to a single, pioneering figure is something quite exceptional in the history of modern science. Physicists working in the domain of relativity or quantum theory may refer to Einstein or Bohr (or other individuals). But their debates have not been massively structured through reference to these individual’s names in the way that evolutionary theory has been and continues to be today (Gayon 1990; Lewens 2007). I know of nothing like “Einsteinianism” or “Bohrism” in physics, whereas “Darwinism” has been a keyword among evolutionary biologists since it was first coined. What can account for such a fact? One explanation might be that Darwinism, just as Marxism, is not only the name of an ordinary scientific tradition, but also of a massive historical phenomenon, ranging across many areas of modern culture and politics. In such cases it is common to identify a tradition of thinking with a person’s name. But although this is perfectly true, we cannot be satisfied with that explanation. The fact is that biologists working on evolution have never stopped returning to Darwin and reading his masterpieces. It is still the case today. And, again, we do not observe anything like this in other areas of the natural sciences. My conviction is that evolutionary biologists’ uninterrupted interest in Darwin since 1859 indicates a strong form of connection, such as that between a model (Darwin) and its successive copies (the successive versions of “Darwinism”). I maintain that there exists some kind of isomorphism between Darwin’s Darwinism and historical Darwinism. By this I do not mean that everything present in Darwin’s evolutionary views has been passed onto the “Darwinian” tradition. I want to say merely that something crucial in Darwin’s own contribution has durably constrained the development of evo-

lutionary theory. This something is not so much a list of particular hypotheses or doctrines (such as a particular interpretation of natural selection, or heredity, or variation, or even descent), but rather a general view related to the structure of evolutionary theory.¹ Or, to be more precise: a general view of the general framework within which evolutionary research makes sense. What matters is the overall structure, not the truth of Darwin's personal hypotheses about this or that element of this structure.

Let us first recall that Darwin referred to his theory in *The Origin of Species* as "Descent with modification through natural selection." (Darwin 1859, 459) This formula² suggests that Darwin's theory was made of two components or even sub-theories: the first component is "descent with modification", that is a theory about what we would call today the general "pattern" of evolution; the second part ("through natural selection") refers to the conjecture that natural selection is the main explanation for the modification of species.

Darwin organized the whole book in such a way that the two parts are always tightly connected to each other. Nevertheless there are good reasons for taking this distinction seriously. First, Darwin was perfectly aware of its importance as he wrote by letter to Asa Gray, dated May 11, 1863: "Personally, of course, I care much about natural selection, but that seems to be utterly unimportant compared to the *Creation or Modification*." (Burkhardt 1985–2007, vol. XI, 403; italicized and bold characters in text) Another reason is that the scientific community did not react to the two parts of Darwin's theory in the same way. "Descent with modification" was quickly renamed "evolution" by Darwin's readers and by Darwin himself, who accepted this term and introduced it in the last edition of *The Origin* (1972), where it appears seven times, as an abbreviation for the "descent with modification" of the previous editions. This part of the theory was so successful and so rapidly adopted in the last third of the nineteenth century³ that it became common to call it "the general fact of evolution", whereas the explanation of this "general fact" through natural selection has been subject to unending controversies

¹ I have been trying for some time to develop this structural view of the history of Darwinism (Gayon 1990, 1995, 1997, 1998, 1999, 2003, 2008, 2009).

² This formula remained the same till the sixth and last edition, where Darwin added one word: "Descent with modification through *variation* and natural selection".

³ Peter Bowler says that this may well have been one of the most spectacular and rapid example of "paradigm shift" in the history of science (Bowler 2003).

since 1859. For these two reasons, the issue of the continuity vs. non-continuity of Darwinism over time deserves being examined from these two different perspectives, and not only from the viewpoint of the theory of natural selection.

2. Descent with modification or “the general fact of evolution”

2.1. Darwin

Darwin did not provide in the *Origin of species* an explicit definition of what he meant by “descent with modification”, which he probably found self-evident: species “descend” from one another and they are “modified”. Nevertheless he had a rather restrictive interpretation of this idea — we might well say a model of it. This model is clearly expressed in the unique illustration given in *The Origin*, the famous branching diagram given in chapter 4. This diagram (see *fig. 1*) was so important for Darwin that he commented on it twice in his book, in chapter 4 (devoted to natural selection) and in chapter 13 (devoted to classification and embryology) (Darwin 1859, 116–126 and 420–422). This diagram expresses a series of conjectures, none of which is trivial:

- [1] Species are subject to modification.
- [2] This modification is slow and gradual.
- [3] Many species go extinct.
- [4] The species that do not go extinct usually split into other species.
- [5] Once two or more species have split, they diverge indefinitely.
- [6] The diagram applies to all taxonomical levels from the lowest local varieties to the most encompassing groups (e.g. “A” may be a variety that leads to a species with eight varieties, or a species that leads to a genre with eight species, or a genre that leads to a family containing eight genres, etc.).
- [7] Postulate [6] implies that classification is entirely determined by genealogy. Therefore there are as many “ranks” as there are branching events of ramification, and all taxonomic categories used in systematics (species, genres, families, etc.) are arbitrary.
- [8] Postulate [6] also implied for Darwin that the entire process of diversification reduces to diversification at the lowest level (varieties and species); supra-specific taxa have no particular role in evolution, they are just an outcome.

