

The Relationship between Microevolution and Macroevolution, and the Structure of the Extended Synthesis

Guillermo Folguera and Olimpia Lombardi

*CONICET – Facultad de Filosofía y Letras de Ciencias Exactas y Naturales
Universidad de Buenos Aires
Espinosa 423 108, C.P. 1405
Ciudad Autónoma de Buenos Aires, Argentina*

ABSTRACT - This article focuses on the relationship between microevolution and macroevolution. The main purpose is to argue that up to the present time in the consolidation of the evolutionary synthesis macroevolution has been always conceived as dependent on microevolution. Such dependence was very clear in the synthesis, but seems to have been left aside by later authors. Nevertheless, we show that the criticisms of the synthesis since the decade of the 1970s did not modify that general trend: the new perspectives reproduced the dependence of macroevolution on microevolution by means of strategies different than those appealed to by the traditional synthesis.

KEYWORDS - Altenberg 16, evolutionary synthesis, Gould, macroevolution, microevolution

Introduction: macroevolution and the promise of an extended synthesis

Since the 1930s, the disciplines grouped together under the biological synthesis played different roles in that dominant theoretical framework. Whereas some of them introduced mechanisms of evolutionary change, others played only a descriptive role in evolutionary biology. According to Arthur (1997), population genetics, evolutionary ecology, and classical genetics belong to the first group; the disciplines of the second group, such as paleontology and comparative anatomy, are confined to describing phenomenological patterns (see also Ghiselin 1980). There is also a third group of “forgotten” disciplines, like embryology and developmental genetics, which did not play a relevant role in the traditional synthesis. In this context, the evolution of populations, or microevolution (m_{ev}), finally turns out to be conceived as the dominant area of evolution,

which relegated the evolution of higher taxa, or macroevolution (M_{ev}), to a secondary position (see Bowler 1998; Folguera 2010; Folguera and di Pasquo 2008).

Over the past years, the idea of an extension of the biological synthesis increased its strength within the evolutionary community (Callebaut 2010; Grantham 2004; Love 2010; Okasha 2005). This extension finds its roots mainly in the expansion and consolidation of Evo-Devo, genomics, and macroevolution (Ioannidis 2008; Love 2003; Scott 2002), and began to be related with certain philosophical problems, including the question about the autonomy of the different areas of knowledge, as well as the disciplinary relationships within the “extended” biological synthesis itself (Callebaut 2010; Love 2010; Rosslénbroich 2009; van der Steen 1993). Some authors have suggested that the extension of the biological synthesis might lead to the consolidation of a pluralistic framework in evolutionary biology (Delisle 2009; Mitchell 2002; Sterenly 1996).

In this article, we will focus on the relationship between m_{ev} and M_{ev} . Like Love, we will use “the interplay between the conceptual and disciplinary levels as a heuristic tool [...] assuming that the conceptual level typically has implications for the disciplinary level” (Love 2003, 312). Our main purpose is to argue that since the consolidation of the evolutionary synthesis up to the present, M_{ev} has been always conceived as dependent on m_{ev} . However, such dependence was expressed through very different strategies. In general terms, the evolutionary synthesis proposed a direct dependence of M_{ev} on m_{ev} , although with some significant variants in the arguments of the different authors. But the criticisms to the synthesis since the decade of the 1970s did not modify that general trend: the new perspectives reproduced the dependence of M_{ev} on m_{ev} by means of strategies different than those appealed to by the traditional synthesis.

For this purpose, the present paper is organized as follows. In the second section, we will point out certain similarities and differences among the stances of the main scientists of the biological synthesis, Theodosius Dobzhansky, Sewall Wright, George Gaylord Simpson, and Ernst Mayr. In the third section, the criticisms leveled against the synthesis’ conception of the relationship between m_{ev} and M_{ev} since the 1970s are critically reviewed. In the fourth section, we will analyze the role played by that relationship in the new extended synthesis proposed by “Altenberg 16.” In addition, we will analyze the relationship among “problem agendas,” structure and pluralism in the biological synthesis, on the basis of the proposal of Alan C. Love. In the last section, we will offer some considerations about the differences among the roles played by the disciplines belonging to the new synthesis and the consequences of this difference

on the problem of the unity of science. Finally, on the basis of the previous considerations, we will argue that the critics of the traditional synthesis could not, nevertheless, free themselves from the idea of the priority of m_{ev} over M_{ev} .

