Is there a unique process which governs macroevolution?

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UDK: 575.8 Izvorni znanstveni rad / Original scientific paper Primljeno: 5. lipnja 2015. Prihvaćeno: 8. listopada2015.

Some philosophers and biologists believe that there is a distinct and unique macroevolutionary process, while others are of the opinion that there is not. Contemporary opinions on this issue are presented in Dietrich's and Erwin's respective essays published in Contemporary Debates in Philosophy of Biology, edited by F. Ayala and R. Arp. Contrary to the paper titles (Microevolution and Macroevolution are Governed by the Same Processes and Microevolution and Macroevolution are Not Governed by the Same Processes), indicating apparently contradictory attitudes, the two authors' viewpoints are much more subtle and nuanced. The set of assumptions of Dietrich's extrapolation view appears to be inconsistent, and the theory may be saved by a shift to paraconsistent logic which, in spite of the contradiction, does not lead to the collapse of the theory. On the other hand, Erwin's hierarchic view implicitly supports the existing logic of the superordinate theory, believing that there is evidence that at least in one case it is possible to prove that macroevolution cannot be reduced to a microevolutionary process. The study of emergence would indicate the acceptability of the claim that geographic range at the species level represents a weakly emergent phenomenon which cannot be explained by being reduced to microevolution processes. Nevertheless, the hierarchical view still seems to lack sufficient convincing evidence for that claim.

Key words: *extrapolation*, *geographic range*, *hierarchical view*, *phenomenon of macroevolution*, *process of macroevolution*.

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Introduction

For some authors macroevolution represents the central concern in evolutionary theory¹, the crucial question being whether macroevolution and microevolution are the same processes or not². Assumptions concerning diverse micro and macroevolutionary processes question the hard core of evolutionary synthesis, according to which microevolution and macroevolution are produced by identical microevolutionary processes. This essay questions the validity of the perspective that implies a revision or extension of the evolutionary synthesis in this case. The first section considers the opposing perspectives on the process or processes that are the bases for microevolutionary and macroevolutionary phenomena. Section Two is aimed at presenting the scope of the topic from the perspective of both views. Section Three reduces the discussion to the exploration of both perspectives in two respects: first, through an internal critique that explores the logical consistency of the set of assumptions of each perspective; and, second, through an external critique that compares selected views towards different ontological hypotheses. An external critique is necessary due to the fact that both positions could be logically consistent, but since they are in opposition to one another, both of them cannot be truthful. Consequently, this type of critique is primarily aimed at verifying whether the premises of the two viewpoints are acceptable, focusing upon the case of species selection. Subjecting both perspectives to two types of critique allows for a clear decision concerning the nature of the causal mechanism in microevolution and macroevolution, as well as an insight into the possible implications of that decision concerning the hard core contemporary synthesis perspective, as it is presented in the fourth section.

1. Standard And Nonstandard Perspective

A majority of scientists perceive macroevolution and microevolution as two distinct³ and well defined phenomena:

Microevolution usually refers to the changes in allele frequency within a species that ultimately affect the phenotype of organisms that make up the species. Macroevolution refers to the changes that are across species, such as when a

¹ D. SEPKOSKI, Macroevolution, in: M. RUSE (ed.), *The Oxford Handbook of Philosophy of Biology*, New York, NY, Oxford University Press, 2008, 211-237.

² F. AYALA and R. ARP, Are Macroevolution and Microevolution Governed by the same Processes? Introduction, in: F. AYALA and R. ARP (eds.), *Contemporary Debates in Philosophy of Biology*, Malden, MA, Blackwell Publishing Ltd., 2009, 165-167.