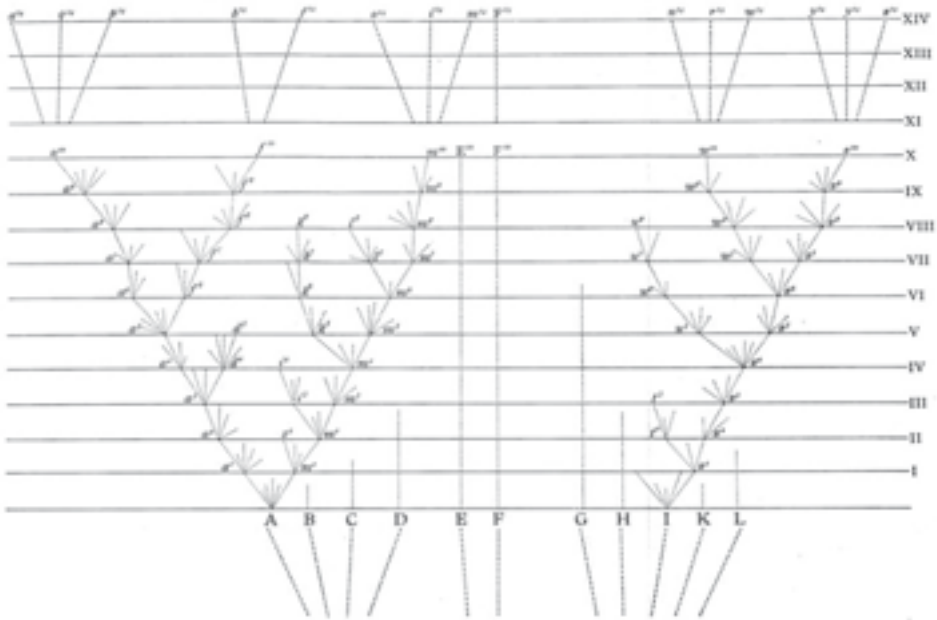


Figure 1. Darwin 1859: contra p. 117. Darwin comments on this figure twice in his book. In chap. IV, the letters “A, B, C ... L” represent “the species of a genus large in its own country”. The roman numbers represent intervals between an arbitrary high number of generations. They produce local varieties which modify and diverge during many generations. At the end of the process, species I (for example) leads to eight species. In chapter XIII, the letters “A, B, C ... L” represent “allied genera” which will lead at level XIV to a greater number of genera (for instance A has differentiated into eight genera forming a family). The same reasoning can be applied to any desired level of taxonomic categories. Darwin explains that what is natural is the genealogical “arrangement”; “ranking” (variety, species, genus, sub-family, or any taxonomic category) is arbitrary.

Darwin’s tree-like diagram had an almost immediate effect upon the entirety of the biological community. Within a short period of time, it became the paradigmatic representation of organic evolution as an established fact, the “general fact of evolution”. The sudden and dramatic effect of this diagram constitutes one of the most spectacular examples of a paradigm-shift in the history of science, to use Thomas Kuhn’s famous terminology. One could not say the same for the theory of natural selection, which opened a long series of controversies.

From a methodological point of view, the characterization of Darwin’s tree-of-life as a “general fact” of nature is misleading. This diagram, with the non-trivial postulates that it illustrates, is a theoretical construction. The kind of theory in-

volved is not a causal theory, although it may be used for explanatory purposes in certain contexts. It is a theory that postulates the general existence in nature of several classes of phenomena. It is a heuristic device, a plausible bet about the general form and pace of the phenomena that constitute evolution as a result, and that call for explanation. Darwin's theory of "descent with modification", as summarized in his diagram, is a low level theory, but nevertheless a theory. It is a conjecture about the general pattern of evolution.

2.2. *After Darwin*

Now the question is: has the scientific consensus about the so-called "fact of evolution", as represented by Darwin's diagram, been significantly threatened since Darwin's time? There have been at least three serious challenges to Darwin's tree-of-life picture. Each of these challenges, or classes of criticisms, relates to the shape of the tree. The first two have been recurrent since the time of Darwin. The third is recent.

The first kind of criticism can be found among those biologists or paleontologists who have advocated a non-gradual or saltationist representation of the origin of species. Since Thomas Henry Huxley, Francis Galton and the early Mendelians, saltationist theories of the emergence of species have been numerous and varied.⁴ Scientists belonging to very different biological sub-disciplines have defended them: morphologists, paleontologists, biometricians, geneticists, and developmental biologists. Today, the most famous and most convincing example is represented by Eldredge's and Gould's (1972) theory of "punctuated equilibria". This theory, first formulated in 1972, postulates that evolutionary change occurs primarily during events of speciation or cladogenesis (i.e. the splitting of a given species into two or more species). Although it may take many generations, this change is rapid at a geological scale.

Whatever the particular form they take, saltationist theories of evolution entail a significant alteration of Darwin's tree. Instead of branches that progressively diverge, the tree will have the shape of successive candelabras. The most famous example is Eldredge's and Gould's "tree" in their 1972 paper (*fig. 2*). This kind of criticism, which focuses on the level of species (or at least on low taxonomic levels) challenges the second, the fifth and the sixth Darwinian postulates listed above: gradualness of change, divergence of species as such, and indefinite divergence after splitting.

⁴ For a systematic examination of the early forms of saltationist theories, see Bowler (1983).