The relationship between microevolution and macroevolution in the synthesis

In the light of our main purpose, the consideration of the main opinions about the relationship between m_{ev} and M_{ev} in the traditional synthesis acquires a particular relevance. The most influential scientists of the synthesis agreed about the following points: i) fossil records were viewed as legitimate phenomena to be accounted for by evolution; ii) population genetics was placed at the “core” of the biological synthesis; iii) paleontology was considered unable to answer the question about evolutionary mechanisms (Depew and Weber 1996; Mayr 1982); and iv) microevolutionary mechanisms were extrapolated (partially or completely, depending on the researchers) to the explanation of macroevolutionary phenomena (Bock 1970; Bowler 1998; Eldredge and Tattersall 1986; Thompson 1983), due precisely to the theoretical inability of the studies of M_{ev} to contribute to the understanding of evolutionary processes (Arthur 1997). Nevertheless, these agreements did not lead to a convergent view about the particular dependence of M_{ev} with respect to m_{ev} .

One of the most influential perspectives about the relationship between m_{ev} and M_{ev} was that proposed by Theodosius Dobzhansky, who introduced some relevant differences between those two domains (Dobzhansky 1965). For instance, while microevolutionary processes are reversible, macroevolutionary processes are irreversible. To illustrate this case, Dobzhansky contrasted the resistance of a certain bacteria to an antibiotic with the irreversible evolution of *Homo sapiens*. For the author, this difference is due to the mechanisms of genetic variation: the number of genes responsible for macroevolutionary processes may be thousands, whereas the genes involved in microevolution are very few. Another difference is related to the determinism of the processes, which was conceived both in epistemic and in ontological terms. According to Dobzhansky, the responses of populations to environmental changes are predictable; on the contrary, in the case of macroevolution there are multiple possible responses. This means that indeterminism in evolution is due not to a mere lack of information, but to ontological causes. The third difference between m_{ev} and M_{ev} is related to a methodological as-

pect. Dobzhansky pointed out that, in contrast to m_{ev} , we have no access to direct evidence of M_{ev} .

Nevertheless, these differences did not cancel the assumption of a priority of m_{ev} over M_{ev} . In fact, the emphasis on population evolution was one of the main features of Dobzhansky's evolutionary thought; that is, population was considered the unit of evolution (Dobzhansky 1937; 1951). On this basis, since the decade of the 1920s, Dobzhansky suggested that almost the entire knowledge about evolution could be derived from the analysis of the biological distribution among and the variability within populations. This focus on the dynamics of populations can also be recognized in Dobzhansky's conceptualization of the speciation process, as resulting basically from genetic isolation of populations (Dobzhansky 1933).

Another point that deserves to be considered is the degree to which the researchers of the synthesis accepted the dichotomy m_{ev} - M_{ev} . In this sense, Dobzhansky introduced a third area, mesoevolution, "placed" between m_{ev} and M_{ev} and endowed with specific features. Although, according to Dobzhansky, mesoevolutionary phenomena have higher complexity than microevolutionary phenomena, the difference is nevertheless only quantitative and, therefore, mesoevolution must be also studied by experimental methods.

The evolutionary perspective of Sewall Wright was different than Dobzhansky's, since he introduced remarkable modifications regarding the importance and the role of the diverse evolutionary mechanisms. Wright specifically analyzed the relationship between m_{ev} and M_{ev} in two articles published at the end of his scientific career, "Character change, speciation, and the higher *taxa*" (1982a) and "The shifting balance theory and macroevolution" (1982b). In these works, Wright presented his shifting balance theory as "a third option" in the debate about the relationship between m_{ev} and M_{ev} . According to this theory, microevolutionary changes are due to the combined action of natural selection and genetic drift. Whereas the action of genetic drift is an important factor for the modification of the genetic frequency in a population, the "motion" from a "peak" representing a high value of fitness to a new "peak" is due to the intense effect of natural selection (see Ridley 2003). Nevertheless, the two mechanisms have relevant effects not exclusively on microevolution. Genetic drift causes changes not only in the m_{ev} domain, but also in other taxonomical levels, in particular the intensity and relevance of the action of genetic drift is higher for M_{ev} . On the other hand, selection might also operate at different scales: there might be selection acting at a local scale and, in addition, another selection acting among different localities at higher scales (Wright 1982b).

Another influential position about the relationship between m_{ev} and M_{ev} was that maintained by George Gaylord Simpson. Certainly, this paleontologist was one of the scientists who became more involved in this problem and its consequences. One of his most relevant contributions was to conceive the possibility of a qualitative difference between the two levels of evolution.