³ M. R. DIETRICH, Microevolution and Macroevolution are Governed by the Same Processes, in: F. AYALA and R. ARP (eds.), *Contemporary Debates in Philosophy of Biology*, Malden, MA, USA: Blackwell Publishing Ltd, 2009, 169-179.

new genus, phylum, or family emerges (form of speciation), or when species go extinct...⁴

The unquestioned distinctiveness of the two phenomena is followed by a dilemma on their meaning and governing processes: which phenomena occur often? It is not clear what real evolution is, since some identify evolution with microevolution, while others believe that real evolution is only macroevolution⁵. Also, the problem is in the determination of the causal processes for both phenomena: the extrapolation position is in line with the evolutionary synthesis, where the existence of unique macroevolutionary process is questioned⁶. The standard position on evolutionary synthesis explains macroevolution as a sequence of successful microevolutionary processes. The key difference between the opposing positions lies in the role and reach of microevolutionary mechanisms. In other words, it is necessary to answer the question, are microevolutionary mechanism able to explain macroevolutionary phenomena of genesis, development and extinction of taxonomy groups above the species level?

1.1 Standard, extrapolation view

Neo-Darwinists explain species multiplication and genealogical patterns of species and organism change through the gradual and slow accumulation of genetic variations, which are then subject to genetic drift, natural selection, and other established microevolutionary processes. The contemporary evolution synthesis explanation is extrapolative: macroevolution processes are an extrapolation of microevolution processes at higher hierarchical levels of taxonomy organization without separate macroevolutionary mechanism. This standard position is not universally accepted, and one of the numerous scientific challenges is saltationism, macromutation theory which claims that a single mutational event can produce phenotypic changes that result in relatively rapid speciation. Also, there is a well supported evidence of Goldschmidt's proposal that changes in developmentally important genes can cause large phenotypic change, which leads to so-called hopeful monsters. New genetic mechanism hold that for a transition from one species toward another it is not sufficient to have a constant gathering of micromutations, but there is also a need for large morphological changes that result in the development of a new species. This new genetic mechanism, systemic mutation, arises due to numerous chromosomal rearrangements which constitute new forms of genetic structure,

⁴ F. AYALA and R. ARP, Are Macroevolution and Microevolution Governed by the same Processes? Introduction, in: F. AYALA and R. ARP (eds.), *Contemporary Debates in Philosophy of Biology*, Malden, MA, Blackwell Publishing Ltd., 2009b, 165-167.

⁵ E. SOBER, *Philosophy of Biology*, Boulder, Westview Press, 2000.

⁶ D. SEPKOSKI, 2008, o. c.

which later form new chemical systems and reaction routes that correspond to new phenotypes. Dietrich believes that there are diverse mechanisms capable of leading to a macroevolution outcome, therefore: »This distinction between process and outcome is crucial for contemporary research...«⁷ Dietrich does not believe the claim that a macroevolution outcome can only be produced by a macroevolution processes. He finds support for his thesis in experiments on Drosophila Ubx genes (hox ultrabithorax genes) that confirm dramatic macroevolutionary changes in body plan and the number of extremities due to microevolution processes that erase or exchange of some R amino acids in the amino acid chain C-terminus. This case is an example of an evo-devo explanation, where small genetic changes produce larger phenotypic changes (such as structural changes in the extremities), and actually have a significant role in the production and maintenance of diverse life forms⁸.

The standard position is not disputing the definition of macroevolution as a change that is above the species level nor does that definition imply a revision of the definition of macroevolution. This occurs due to the fact that higher level taxonomic groups such as Genus, Familia or Phylum are perceived as an epistemological convention and not as an ontological reality⁹. In cases when the ontological species reality is recognized¹⁰ as a separate entity with properties of an individual¹¹ that is born and dies, the question becomes, does Stanley's¹² species selection present a unique macroevolutionary process. Does it separate species selection from species sorting, differentiating the birth and death of single entities in a population? Dietrich suggests the existence of the rare separate macroevolutionary processes of small value:

Rather than deny that distinct macroevolutionary processes are possible and present in nature, I claim that such processes are possible in the case of species selection, but are relatively rare and so are of minor evolutionary consequence when the entirety of the domain of evolutionary biology is considered¹³.