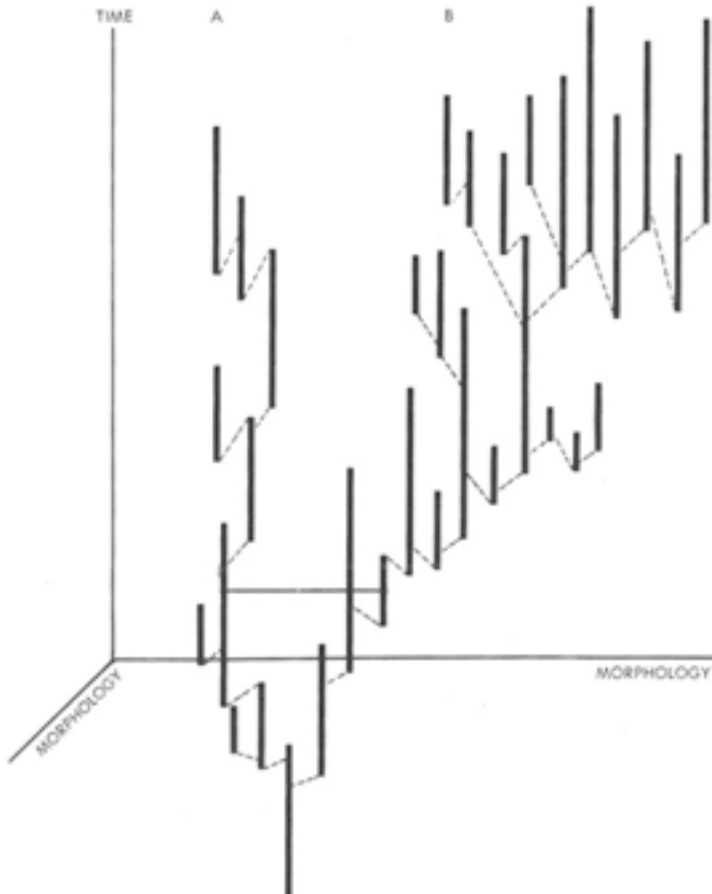


Figure 2. Eldredge and Gould 1972, 113. Original legend: “Three-dimensional sketch contrasting a pattern of relative stability (A) with a trend (B), where speciation (dashed lines) is occurring in both major lineages. Morphological change is depicted here along the horizontal axes, while the vertical axis is time. Though a retrospective pattern of directional selection might be fitted as a straight line in (B), the actual pattern is stasis within the species, and differential success of species exhibiting morphological change in a particular direction.”

A second class of criticism emphasizes the view that evolution is something that does not happen only at the level of varieties and species, but also takes place at higher taxonomic levels. This kind of criticism has also been extremely popular since Darwin, especially among morphologists and paleontologists. In its commonest expression, it states that higher taxa tend to appear and diversify rather suddenly, giving rise to morphological types that remain stable ever after. In such a view, modification and multiplication of species are superficial phenomena, not the core of the evolu-

tionary process. Biologists and paleontologists who adopt this view do not accept Darwin's "tree"; they refer to the image of a "bush" with parallel twigs arising from a given level. In 1929, the French morphologist Louis Vialleton gave a vivid summary of the shift from traditional Darwinian trees to "bushes" in systematics at the end of the nineteenth century and at the beginning of the twentieth century:

Genealogical trees, by illustrating in a simple way a number of infinitely complex relations in the real world, were very useful to the transformist theory; they provided the concrete examples of transformation that Lyell demanded from Darwin. . . . The first diagrams were quite satisfying. They strikingly represented the evolutionary unfolding of beings and seemed to be able to provide their natural relationships that had been sought for such a long time. But disillusion came fast. . . . Taking into account the time of appearance of various forms [and not only this or that morphological criterion], it soon appeared that genealogical trees looked quite different from how they looked before. Instead of showing a more or less elongated trunk during the period when only the supposed initial form existed, they had the shape of bushes whose twigs stemmed from approximately the same height above the ground, and moved away in a parallel way from each other, each of them being more or less ramified (Vialleton 1929).

To illustrate these doubts about Darwinian "trees", Vialleton gave two different representations of the genealogical tree of Mammals: one was borrowed from the American paleontologist Henry Fairfield Osborn (*fig. 3*), the other was Vialleton's representation of exactly the same data and interpretation (*fig. 4*). Vialleton's representation emphasizes the idea that something decisive occurs at high taxonomic ranks. To be fair, Vialleton was as anti-Darwinian as one can imagine: he thought that "transformism" (his name for Darwinian evolution — i.e., gradual modification and splitting of species) was only a superficial phenomenon, whereas genuine "evolution" was the generation or "creation" of major morphological novelties in groups that suddenly appeared and remained approximately stable thereafter.

More recently, Eldredge's and Gould's punctuated equilibria have provided a totally new version of the old idea that evolution is not confined to the level of species. The famous diagram reproduced in *fig. 2* illustrates the hypothesis that a given evolutionary trend in a taxonomic group (either stasis or directional evolution) might well result from changes above the level of species. For instance, in lineage "B", the evolutionary trend results from differential success of (static) species exhibiting morphological change in a particular direction. Although this way of thinking is far from Vialleton's typological approach (and, in that sense, much closer to Darwin), it exemplifies another manner of advocating evolution above