Macro-evolution involves the rise and divergence of discontinuous groups, and it is still debatable whether it differs in kind or only in degree from micro-evolution. If the two proved to be basically different, the innumerable studies of micro-evolution would become relatively unimportant and would have minor value in the study of evolution as a whole. (Simpson 1944, 97)

Certainly, Simpson's position experienced substantial changes throughout his life. For instance, in his book *Tempo and Mode in Evolution* (1944), he claimed that paleontology is the only scientific field that can study phenomena at long time scales. In turn, he did not understand M_{ev} merely as a process that gives rise to genetic groups, e.g., species and genus. From his perspective, biological evolution has also occurred at higher levels of the evolutionary hierarchy. Accordingly, he proposed a "megaevolution" as the domain corresponding to the evolution of higher taxa. Macroevolution and megaevolution exhibit significant differences. One of them is related to the existence (or not) of gaps in fossil record. In general, there are no discontinuities in the case of macroevolution, but they are very frequent and important in the case of megaevolution. "When the record does happen to be good, it commonly shows complete continuity in the rise of such taxonomic categories as species and genera and sometimes, but rarely, in high groups" (Simpson 1944, 105). Two different theoretical interpretations were elaborated to explain those differences. According to one of them, the absence in the fossil record of intermediate forms is "caused by nondeposition of middle strata or fossil and to sampling of migrants instead of min lines" (Simpson 1944, 105). For the second interpretation, on the contrary, discontinuities are real phenomena and not a shortcoming of the fossil record. What position does Simpson take with respect to this problem? On the one hand, Simpson acknowledged that discontinuities are not due to chance.

In the early days of evolutionary paleontology it was assumed that the major gaps would be filled in by further discoveries, and even, falsely, that some discoveries had already filled them. As it became more and more evident that the great gaps remained, despite wonderful progress in finding the members of lesser transitional groups and progressive lines, it was no longer satisfactory to impute this absence of objective data entirely to chance. (Simpson 1944, 115)

However, in spite of the fact that Simpson admitted the non-random character of the discontinuities in the fossil record, he denied the idea of saltational evolution, since it is

very unlikely, if not impossible, that such major saltations have occurred, according to present understanding of the genetic mechanism. The most nearly concrete suggestion of a mechanism adequate for saltation is that of Goldschmidt (1940), and he quite fails to adduce factual evidence that his postulated mechanism ever has produced or ever really could produce such an effect. (Simpson 1944, 116)

Another proposal for explaining the discontinuity of the fossil record in case of megaevolution is based on the existence of changes in mutation rates. However, Simpson did not accept this explanation.

There is no direct factual evidence for it, however, and it is not necessary postulate. Moderate mutation rates, more or less like those known in the laboratory, are necessary: but very high rates, even if there were such rates, would not suffice to explain these transitions unless also accompanied by the other special conditions [...]. (Simpson 1944, 122)

What is, then, the explanation of those gaps in the fossil record? Simpson found his answer in certain theories coming from the genetics of populations, by recalling that the rates of evolution depend on the population size.

According to the theories of population genetics previously summarized, such unusually high rates of evolution are very improbable in large populations and are most consistent with the postulate that the transitional populations were small. (Simpson 1944, 121)

But population size is not the only factor considered by Simpson. For instance, other factors, like ecological zone, environmental instability, and individual size, are also very important. Therefore, the gaps observed in the case of megaevolution's fossil record are due to "exceptionally rapid rates" in small populations. In this context, the relevant question is: what are the mechanisms that explain those paleontological records? According to Simpson, the main mechanism is natural selection, which allows taxa to rapidly evolve to a new status (Simpson 1944). Therefore, there is no qualitative difference among the evolutionary mechanisms of m_{ev} , M_{ev} and megaevolution.

Qualitatively similar processes, less only in duration and in the degree of ecological change involved, seem certainly to occur in macro-evolution and even in micro-evolution. The materials for evolution and the factors inducing and directing it are also believed to be the same at all levels and to differ in megaevolution only in combination and in intensity. (Simpson 1944, 124)

In a later book, *The Major Features of Evolution* (1953), Simpson reinforced the idea that genetics of populations plays a direct role in the explanation of the phenomenological patterns of evolution of higher taxa by means of natural selection as the main mechanism. As we can see, the core position of natural selection in Simpson's theoretical framework is clearly noticeable. As Beatty points out, the only "law" about the course of evolution is the fact that it is "generally adaptive" (Beatty 2008).