Species selection has been rarely observed because the geological process of change is slow. This epistemological limitation is introduced by Dobzhansky¹⁴

⁷ M. R. DIETRICH, 2009, o. c., p. 172.

⁸ J. S. ROBERT, Evo-devo, in: M. Ruse (ed.), *The Oxford Handbook of Philosophy of Biology*, New York, NY, Oxford University Press, 2008, 291-310.

⁹ D. SEPKOSKI, 2008, o. c.

¹⁰ While taking into account differentiation category of species and species as taxa. The success of practical definition of species does not imply their ontological reality.

¹¹ S. M. Stanley (1975), D. Hull (1992), K. De Queiroz and M. J. Donoghue (1998) and S. J. Gould (2002) are some of those who advocate species as individuals.

¹² S. M. STANLEY, A theory of evolution above the species level, *Proceedings of the National Academy of Sciences* (USA), (1975) 72, 646-650 and S. M. STANLEY, *Macroevolution: Pattern and process*, W. H. Freeman, San Francisco, 1979.

¹³ M. R. DIETRICH, 2009, o .c. p. 176.

¹⁴ T. DOBZHANSKY, *Genetics and the origin of species*, New York, Columbia University Press, 1937.

as a reshaped ontological determination »...reluctantly to put a sign of equality between the mechanisms of macro and micro-evolution...« and methodological obligation »...what could be known with the program of experimental evolutionary genetics...«¹⁵. The standard position claims numerous, more frequent and more important selections at the level of individual organisms than at the level of species and above.

1.2 Non-standard, hierarchical view

Sepkoski writes that many doubt in the strength and reach of the microevolutionary explanation of evolution:

...the mechanisms of microevolution only explain the emergence and survival of small variations within populations (a slightly brighter coat, a minutely sharper beak, etc.)¹⁶.

Naturally, the size of phenotype changes does not represent a crucial value here: it is rather whether there are processes producing a new species operating exclusively at the species level or higher. The nonstandard, hierarchical position, assumes diverse nature of microevolutionary and macroevolutionary process, and irreducibility of macroevolution patterns on microevolution. Erwin writes that challenges to the idea of sameness of microevolution and macroevolution come from three different areas:

...1) Selection among species, (2) the sources of variation and constraint, and (3) the non-uniformitarian nature of the evolutionary process itself¹⁷.

Erwin believes that a confirmation of differences among micro and macroevolutionary processes requires a determination of an exclusive disjunction in at least one of the listed cases. In the first case it should be determined that macroevolutionary trends reflect selection among species and not within species; in the second case it should rely on all comprehensible sources of variation and limitations at the molecular level, some of which suggests the existence of a separate macroevolutionary mechanism (without defining the mechanism type); in the third case it is necessary to make sure that those experiments which assume evolutionary rates, mechanisms and processes that can be carried out today, are not sufficient for the explanation of the change of evolutionary patterns that are measured by the geological timeline, as evolutionary uniformitarians claims¹⁸. The theory of punctuated equilibrium, currently the

¹⁵ M. R. DIETRICH, 2009, o. c. p. 170.

¹⁶ D. SEPKOSKI, 2008, o. c. p. 212.

¹⁷ D. H. ERWIN, 2009. Microevolution and Macroevolution are Not Governed by the Same Processes, in: F. AYALA and R. ARP (eds.), *Contemporary Debates in Philosophy of Biology*, Malden, MA, Blackwell Publishing Ltd, 2009, 180-193, p.181.

¹⁸ D. H. ERWIN, 2009, o. c.

strongest scientific objection to the natural selection principle as the universal micro and macro mutation causal process¹⁹, perceives species as evolutionary independent individuals that suddenly appear and diminish in the fossil record and does not bring into question the role of the microevolution mechanism but rather points to the possibility that:

... these unrevised microevolutionary mechanisms do not hold exclusive sway in evolutionary explanation, and that their domain of action must be restricted (or at least shared) at the level of macroevolutionary pattern over geological scales $...^{20}$.