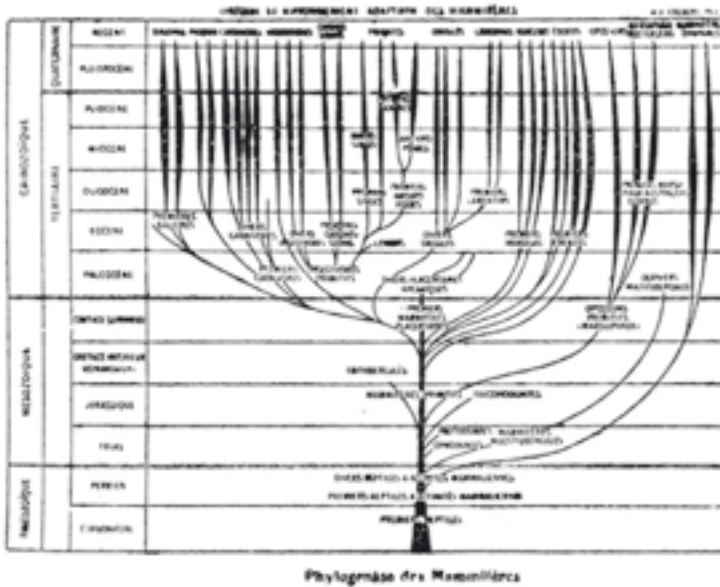


Figure 3. Vialleton 1929, 183. Original legend “Arbre généalogique des mammifères (d’après Osborn)” [Genealogical tree of Mammals (from Osborn)]. Vialleton refers to Osborn 1917.

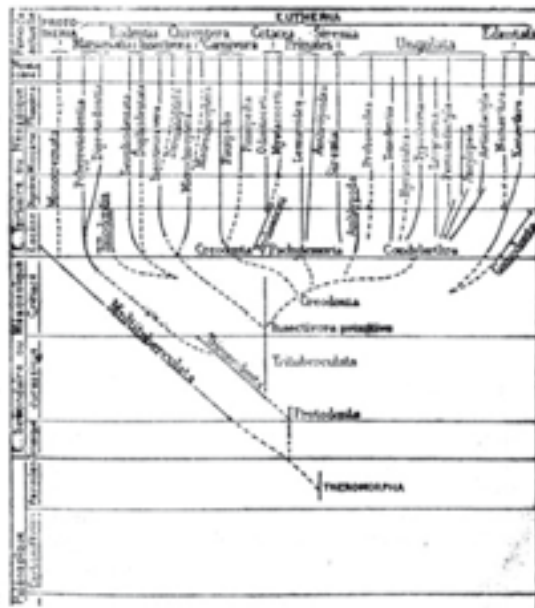


Figure 4. Vialleton 1929, 181. Original legend “Arbre généalogique des mammifères” [Genealogical tree of Mammals].

the species level, and consequently of challenging the Darwinian postulates [6] and [8] listed above (and, also, [5]: the entities that “diverge” are not necessarily species). Most of the literature in paleobiology since the mid 1970’s illustrates a similar search for specifically macroevolutionary patterns (For a comprehensive review, see Stanley 1998). The third class of criticism of Darwin’s diagram is more recent and, in a sense, more radical. The suspicion is that this diagram represents only a fraction of the real pattern of the history of life. Darwin’s tree involves the conviction that a tree of irreversible divergence *of species* adequately and sufficiently represents the history of biological diversity. Although Darwin did not explicitly say this, his diagram has been understood as meaning that there actually exists one single “tree of life”, the branches of which (namely, species) become, at some time or another, totally isolated from any other in terms of reproduction and hereditary transmission. An increasing number of phenomena challenge this view of species as (material) monads “without any doors or windows”, to freely pastiche Leibniz’s famous formula. These two phenomena are lateral gene transfer and symbiosis.

Since the end of the 1990s, lateral gene transfer has been known to be a major phenomenon among prokaryotes (Eubacteria and Archaea). Prokaryotes are single-celled organisms without a membrane-bound nucleus. Since Carl Woese’s pioneering work in the 1970s and 1980s, they are divided into two “domains”: Bacteria and Archaea. Eukaryotes constitute the third “domain”: they include all single-cell and multicellular organisms with a membrane-bound nucleus. At the beginning, the application of molecular techniques to prokaryotes generated the hope of reconstructing the unique and universal tree of life (Woese 1987). But an increasing number of anomalies led to the discovery that gene transmission among prokaryotes is not only vertical, it is also horizontal. The magnitude of this phenomenon has been fiercely debated for almost twenty years now. It is now clear that it is important enough to cast serious doubts on the very existence of a unique tree representing the natural relationships among all cellular organisms, or, at least, on the possibility of reconstituting this tree if it exists (for a review, see McInerney, Cotton, and Pisani 2008). This is due to the fact that almost all (if not all) prokaryotic genes have been subject to lateral gene transfer. Whether this turnover of genes in Eukaryotes is significant remains a debated issue. Nevertheless, we now observe an intense controversy between two ways of representing the genealogical pattern of the history of life: tree and network.

It is presently uncertain whether the “tree of life hypothesis” will be able to successfully combat the “network of life hypothesis”. In reality, it is likely that both the “tree” and the “network” will have to coexist in a pluralistic view of evolution-

ary patterns, where *several* histories are told by several methodologies. In fact, evolutionary biologists seem now to admit that Darwin's diagram, which focuses exclusively at the level of species, encapsulates only one fraction of the history of life. In the case of prokaryotes at least, lateral gene transfer has been important enough to obliterate, and, perhaps, overcome "vertical transmission" at a large historical scale.