These considerations show that Simpson shared the idea of the pre-eminence of m_{ev} with the other authors of the biological synthesis. However, his position in the debate was particularly significant because he "inserted" paleontology into the synthesis. With respect to the importance of this move, it is worth recalling his own words about the integration of paleontology and genetics, which "may be particularly surprising and possibly hazardous" (Simpson 1944, xv). The insertion of paleontology, however, did not have the effect on the relationship between m_{ev} and M_{ev} that one might expect. In fact, according to Simpson, paleontology is autonomous only with respect to phenomenological issues, but not about macroevolutionary processes. In other words, the role of paleontology is restricted to the presentation and description of fossil records, but it cannot propose specific processes to explain fossil patterns. It is precisely for this reason that Eldredge and Tattersall (1982) "accused" Simpson of being the scientist responsible for the "silence" of biology about macroevolutionary mechanisms.

In general, Ernst Mayr conceived M_{ev} as the origin of higher categories and the domain of the development of new organic systems. In other words, M_{ev} was understood as a process that encompasses all the evolutionary processes that last for long periods of time and that involve entities belonging to higher levels. However, Mayr stated that,

[a]ll the processes and phenomena of macroevolution and the origin of the higher categories can be traced back to intraspecific variation, even though the first steps of such processes are usually very minute. (Mayr 1942, 298)

Therefore, the study of intraspecific variations was the central goal of Mayr's analyses (Mayr 1996). Genetics and microevolutionary factors should explain macroevolutionary phenomena.

With respect to the disciplinary role of paleontology, two arguments underlying Mayr's position need to be stressed. On the one hand, he denied the capacity of paleontology to generate theories that can explain its own phenomena. In addition, he questioned the status of fossil records by considering them not as inappropriate, but as insufficient

(Mayr 1982). On the other hand with respect to the processes leading to species and higher level entities, Mayr proposed mechanisms based on the dynamics of populations. This clearly implies that, for him, M_{ev} owes its features to m_{ev} .

The phenomena of macroevolution cannot be understood unless they are traced back to populations that are incipient species, and to neospecies. Major macroevolutionary processes are initiated during peripatric speciation. (Mayr 1982, 1131)

In summary, Mayr's stance about the relationship between m_{ev} and M_{ev} admits the possibility of reducing macroevolutionary phenomena to microevolutionary mechanisms, and it implies the denial of the autonomy of paleontology. In fact, these ideas should be contextualized in the general notion of "population thinking," the way chosen by Mayr to discredit essentialist styles of thought within biology (Sober 1980). Although the point is not the main purpose of this work, it is interesting to identify the many causes that may have influenced Mayr in this respect. Beatty (1994) suggests that the distinction between "essentialism" and "population thinking" might have been important in his view of evolutionary biology, as well as "a means of legitimizing philosophy of biology as a special area of inquiry" (Beatty 1994, 353).

This brief summary clearly shows that, in spite of the differences among their general positions, the main representatives of the traditional biological synthesis agree in the assumption of an asymmetric relationship between m_{ev} and M_{ev} . The mechanisms of evolution are supposedly confined to the microevolutionary levels and, as a consequence, the phenomena of macroevolution have to be reductively explained by those mechanisms. This position began to be challenged in the decade of the 1970s with the advent of the criticisms to the traditional synthesis.

The reconfiguration of the relationship since the seventies

The relationship between m_{ev} and M_{ev} has been frequently revised since the 1970s. One of the most discussed topics has been the rate of the evolutionary change, in particular, whether the rate is constant or not. This was an issue explicitly addressed by the theory of punctuated equilibrium, proposed by Niles Eldredge and Stephen Jay Gould (1972). In a simple but clear characterization, the theory states that "species are morphologically static throughout most of their history and have distinct and rapid births and deaths" (Lieberman and Vrba 1995, 394).

This hypothesis was elaborated for the purpose of giving an account of the interspecific patterns coming from a differential distribution of phenotypic evolution among lineages (Gould and Eldredge 1977; Vrba 1984). In fact, phenomenological patterns show a “relative lack of accumulation of phenotypic change throughout the known duration of a species once it appears in the fossil record” (Eldredge 1992, 146).

The debate opened up by the theory of punctuated equilibrium also involved the comparison between genetic patterns and fossil phenomenological patterns, in the line of Simpson’s words about the topic in *Tempo and Mode in Evolution* (Shubin and Marshall 2000). The debate naturally led to a critical analysis of the possibility that microevolutionary mechanisms explain macroevolutionary phenomena. In fact, according to the theorists of the punctuated equilibrium, the reason why abrupt changes in fossil patterns were ignored by the synthesis was the assumption that fossil records could be accounted for by gradual genetic variations in populations.