Contemporary thought on this issue is directed towards questioning the existence of emergent properties at the species level²¹. Geographic range could be an example of the emergent properties:

To the extent that geographic range is a result of such complex and non-linear processes, it is not explainable as a result of microevolutionary processes and is emergent²².

The argument which supports a unique macroevolutionary process is that the directions of long-term macroevolutionary processes oppose the trends of microevolutionary processes operating in the same species. Some of these long-term morphological directions and limitations survived despite radical changes in environment and even through mass extinctions²³. For Erwin mass extinctions are another example of macroevolutionary processes that are not governed by microevolution. In pre-theoretical belief, it appears that mass extinctions represent the principle of destruction and restrictions rather than creating evolutionary novelties. Nevertheless, new comprehensions that have originated in the evo-devo area (parallel development of animals from diverse monophyletic groups) show mass extinctions represent another important possible source of variation, by forming new niches within emerging ecosystems. The third challenge to the standard explanation is in its denial of its hard core, the principle of evolutionary uniformitarianism which assumes the timely invariance of the properties of biological entities. Evolutionary uniformitarianism assumes that the contemporary experiments of evolutionary rates, mechanisms and processes are sufficient to explain the change of geological evolutionary patterns. Nevertheless, Erwin believes that:

¹⁹ J. TRAVIS and D. N. REZNICK, Adaptation, in: M. RUSE and J. TRAVIS (eds.), *Evolution: The First Four Billion Years*, Cambridge, MA, The Belknap Press of Harvard University Press, 2009, 105-131.

²⁰ S. J. GOULD, *Punctuated Equilibrium*, Cambridge, MA, Belknap Press of Harvard University Press, 2007, p. 58.

²¹ S. J. GOULD, *The Structure of Evolutionary Theory*, Cambridge, MA, Belknap Press of Harvard University Press, 2002, p. 673. writes that: »Emergent characters belong exclusively to the species.«

²² D. H. ERWIN, 2009, o. c. p. 185.

²³ D. H. ERWIN, 2009, o. c.

There is no necessary reason why evolutionary uniformitarianism should be correct; it is simply an implicit assumption of most evolutionary biologists²⁴.

Evolutionary uniformitarianism has certain weaknesses. The first deficiency is in its restriction on a shorter time period that narrows the study of the entire dynamics of evolution since it is not possible to precisely distinguish the time needed for observation of environmental events over a longer time²⁵. The second deficiency stems from the variability of evolutionary changes that have themselves evolved²⁶. Smith and Szathamáry present the idea that diverse levels of selection narrow the ontological and reproductive ability of biological entities and strength of natural selection as unique principal of evolutionary change. The diverse levels of selection stand in support of the variability of evolutionary changes and one feature is common to many of the transitions. Because of that entities that were capable of independent replication before the transition can replicate only as part of a larger whole after it²⁷.

Also, selection pressure on the lower level entities (replicating molecules, prokaryotes, asexual protists etc.) interferes with the integration of entities that are at a higher hierarchical level (chromosomes, eukaryotes, sexually proliferating species, multicellular species etc.). These changes form new (emergent) evolutionary structures that are hardly accessible or inaccessible by direct experimental observation »...because they have changed the rules of the game, and changed the nature of the variability upon which selection can act.«²⁸.

For the non-standard, hierarchical view, macroevolution is governed by a distinct process, and microevolution and macroevolution present many diverse evolutionary patterns and processes that occur on different hierarchical levels. Erwin believes that discussion on reducibility of macroevolutionary phenomena on microevolutionary processes is an empirical and not theoretical (philosophical) question.

2. Internal And External Critique Of Two Positions

The internal critique investigates the logic consistency of a system of thought, making sure that it does not contain any contradictory claims. This type of critique audits use of the basic and overall assumption which is in the basis of the system. Nevertheless, if the principal assumptions are metaphysical axiom, the whole evaluation requires an external critique. This type of critique

²⁴ D. H. ERWIN, 2009, o. c. p. 188.