Another process that jeopardizes Darwin's representation of genealogy is symbiosis. Symbiosis has probably been a major evolutionary process, especially at the level of cell evolution (Margulis and Sagan 2002). Symbiosis is much more rare than lateral gene transfer; but when it occurs, it may have dramatic effects because it implies the coexistence of two full genomes. Symbiosis seems to have been a key process in the emergence of a number of major groups of unicellular eukaryotic organisms, and of eukaryotes themselves. Symbiosis does not challenge the notion of irreversible divergence of *species*, because separate organisms that fuse initiate new species that diverge from others. But fusion events between organisms introduce complications that cannot be assimilated by an exclusively tree-like pattern of phylogeny. *Fig. 5* illustrates the kind of anastomosis that result from such conjectures.

I now conclude on the first aspect of Darwin's theory (Descent with). Darwin's diagram has proved immensely fertile. It remains the basic intuition behind most of the work on phylogenies. But it is not true that the diagram has remained unchanged. Several of the postulates embodied in Darwin's representation appear not to be false, but rather a simplified view. At least four of the seven postulates that I have listed have been seriously challenged: [2] (gradualness of modification), [5] (irreversible divergence of species), [6] (uniform validity of the tree-like diagram at all levels), and [8] (evolution above the species level). Modern evolutionary biologists are not in agreement regarding the assertion that modification of species is *always* slow and gradual (against [2]). Indefinite divergence after splitting is not strictly false, but it is only one part of the story of life: important horizontal relations must be taken into account (against [5] and [6]). Finally, many contemporary biologists (especially paleobiologists) deny that evolution is nothing more than modification of species (against [8]).

To summarize in a single sentence, then: Darwin was successful in imposing a view of the history of life in terms of genealogy and modification, but the particular model that he offered has been repeatedly discussed.

3. Natural selection as an explanatory principle

The second half of “Darwin’s theory” was the theory of modification through natural selection. Whereas “descent with modification” was a first-level theory about the general pace of evolution, natural selection was for Darwin an explanatory hypothesis that aimed at unifying the entirety of evolutionary phenomena under a common set of law-like statements. Just as in the case of “descent with modification”, I will first remind the reader of Darwin’s views about the theoretical status of natural selection. Then I will compare the post-Darwinian history of evolutionary biology with Darwin’s conception of his explanatory theory.

3.1. Darwin

In *The Origin of Species*, Darwin used a double strategy for justifying the principle of natural selection. The first strategy consisted in providing inductive arguments in favor of the existence of natural selection as a process. The second strategy was hypothetico-deductive: it consisted in showing that natural selection explains and unifies various classes of independent facts. Strangely, Darwin did not make this double strategy explicit in the text of the *Origin*, although the overall structure of the book corresponds more or less to it: on the whole, chapters 1 through 5 of the first edition establish the plausibility of the existence of variation and natural selection on the basis of a mixture of empirical generalizations and deductions; chapters 7 through 13 are devoted to establishing its explanatory power (and also its limits: chap. 8 on hybridism).

In fact, it is only in the introduction to *The Variation of Animals and Plants Under Domestication*, published nine years after the first edition of *The Origin of Species*, that Darwin made perfectly explicit his argumentative strategy:

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 undulations of the ether and even its existence are hypothetical, yet every one now admits the undulatory theory of light. The principle of natural selection may be looked at 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 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 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 (Darwin 1868, 8–9).

In an extremely dense formulation, Darwin distinguishes two levels of justification of natural selection.

At the first level, natural selection is a “mere hypothesis” that is “rendered probable” by empirical arguments. Two different sorts of arguments are invoked. One is analogical: artificial selection, which shares some preconditions with the hypothetical process of natural selection (variation, heredity, biases in survival or reproductive rates) does modify species. This argument was crucial to Darwin, since he had no direct evidence for the existence of natural selection in nature (chap. 1 and 2 of *The Origin*). The second kind of argument invoked at this level is based upon empirical generalizations about the two specific preconditions of natural selection, relative to the rate of reproduction of organisms and the limitation of resources (chapter 3 of *The Origin*), and the notion of more or less heritable and “favourable” (or unfavourable) variations (chapter 4 of *The Origin*). Taken together, these arguments establish the plausibility of natural selection as a very general process existing in nature, in all species, for many characters and at all times.

At the second level, Darwin says, “this hypothesis may be tested” through its capacity to “explain” a large array of “independent classes of facts”. This refers to chapters 7 through 13 of *The Origin*, and Darwin mentions some of the facts explained in the passage quoted. One might disagree about exactly what the list should contain; but, on the whole, Darwin claims that natural selection explains at least: adaptations (morphological and instinctual), the geographic distribution of species, the stratigraphic distribution of fossils, extinction, divergence, homologies, the relation between development and evolution, and taxonomic patterns. This second level of justification of natural selection was crucial to Darwin, since it is at this level that the “mere hypothesis” becomes “a well-grounded theory”, a theory that deserves being “received”.

The Newtonian style of the entire argument has been underlined by a number of commentators (Kavaloski 1974; Ruse 1975; Hodge 1987). What I want to stress here is that this argumentative structure provides a powerful tool for the understanding of the structure of evolutionary research since Darwin. The first level led to the development of population biology, with a careful exploration of the bases and modes of natural selection as a widespread principle in nature. The

second level provided a theoretical principal for the reframing of the entire field of natural history. At that second level, natural selection is not only a common and fascinating process in nature, but also a principle that unifies many classes of facts, and, ultimately, biology as a whole. *Fig. 5* gives a schematic representation of this argumentative structure.