Because the population-dynamic formalisms operated on the assumption of continuous and incremental genetic variation, all nongradualist forms of evolutionary change were excluded. (Pigliucci and Müller 2010, 13)

In turn, as one might expect, the assumptions about the relationship between evolutionary levels were inextricably linked with the already intensively discussed issue about the comparative status of the different disciplines belonging to the synthesis. In this sense, it is not surprising that two of the most active representatives of the 1970 reaction, Eldredge and Gould, are both well-known paleontologists.

That debate was just the beginning of a deep revision of the relationship between m_{ev} and M_{ev} . In this respect it is possible to recognize two faces in the positions sustained by the new theorists: “negative” arguments (criticisms to the theses of the biological synthesis) and “positive” proposals (theories alternative to those theses). Both faces can be identified in the same quotation from Gould.

If every evolutionary principle can be seen in a *Drosophila* [sic] bottle or in the small and immediate adjustment of local populations on the *Biston betularia* [sic] model, then paleontology may have nothing to offer biology beyond exciting documentation. But if evolution works on a hierarchy of levels (as it does), and if emerging theories of macroevolution have an independent status within evolutionary theory (as they do), then paleontology may become an equal partner among the evolutionary disciplines. (Gould 1980a, 98)

The acknowledgment of the presence of these two argumentative

positions is relevant to the purpose of the present paper. Certainly, the negative arguments gained, at least, a partial success in the biology academic community. The difficulties of microevolutionary mechanisms in explaining macroevolutionary patterns were in general admitted by evolutionary biologists. But the agreement about the limitations of microevolution opened up a new question: which are the macroevolutionary processes that could explain fossil records? This positive search for macroevolutionary mechanisms found obstacles much more serious than those derived from the negative arguments. This problem was anticipated by some researchers in the 1970s.

Paleontologists have supplied most of the direct observations of major phyletic evolution in plants and animals, but they have been severely limited in their efforts to clarify the associated evolutionary mechanisms because of the nature of the fossil record. (Bock 1970, 704)

Among the several requirements to which the search for evolutionary processes was subject throughout the twentieth century, an important one was methodological. According to some authors, certain disciplines cannot contribute to the understanding of evolutionary mechanisms because they deal with “higher levels of structural organization inaccessible to laboratory genetic approaches” (Love 2006, 319; see also Ayala 1982; Futuyma 1998; Lande 1976). It is quite clear that the requirement of being accessible to laboratory experiments is only fulfilled by disciplines like population genetics, but not by paleontology.

Nevertheless, in spite of the difficulties, the critics of the biological synthesis persisted in the search for alternative evolutionary mechanisms appropriate for the levels of macroevolution. The main proposal in this direction was the mechanism of selection.

[S]election is the interaction between heritable, varying, emergent characters of individuals and the environment that causes differences in birth and/or death rates of those individuals. (Lieberman and Vrba 1995, 394)

Selection was, then, introduced as a general mechanism, of which natural selection of populations and of species are particular cases.

The positive proposals of the 1970s did not achieve wide acceptance in the academic community due to diverse reasons, whose analysis is beyond the purposes of the present paper. Although in the mid-1980s some aspects of the new theoretical perspective were (at least partially) accepted, like certain theses of the punctuated equilibrium theory (Gould and Eldredge 1986), problems subsisted. Indeed, Gould admitted some difficulties regarding the adoption of hierarchical perspectives

within biology, in particular those derived from taking the possibility of multiple units of selection not seriously enough.

Although arguments for a multiplicity of units of selection have been advanced and widely discussed, evolutionists have generally held fast to the overwhelming predominance, if not exclusivity, of organisms as the object sorted by selection. (Gould 1982, 384)

The problems persisted during the following years. However, at the beginning of the present century, the idea of an extended synthesis came back. In the following sections we will analyze the general features of this return.

“Altenberg 16” and the hierarchies in the context of the extension of the biological synthesis

Hierarchies in the context of the extension of the synthesis

The need of extending the biological synthesis was put forward from different perspectives during the following years. In 2008, fourteen biologists and two philosophers (known as “Altenberg 16”) introduced a formal and explicit proposal of an extended synthesis. The members of this group collaborated in the writing of a motivating book entitled *Evolution: The Extended Synthesis*, edited by Massimo Pigliucci and Gerd Müller (2010), where the current situation of the biological synthesis is thoroughly analyzed. In that work, at least three aspects of the biological synthesis are revised: first, the predominance of the focus on gradual patterns in paleontological records; second, the exclusive attention on natural selection as the main evolutionary mechanism; and third, “genocentrism,” that is, “[t]he focus on the gene as the sole agent of variation and unit of inheritance, and the dogmatic insistence on this stance by the popularizers of the Synthesis” (Pigliucci and Müller 2010, 14).