²⁵ D. H. ERWIN and R. L. ANSTEY, Speciation in the fossil record, in: M. RIDLEY (ed.), *Evolution*, New York, NY, Oxford University Press, 2004, 185-197.

²⁶ D. H. ERWIN, 2009, o. c.

²⁷ M. J. SMITH and E. SZATHAMÁRY, *The major transitions in evolution*, New York, NY, W. H. Freeman, 1995.

²⁸ D. H. ERWIN, 2009, o. c. p. 189.

is necessary because both positions could be logically consistent, but since they are in opposition both of them cannot be truthful. External critique is interested in relation of metaphysical-epistemological basis of studied system towards theoretical contributions of new insights in approaching the truth.

2.1 Internal critique

In his paper Dietrich does not want to polarise those views in accordance with the principle of »all or nothing«, but rather seems to be directing the discussion towards the question of the relative importance of distinct micro and macroevolutionary processes. According to him, microevolutionary processes are much more frequent than unique macroevolutionary processes and are therefore of greater significance in explaining the emergence of both microevolutionary and macroevolutionary phenomena. Dietrich claims the existence of distinct macroevolutionary processes (explicitly in the case of the species selection) and a possibility of discovering new macroevolutionary processes. It is by these claims that the set of hypotheses in the solid core of evolutionary theory, coupled with classic logic, are rendered inconsistent with regard to that same logic, and inconsistency is one of the modes in which a failure of a theory emerges or becomes manifest. If we were to think of Dietrich's hypotheses as premises pertaining to a logical set of well-formed formulae (wwf), they should be followed by an argument conclusion. The argument is logically valid if the conclusion follows from the premises in all interpretations of the formal language, i.e. the conclusion results from the premises if and only if it is true in all the interpretations of non-logical terms in which the premises are true. In this case the set of all the sentences ensuing from that set could be referred to as a theory based on these assumptions. Consistency means that if within the theory there is truth-bearer A, it is impossible for both A and \neg A to be true. Furthermore, as classic logic maintains, if one theory is consistent, some sentences do not ensue from it. In accordance with this, the set of assumptions of evolutionary theory, as interpreted by means of the extrapolation view, coupled with classic logic, would seem to be inconsistent due to the fact that classic logic observes the principle ex contradictione quodlibet (ECQ), according to which, in case of at least one contradiction, the theory is rendered inconsistent and is consequently not logically valid. The theory can be saved by means of a change in logic. As paraconsistent logic has it, it is not true that anything following from contradictory premises is explosive (ECQ).²⁹ The logical validity of the extrapolation view of evolutionary theory can be preserved by departing from the trivialism of classic logic which demands the truth of everything. Tanaka be-

²⁹ For standard and some other definitions of paraconsistency see G. ROBBLES, Weak consistency and strong paraconsistency, *Open Access Journal for a Global Sustainable Information Society* (2009) 7, 185-193.

lieves this to be possible because inconsistency is pervasive in our rational life and trivialism is rationally unacceptable³⁰. Practical rationality may require a choice between incompatible convictions. However, Tanaka's claim may prove to be too strong since no one seems to wish for inconsistency in their system of thought. On the contrary, theoretical rationality calls for the elimination of inconsistency wherever it is detected. But, it seems that Dietrich's claims shows the inconsistency of the extrapolation view as a local phenomenon which does not result in the global destruction of his viewpoint and evolutionary theory, thereby rendering the extrapolation view paraconsistent. Dietrich's viewpoint is paraconsistent because it does not bring about a collapse of evolutionary theory, but seems to be, on the other hand, weakly inconsistent according to at least one definition³¹ since it contains a negation of a superordinate logic, in this case evolutionary theory. The hierarchic view assumes, either explicitly or implicitly, premises leading to a different conclusion.³² (i) microevolutionary process is not sufficient to explain the emergence of macroevolution; (ii) there is evidence that in at least one case macroevolution can be explained by the macroevolutionary process. The hierarchic view would therefore represent a theory of a lower order, comprising assumptions (i) and (ii) which seem to be contradictory to the superordinate logic of evolutionary theory since they claim that macroevolutionary phenomena cannot be satisfactorily explained by the neo-Darwinist paradigm. However, this is where the author implicitly supports the existing classic logic of the superordinate theory, maintaining his premises to be true and the issue of macroevolution being reducible to microevolutionary processes to represent an empirical question. It therefore becomes necessary to see whether there exist processes producing new species that work only at the species level or higher, whereas Erwin claims this to be the case with the geographic range which is not explainable as a result of microevolutionary processes and is emergent. This case will be examined in the next Sub-chapter with great care.