3.2. After Darwin

3.2.1 Brief historical survey (1859–1950)

Let us now assess the fate of this grand scheme. The first hundred years of evolutionary theory after Darwin may be summarized in a rather simple way. For a period of approximately seventy years after the publication of *The Origin* (1859), most of discussions and criticisms were targeted at the very existence of natural selection as a process, and of its capacity to account for adaptation. The reason for this was the absence of a convincing theory of variation and heredity. Of course, if this level was problematic, the second was even more so. In the 1920s and 1930s, it became clear that Mendelian genetics was able to reformulate Darwin's hypothesis (or a particular model of it, I would say) in a way that made it testable and predictive (on this complicated story, see Gayon 1998).

Then came the “modern synthesis”, built in the period 1930–1950. As Julian Huxley said when he coined this expression, this period consisted in a “rebirth of Darwinism” (Huxley [1942] 1978, 26). Since population genetics was able to prove the existence and efficacy of natural selection, the time became ripe for developing the second aspect of Darwin's theory. The modern synthesis consisted in an attempt to show, in its modernized genetic version, that natural selection was indeed a major principle for the explanation of such phenomena as geographical variation, long-term modification of species (anagenesis), speciation (cladogenesis), extinction, the tempo of evolution and phylogenetic trends. This enterprise was genuinely collective. A number of different disciplines and scientists all over the world contributed to this “synthesis”: theoretical population geneticists (Fisher, Haldane, Wright), field and experimental population geneticists (Dobzhansky, Teissier, L'Héritier, Timofeeff-Ressovsky), cytogeneticists (Darlington, White), animal and plant systematists (Mayr, Stebbins), paleontologists (Simpson, Newell), embryologists (Schmalhausen, Waddington), ecologists (Lack) and specialists in human evolution (Rensch), to mention just a few (Mayr and Provine 1980; Smocovitis 1996). In the 1950s the triumph of natural selection as an explanatory principle seemed to have no limit (see for instance Mayr 1959). These years corresponded to

the time when evolutionary biology was institutionalized as a discipline. In subsequent years, however, evolutionary biologists became more circumspect. Two kinds of criticisms developed, at the levels of microevolution and macroevolution.⁵

3.2.2. *Criticisms of natural selection at the level of microevolution*

At the level of microevolution, what natural selection explains is first and above all adaptations. One should observe that since the modern synthesis, this ambition has never been seriously challenged. For almost all contemporary biologists, natural selection is the sole explanation for adaptations. This was true sixty years ago, and it is even truer today. Many modern textbooks on evolutionary biology can testify to this.⁶ However, three main criticisms have been addressed to natural selection at the microevolutionary level over the past fifty years.

First, at the molecular level, the discovery of an unexpected amount of polymorphism in proteins and DNA has led to the recognition that most of this polymorphism is approximately neutral with respect to natural selection. This has been the central tenet of the “neutral mutation — random drift hypothesis of molecular evolution” (Kimura 1968; 1973). This theory has generated one of the most intense controversies in population genetics in the second half of the twentieth century, precisely because it challenged the idea that natural selection controls the evolution of biological phenomena at all levels.⁷ The theory is now widely admitted. It states that natural selection does not control everything at the molecular level, especially DNA; it controls only the limited fraction of mutations that affect the phenotype at a given time in evolution.

Secondly, there has been a huge debate about group selection. Darwin and most population geneticists in the middle of the twentieth century denied the existence of group selection, or at least its ability to generate adaptations. Here also, things have changed. Group selection, which was first perceived as a threat to Darwinism (because it went against the particular model of natural selection that was favored by Darwin and by population biologists in the period 1930–1980) is now treated as a legitimate model of natural selection, which appears to be important for the

⁵ For a more detailed exposition, see Gayon 1990, 1997, 2003, 2008, 2009.

⁶ See for instance Ridley 1996, chap. 13, pp. 338–368. The first three sections of this chapter are entitled: “13.1. Natural selection is the only known explanation for adaptations”; “13.2. Pluralism is appropriate for the study of evolution, not of adaptation”; “13.3. Natural selection can, in principle, explain all known adaptation”.

⁷ The best image of this controversy can be found in Lewontin 1974.

explanation of the origin of major biological phenomena such as sex and a number of phenomena of cooperation.⁸

Thirdly, theoretical biologists in the name of complexity have formulated strong attacks against Darwinism at the microevolutionary level. The claim, here, is that complexity imposes strong limits to the modifying power of natural selection. Because of the large amount of connectivity existing in genetic systems, natural selection may fail to increase the mean fitness of the population, whatever the intensity of selection (Kauffman 1993).

These challenges to Darwinism at the level of microevolution are important. All of them have led to the development of new and fertile domains of research in evolutionary biology. The first and the third (neutral theory of molecular evolution and complexity theory) share a similar character: both of them relativize the idea of natural selection as an all-sufficient principle in evolution. Natural selection does not operate on a passive field of variation. Its action is limited by formal constraints such as stochasticity and generic properties of self-organized systems. The second challenge (group selection) is different: by admitting multilevel models of natural selection, it increases the theoretical content and explanatory power of natural selection rather than restricting it. It also makes natural selection much more complicated, much less intuitive, and probably difficult to test. Ultimately, none of these criticisms has challenged natural selection as the only acceptable explanation for adaptations. Therefore, on the whole, all attempts to challenge the explanatory power of natural selection at the microevolutionary level have resulted in enrichment rather than a decline of Darwinism.