It is interesting to compare this position about the relationship between m_{ev} and M_{ev} with the criticisms raised in the decades of the 1970s and the 1980s. Both perspectives stress the need of a hierarchical structure to account for evolution.

Documentation and analysis of macroevolutionary patterns in living and fossil organisms amply demonstrate the need to more fully incorporate scale and hierarchy into the Evolutionary Synthesis. (Jablonski 2010, 349)

This means that the Altenberg 16 favors the incorporation of different levels in the account of evolutionary processes. In a way similar to the previous proposal, the Altenberg 16 accepts a multilevel selection theory, recognizing its high “potential for empirical and theoretical advances” (Jablonski 2010, 344) and claiming that it is “essential to understanding long-term evolutionary processes” (Jablonski 2010, 350). In this context, the question about how the relationship between m_{ev} and M_{ev} is characterized by this proposal is particularly relevant in the light of our main objective.

Multilevel processes, or at least a failure of simple extrapolation from short-terms, local processes, are often evident in the dynamics of evolutionary trends, which can unfold via differential origination [...], differential extinction [...], or directional speciation [...]. Although clades may evolve in directions consistent with patterns of intraspecific variation [...] simple extrapolation from short-term processes often breaks down – as might be expected, given the scarcity of directional species-level evolution over geological timescales. (Jablonski 2010, 344)

In other words, microevolutionary and macroevolutionary processes may evolve in different “directions” depending on the case under consideration. Even in the situation of the selection on organisms, which is strongly correlated with clade dynamics, multilevel analysis is desirable because “the combined forces will be more effective in driving large-scale change than either would be independently” (Jablonski 2010, 344). In summary, there are telling points of contact between the proposals of the Altenberg 16 and the negative arguments developed by the 1970 critics with regard to the conception of evolutionary processes. Both perspectives point to the limits of natural selection and stress the need of searching for alternatives to the central role traditionally assigned to the gene. In addition, the new theoretical framework does not introduce significant “novelties” when compared with the positive proposals of those 1970 works. In this respect, one of the scientists of the Altenberg 16 asserts that “the revival of the [multilevel selection] theory shows that it continues to be an important extension in contemporary research” (Wilson 2010, 88). It seems to be clear that the viewpoint of the Altenberg 16 still stands very close to the selective scenario, but in a hierarchical version.

Structure and interdisciplinary relations

At this point, it is pertinent to analyze whether the recently proposed extension only involves the incorporation of “new” areas of knowledge

(genomics, Evo-Devo and M_{ev}), or whether it also modifies the relationships among disciplines. With respect to this question, one of the philosophers of the Altenberg 16, Alan C. Love, contributes to the 2010 book with a relevant chapter, suggestively entitled “Rethinking the structure of evolutionary theory.” Love emphasizes the importance of distinguishing between structure and content in the biological synthesis. In his own words, content includes “empirical findings, dynamical models, and key concepts, among other items” (Love 2010, 435), whereas structure refers to “how the content is organized” (Love 2010, 405). As we have seen, since the 1940s to the 1960s the relationships between disciplines were considered as clearly asymmetric, as a consequence of the extrapolation of the microevolutionary processes to the M_{ev} domain. Therefore, the proposal of new evolutionary mechanisms to explain the higher levels of the structural organization of the phenomenon of evolution is an unavoidable step toward revoking that asymmetry. This means that the new structure of evolution will immediately be reflected in the structure of biology itself, which will incorporate interdisciplinary links different than those implicitly or explicitly accepted in the traditional synthesis.

The analysis of the structure of the extended synthesis clearly shows its multidisciplinary character. The multidisciplinary approach of the new synthesis should lead not to a mere juxtaposition of disciplines, but to an integration that will give rise to novel results: “[e]volutionary theory needs to be a synthesis of disciplinary approaches in order to produce an integrated or cohesive body of scientific knowledge” (Love 2010, 421-422). This point establishes a direct link between the problem of the role of disciplines in evolutionary biology with the own structure of the biological synthesis. “An erotetic structure for evolutionary theory in terms of an organization of problem agendas with diverse disciplinary contributors provides a standpoint for prospects and possibilities of an extended synthesis” (Love 2010, 433). In the case of the proposal of the Altenberg 16, one of the most criticized topics is the “gene-centrism” of the biological synthesis. In this sense, Gregory A. Wray claims:

Information from molecular biology, developmental biology, and, most recently, genomics are prompting substantial changes to the gene centered view that emerged during and shortly after the Modern Synthesis. (Wray 2010, 110)

From a similar standpoint, Pigliucci asserts that in the extended synthesis, “genes could come to be seen as ‘followers’ rather than leaders in the evolutionary process, a change that may have little impact on, say, research in molecular genetics, but that would represent a major conceptual shift in evolutionary theory” (Pigliucci 2010, 370). But, what

are the changes that are producing the extension of the structure of the biological synthesis?