³⁰ K. TANAKA, F. BERTO, E. MARES and F. PAOLI, Paraconsistency: Introduction, in: K. TANAKA, F. BERTO, E. MARES and F. PAOLI (eds.), *Paraconsistency: Logic and Applications*, Dordrecht, Springer, 2013, 1-15.

³¹ G. ROBBLES, 2009, o. c.

³² The paper lists the assumptions in a logically more coherent and comprehensible form, based on the original parts of Erwin's paper. They can be encountered in his paper in several places, and here the following have been selected: assumption (i) taken from the quotation »...that novel mechanisms may be responsible for macroevolutionary change.« (D. H. ERWIN, 2009, o. c. p. 190); and assumption (ii) taken from the quotation »Convicting demonstrations have been provided that geographic range is a weakly emergent, heritable trait that cannot be reduced to microevolution.« (D. H. ERWIN, 2009, o. c. p. 190).

2.2 External critique

While the previous chapter dealt with the logical validity of the conclusions drawn from two different views, in this chapter the acceptability of their premises, i.e. soundness of their arguments need to be considered. The external judgment of two opposite positions on the nature of micro and macroevolution processes weight their ontological and epistemological relation towards the issue in question: is there a distinct macroevolutionary process that is independent of the observer and is it possible to achieve reliable scientific knowledge about that process? While determining micro and macroevolution, Ayala and Arp³³ place the demarcation line for the two phenomena at the species level. Species is the criterion of the separation, and the basic processes whose nature determines the possible existence of unique macroevolutionary process. The ontology of hierarchical levels of life is crucial in selecting between two positions, and the main dispute is in the concept of species selection. Thus Sepkoski writes:

This question largely hinges on the issue of hierarchy: Do major taxonomic groups represent real, ontologically distinct entities with their own emergent properties, and are the factors that govern their development discontinuous with the mechanisms that produce variation and fitness among individuals³⁴?

Eldredge and Gould's Theory of Punctuated Equilibrium has established the ontological reality of the species, making it possible to determine species as individuals, which was done by Ghiselin³⁵, Hull³⁶ and Lieberman and Vrba³⁷. The major contribution of the Theory of Punctuated Equilibrium lies in the species concept because it seems to have created the possibility of the existence of an independent area of macroevolution:

Species represent the basic unit in theories and mechanisms of macroevolutionary change... I presented the case for treating species as individuals in an earlier section of this chapter (pp. 603-608), noting that punctuated equilibrium greatly aids such delineation...³⁸

The species can now play the same role of fundamental individual that organisms assume in microevolution³⁹, whereby species have a birth and extinction, similar to organisms which are born and die. It is in this way that the

³³ F. AYALA and R. ARP, 2009, o. c.

³⁴ D. SEPKOSKI, 2008, o. c. p. 212.

³⁵ M. T. GHISELIN, A radical solution to the species problem, *Systematic Zoology*, (1974) 23, 536-544.

³⁶ D. L. HULL, Individuality and selection, Annual Review of Ecology and Systematics, (1980) 11, 311-332.

³⁷ B. S. LIEBERMAN and E. S. VRBA, Stephen Jay Gould on species selection: 30 years of insight, *Paleobiology* (2005) 31 (2, Supplement) 113-121.