3.2.3. Macroevo­lutionary criticisms of natural selection

Over the past forty years it is mainly at the level of macroevolution that major cracks in the Darwinian edifice have occurred. Remember here that for Darwin, the crucial test for the “acceptability” of natural selection was the ability of this hypothesis to explain “independent classes of facts”: not only adaptations, but also extinction, divergence and other macroevolutionary phenomena (the boxes at the bottom of *fig. 5*). What has become problematic over the past forty years is precisely the claim that natural selection suffices for the explanation of *all* macroevolutionary phenomena. Here, I will just give two examples.

⁸ For a synthesis, see Sober and Wilson 1998.



Figure 5. The two levels of the diagram (above and below “hypothesis of natural selection”) represent the two levels of justification of Darwin’s hypothesis of natural selection (from Gayon 1997, 270).

The first example is extinction. In the traditional Darwinian view (i.e. that of Darwin himself and of classical theories of extinction in the mid- twentieth century), extinction is just a large-scale effect of natural selection within species: as natural selection transforms biological species, some happen to be fitter in the competition with other species. The less favored species (those which evolve more slowly) decrease in numbers and go extinct. But paleobiologists have shown that such an explanation does not work in the case of mass extinction. In episodes of mass extinction (a phenomenon that has occurred many times in the history of life, at different scales), species go extinct not because of their relative success when competing with other species for places in the ecological theatre, but because they are ill equipped to face a brutal perturbation of their physical environment. For instance, if diatoms survived better than other planktonic forms during the great Cretaceous extinction, it is because they were endowed with a capacity of becoming encysted. This feature had evolved for reasons that had nothing to do with the environmental conditions that generated the mass extinction of the Cretaceous. The diatom’s dormancy is an adaptation to life in cold water that had been acquired long before. As David Raup said in his magisterial book on extinction, when species go extinct in mass extinction events, this is not due do “bad genes” but to “bad luck” (Raup 1991).

Another example is divergence. Following Eldredge and Gould's seminal paper on punctuated equilibria, a number of paleobiologists have denied that morphological divergence is necessarily the result of continued selection within species. They have supported alternative explanations, according to which divergence can also be a consequence of repeated events of speciation and extinction of species, either because of species selection, or because of "species drift" (resulting itself from stochastic considerations or from some kind of developmental constraint). This kind of theory is now currently being debated among paleobiologists (Stanley 1975; 1998).

Another kind of criticism that deserves being mentioned has come from the "evo-devo" (evolution-development) school. It emphasizes the importance of major morphological and embryological constraints that affect the evolutionary process. Evo-devo insists that the level of the elementary hereditary material (the genetical level) is insufficient for explaining the mechanisms responsible for evolutionary change: epigenetic heritable traits (such as developmental pathways) should also be taken into account. It is unclear whether advocates of evo-devo claim that such higher level traits canalize evolution or constitute another level of selection (Amundson 2005 gives a remarkable analysis of this school of thinking).

Other examples could be used, showing that the predominance of natural selection in the explanation of macroevolutionary phenomena is seriously contested today. This is not to say that contemporary evolutionary biologists deny that natural selection is a major force that should always be taken into account when studying the history of life. But the majority of them think that things are more complicated: other principles are needed, and perhaps there is no hope of deducing everything in the history of life from a short list of theoretical principles.

3. Conclusion: death or persistence of Darwinism?

Let us now come back to the question posed at the beginning of this paper. What do the modern evolutionary biologists' repeated and contradictory references to Darwin mean? I would like here to take the evolution of Stephen Jay Gould's attitude on this issue as a key example.

In 1980, Gould published a paper provocatively titled "Is a new and general theory of evolution emerging?" This paper was probably the most radical attack against Darwinism that Gould ever published. It provides an exceptional landmark for anyone who wants to understand what was at stake when a number of evolutionary biologists began to say, around 1980, that the classical "Darwinian" view of evolution was in deep crisis.

Let us first point out the precise target of Gould's attack. Although he often writes of "Darwinism", it is only a particular version of Darwinism that he has in mind — the modern synthesis. In the first section of the paper, entitled "The modern synthesis" (Gould 1980, 119–121), Gould quotes the following passage from Mayr:

The proponents of the synthetic theory maintain that all evolution is due to the accumulation of small genetic changes, guided by natural selection, and that transpecific evolution is nothing but an extrapolation and magnification of the events that take place within populations and species (Gould 1980, 120).

And Gould adds:

... if Mayr's characterization of the synthetic theory is accurate, then that theory, as a general proposition, is effectively dead, despite its persistence as text-book orthodoxy (Gould 1980, 121).

What were Gould's arguments supporting the "death" of the synthetic theory? The 1980 paper advocates a "hierarchical approach" to evolution, with three main levels: variation within populations, speciation, and patterns of macroevolution. Gould defends the claim that at each of these three levels, the conception of evolution as an accumulation of small genetic changes, guided by natural selection, has been refuted.

At the level of population genetics, Gould evokes the neutrality of most genetic change.

At the level of speciation, he refers to various models of speciation (especially White's parapatric model) showing that reproductive isolation is not a by-product of adaptation, but rather a rapid and stochastic event. He also emphasizes heavily the revival of Goldschmidt's "hopeful monster" (Gould 1980, 122–125).