Microevolution, macroevolution and pluralism

Let us recall the positive strategy adopted by the 1970 reaction, with its postulation of selection as a general multi-level selective mechanism. It is certainly true that such a mechanism cannot be uncritically identified with natural selection and that it does not amount to a mere repetition of microevolutionary mechanisms in the context of M_{ev} (Gould 1980b). In fact, Gould and other scientists made sustained efforts to clarify the differences between selection and natural selection. Whereas selection is understood as the “differential birth and death among varying organisms within a population” (Vrba and Gould 1986, 217), natural selection is only one of its possible causes. This argumentative strategy shows that, according to the 1970 reaction, not all cases of selection are due to natural selection (Lieberman and Vrba 1995). However, this conclusion does not cancel the fact that, in this new view, the processes of m_{ev} and M_{ev} still have an analogous structure (Folguera and Rendón 2010). Sometimes this analogy is even explicitly admitted: “selection operates, in a manner analogous to Darwinian natural selection, at several levels in addition to genes and organisms” (Lieberman and Vrba 1995, 394). This means that, in a certain sense, m_{ev} is analogically expanded to other domains of evolution, in particular, to M_{ev} .

But complexities arise when we expand the concept of selection hierarchically, and more precision is required in a statement of selection that applies equally to sorting among genomic constituents and among species. (Vrba and Gould 1986, 218)

One of the main purposes of the 1970 critics of the biological synthesis was, of course, to modify the traditional relationship between m_{ev} and M_{ev} (see, for example, Lieberman and Vrba 1995; Vrba and Gould 1986). However, their analogical strategy still implies the priority of m_{ev} over M_{ev} . Such priority, although non-reductive, derives from the fact that m_{ev} is taken as the model for evolution at all levels. In other words, there is no novelty in the macroevolutionary levels to the extent that their mechanisms are analogically extrapolated from the levels of microevolution. As a consequence, despite their explicit purpose, those theoretical positions that emerged in the 1970s reproduce, although in a different way than in the case of the traditional synthesis, the asymmetry between m_{ev} and M_{ev} .

In turn, the authors of the Altenberg 16 also recognize the need of finding macroevolutionary mechanisms: “Here, too, evolutionary mechanisms are poorly known” (Jablonski 2010, 341). As we have seen, in general they agree with the positive strategy adopted by the 1970 reaction. In fact, they support the idea of selective processes at different levels. Nevertheless, they do not revise the analogical extrapolation of mechanisms from m_{ev} to M_{ev} . This means that both the hierarchical evolutionary domain and the disciplinary domain continue to display an asymmetric structure (Folguera and Rendón 2010). Summing up, in spite of the words of Love cited above, those referred to the revision of “the gene-centered view,” the Altenberg 16 could not succeed in introducing a substantial modification in the relationships between evolutionary levels and between biological disciplines with respect to the traditional synthesis.

However, this extension of the biological synthesis involves other important complexities that lead us to a more detailed analysis. Undoubtedly, one of the areas that has implied deep re-examination and changes within biological synthesis is Evo-Devo. In this area, different concepts and theories were elaborated (and recovered), which have converged toward the gradual unfolding of a new scenario in the evolutionary biology. For instance, a concept like epigenesis is a clue in the attempt to turn genes into mere “followers” rather than leaders in evolutionary process. However, the extent of the involved changes is not clear yet. In the example of epigenesis, it is an open question concerning the empirical and theoretical scope associated to phenomena such as genetic assimilation, environmental influences, or transgenerational epigenetic inheritance; that is, “the inheritance of phenotypic variation in cells and organisms that do not depend on variations in DNA sequence” (Jablonska and Lamb 2010, 143). In the context of this conceptual framework, the main challenge of any extended synthesis involves not only a review of the content of evolution, but also the need of rethinking the structure of evolution, with its levels and the links among them. With respect to this problem, although Love admits that the positive program of finding alternatives to the synthesis is not an easy task, he suggests a kind of pluralism as a promising perspective.

If evolutionary theory is composed of multiple problem agendas that require contributions from diverse disciplinary perspectives, there is no “fundamental” viewpoint or level to which we can reduce our picture of the evolutionary process. [...] This plurality of biological disciplines, offering complementary and competing contributions to multidisciplinary explanations of phenomena related to problem agendas, is suitably matched with a pluralism about structure in evolutionary theory [...]. (Love 2010, 433)

A pluralism of this kind rejects any assumption of priority of certain levels on the others. In turn, this requires a reassessment of the role that each discipline plays in the context of the biological synthesis. Certainly, these revisions are not exempt from new problems, some of which will be discussed in the next and last section.

The role of the disciplines and the problem of integration

The previous sections suggest the need of facing the following new question regarding this pluralistic proposal of extension: how can the integration among the different areas of biology be performed? Regarding this problem, William Bechtel notices that, in the history of biology,

[t]he most common model for accomplishing unification has been the logical positivists' model of theory reduction, according to which theories of one discipline are derived from theories of other disciplines (together with necessary bridge laws and boundary conditions). (Bechtel 1993, 277)

Certainly, this strategy of integration by reduction has been very common in biological sciences. However, this strategy offers less results than expected.

Perhaps the strongest vision of unity appeared in the theory-reduction model of the logical empiricists. This model was attractive because it suggested that logic might provide a powerful way to unite the results all scientific inquiries by showing higher-level theories to be derivable from lower-level ones. Not only were serious objections raised against this model, but as we have seen, much of the unity that appears to result is illusory. (Bechtel and Hamilton 2007, 40)

In biology, the cases of reduction (*sensu strictu*) have not been frequent (Burian 1993). In the particular case of the relationship between evolutionary domains, the phenomena at the macroevolutionary levels could never be strictly explained or derived from the mechanisms and processes at the microevolutionary levels. Therefore, on what basis did traditional synthesis perform the desired integration? The integration sustained by that theoretical framework was based not on deductive reduction but on the assignment of different roles to the disciplines belonging to the synthesis. As we have seen, according to that view the explanatory role in biology was reserved exclusively for population genetics, whereas paleontology was conceived as a merely descriptive discipline. In addition, the assignment of different roles can be detected in other proposed mechanisms; see, for instance, the notion of changes in

the genetic regulatory program for the development of the body plan (Davidson et al. 2002; Davidson and Erwin 2006).

Certainly, the strategy of the architects of the biological synthesis was efficient for attaining the desired result of integration. However, this strategy also produced a highly negative effect on the role of the “secondary” disciplines.

The proliferation and heterogeneity of life science disciplines and methodologies following the advent of molecular biology had led to a centrifugal force within, making it difficult to recover a single big-picture or “grand unified theory”. (Love 2010, 433)

This “centrifugal force” did have a strong disruptive effect in biology. This means that there is a considerable tension between the need of integration and the negative effect of the traditional integrative strategy on certain disciplines and their domains of research. The acknowledgment of such a tension, as well as the attempt to overcome it, represents the most important challenge that an extended synthesis must face in the next years.

The difficulties of the traditional approach to integration open up the possibility of exploring new “bridges between theories without either one being reduced to the other” (Bechtel and Hamilton 2007, 22). One of these new proposals of integration is based on the interesting notion of “field,” which Darden and Maull characterize in terms of

a central problem, a domain consisting of items taken to be facts related to that problem, general explanatory facts and goals providing expectations as to how the problem is to be solved, techniques and methods, and sometimes, but not always, concepts, laws and theories which are related to the problem and which attempt to realize the explanatory goals. (Darden and Maull 1977 cited in Bechtel and Hamilton 2007, 22)

In this way,

Interfield theories sometimes serve simply to bridge existing disciplines, allowing practitioners in each discipline to utilize techniques developed and knowledge procured in the other. In the most interesting cases, however, constructing a bridge between fields or disciplines results in the construction of a new discipline. (Bechtel and Hamilton 2007, 23)

What should the integration strategy be in the case of evolutionary synthesis? As explained, we have detected different kinds of relationships among evolutionary areas. In each proposal, we found a different sort of dependence of M_{ev} on m_{ev} . In this context, it might be suggested

that Evo-Devo could play a relevant role in the desired extension of biological synthesis, by building up a meaningful bridge between the two areas of evolution: m_{ev} and M_{ev} . However, the ability of Evo-Devo to play this role is still a very controversial matter. In our opinion, the goal does not consist merely in the generation of new areas of knowledge corresponding to the relationships between different fields, in particular, between m_{ev} and M_{ev} . In any case, we consider that it is also necessary to redefine the roles of the different disciplines pertaining to the biological synthesis.

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