Finally, at the level of macroevolution (Gould 1980, 125–128), Gould primarily discusses punctuated equilibria, and proposes that evolutionary trends are not a mere extrapolation of intra-specific evolution, but result from differential rates of speciation and extinction among species.⁹

⁹ "... if species originate in geological instants and then do not alter in major ways, then evolutionary trends cannot represent a simple extrapolation of allelic substitution within a population. Trends must be the product of differential success among species (Eldredge and Gould 1972; Stanley 1975). In other words, species themselves may be inputs, and trends the result of their differential origin and survival. Speciation interposes as an irreducible level between change in local populations and trends in geological time. Macroevolution is, as Stanley argues (1975, 648), decoupled from microevolution." (Gould 1980, 125–126) The full reference of Stanley 1975 is given in the bibliography of the present paper.

Thus Gould's 1980 paper leaves the reader with the conviction that the traditional "Darwinian" or synthetic theory of evolution has broken down, and has been, or will soon be, replaced with another theory, where natural selection of small individual-level inherited variation is just one process among others, and definitely not a unifying principle for the evolutionary process as a whole.

If we now look at Gould's testament, the luxuriant book published in 2002, the very year of his own death, under the title *The Structure of Evolutionary Theory*, we observe a rather different attitude regarding Darwinism. The first chapter is wholly devoted to summarizing the entire argument of the book. Gould, again, explains the structure of the new theoretical framework through a comparison with the former classical, or purely Darwinian, framework. But this time he refers to Darwin himself rather than to the synthetic theory. He maintains that the new theoretical framework of evolutionary biology is neither an "extension" of the older Darwinian theory, nor a "destruction" or "replacement" of it. This vocabulary, which the author uses very carefully, is both puzzling and stimulating. In Gould's terms, "extension" would mean that the same principles have been applied to a wider spectrum of phenomena. "Replacement" would mean that other principles are now at the heart of evolutionary theory. Instead of these two terms, Gould prefers "expansion". "Expansion" means that the same principles remain central to the theory, but they have been "reformulated" in a way that gives a truly different aspect to the entire edifice (just as an architect makes a new edifice from an older one, by adding new parts to the existing unchanged ones, which themselves constrain the whole building).¹⁰

This notion of expansion is rather unorthodox in terms of current philosophy of science. "Extension" would make philosophers think of a wider explanatory scope. "Replacement" irresistibly evokes Thomas Kuhn's "paradigm shift". But, obviously, Gould wants to avoid these two classical ways of interpreting scientific change. What, then, does he mean precisely by "expansion"? He defines the "Darwinian framework" (which he also calls "the Darwinian logic") as a conjunction of three principles:

¹⁰ "I do believe that the Darwinian framework, and not just the foundation, persists in the emerging structure of a more adequate theory. But I also hold . . . that substantial changes, introduced during the last half of the twentieth century, have built a structure so expanded beyond the Darwinian core, and so enlarged by new principles of macroevolutionary explanation, that the full exposition, while remaining within the domain of Darwinian logic, must be construed as basically different from the canonical theory of natural selection, rather than simply extended." (Gould 2002, 3)

1. “Agency”: natural selection works almost entirely at the level of organisms.
2. “Efficacy”: natural selection is the mechanism responsible for the emergence of evolutionary novelty, the exclusive factor that shapes evolutionary change.
3. “Scope”: the extrapolation of minute, incremental changes, can explain the entirety of the history of life (Gould 2002, 14–15).

Gould, of course, refuses these three principles in their crude formulation. Natural selection *does not* work only at the level of organisms: species selection or even clade selection is essential to him (this is indeed the major commitment of his 2002 book). Selection *is not* the only mechanism of evolutionary novelty: morphological constraints, developmental constraints and historical constraints canalize evolutionary pathways. Finally, Gould does not admit that the entirety of life is explained by extrapolating from small intra-specific changes to macroevolution.

Why, then, does Gould say that Darwin’s principles have been “expanded” rather than “replaced”? “Expansion” seems to be a convenient word for the expression of two ideas:

1. Generalization of Darwinian (or more precisely synthetic) principles: species selection, species drift, clade selection and clade drift are obvious examples of this strategy. Gould’s final judgment is that he and other paleobiologists have applied Darwinian schemes to entities that were not considered by Darwin (Gould 2002, 6).
2. Addition of new principles, such as morphological, developmental and historical constraints.

To make these ideas more intuitive, Gould makes use of an image. He compares the relationship between Darwinism and the new theoretical framework with a coral. At its basis, this coral has a trunk with three successive branches. The central trunk represents the theory of natural selection and cannot be severed. The branches represent the three “Darwinian principles” (agency, efficacy, scope). These principles remain at the basis of the new theoretical framework, but each of them has been “truncated” at a rather low level, so that they all “expand” and “develop” into an “organism” substantially different from the original one.

Thus, in Gould’s terms, a new theory has not replaced the classical theory of evolution; rather, it has *developed* into a new one. What Gould means by this metaphor is the relationship between Darwin and the historical Darwinism is not only a question of genealogical influences. The claim is that there is a genuine con-

ceptual similarity or “isomorphism” (not identity) between the two theories. In other words, the relation between Darwin, Darwinism and the modern evolutionary theory is not only historical; it is also a formal relation. This brings me back to the previous part of this paper, where I exposed my own view of the relationship between the original Darwinism (Darwin’s own view of evolution) and Darwinism as historical tradition. Just like Gould, I am convinced that the repeated references made to Darwin by so many evolutionary biologists since 1859 are not only a matter of “genealogy”. In a very strong sense, Darwin settled a framework that constrained the very structure of evolutionary theory for a long time, though certainly not the entirety of its empirical and theoretical content.

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