³⁸ S. J. GOULD, 2007, o. c. p. 703-4.

³⁹ S. J. GOULD, 2002, o. c.

species could have become a concept that could be conceived of as individual evolutionary units that, to some degree independently of population-level selection, have adaptive traits of their own⁴⁰. The Theory of Punctuated Equilibrium denies that the synthetic view of gradual accumulation of microevolutionary change could satisfactorily explain the change at higher taxonomic levels. This seems to have opened a possibility »... for a new wave of macroevolutionary investigation, ultimately leading to the 'hierarchical view of life«⁴¹. As the hierarchical view maintains, evolution operates on different levels of the hierarchy (the gene, the organism, the population, the species, taxonomic taxa, etc.) through different kinds of processes. The hierarchical view derive their disputable claims:

(a) Properties and processes at higher levels can affect the course of evolution, and (b) these higher-level properties and processes cannot be reduced to lower-level properties and processes...: (c) A fully adequate theory of evolutionary dynamics must recognize these irreducible higher-level properties and processes⁴².

To Dietrich species selection represents the most clearly articulated macroevolutionary process, but the definition of species selection seems to be arguable since some theorists support an emergent character approach (Vrba), while some others seem to be more inclined towards adopting an emergence fitness approach (Loyd, Gould). In the second place, Dietrich admits that species selection represents the best case of an isolated causal process, operating exclusively in macroevolution. However, he believes that it is the frequency of these events that represents the real question, the one that needs to be answered. Namely, the very proponents of the hierarchical view admit there is too small an amount of evidence to corroborate the hierarchical view of macroevolution⁴³. Furthermore, Grantham himself mentions different denials of this evidence. The best known proof that macroevolution cannot be merely reduced to microevolutionary processes is represented by geographical range. In an influential paper entitled »Is macroevolution more than successive rounds of microevolution?«44 Grantham considers the relations between micro and macroevolution, different concepts of emergence and biology of geographical range, writing as follows:

⁴⁰ D. SEPKOSKI, 2008, o. c. p. 221.

⁴¹ D. SEPKOSKI, 2008, o. c. p. 372.

⁴² T. GRANTHAM, Hierarchical Approaches to Macroevolution: Recent Work on Species selection and the »Effect Hypothesis«, *Annual Review of Ecology and Systematics*, (1995) 26, 301-321, p. 302-303.

⁴³ T. GRANTHAM, 1995, o. c.

⁴⁴ It seems necessary to draw attention to the fact that Grantham places the questionnaire immediately below the paper title.

Thus, if geographical range is weakly emergent, it provides a basis for arguing that macroevolutionary phenomena cannot be fully explained by microevolutionary processes⁴⁵.

Grantham further claims that the geographical range is weakly emergent and blocks the attempt to explain all macroevolutionary phenomena in terms of microevolutionary processes. The problem lies in Grantham's admission that geographical range size can be emergent without being heritable at the species level, whereas true species selection for geographical range has to be heritable⁴⁶. Dietrich maintains that the term geographical range, as employed in Grantham's study, seems like an emergent character, but if the geographical range is dependent on an organismal trait, like his first evidence for hierarchical explanation of macroevolution (Larval Ecology in Marine Invertebrates), then it seems like an aggregate character⁴⁷. On the other hand, when it comes to defining species selection, some are inclined to distinguish between selection operating on aggregate, organismal characters and selection acting on true species-level characters⁴⁸, whereby only the selection operating on the species level characters qualifies as species selection⁴⁹. Similarly, Jablonski and Hunt, on the basis of the emergence fitness approach, claim that geographical range represents genuine species selection, with no proof that geographical range is itself an emergent character. The claims taken from the discussion of this chapter represent the basis for the analysis of acceptability of the premises of two viewpoints under consideration: the extrapolation view assumes that macroevolution is caused by both micro and macroevolutionary processes, the microevolution processes being however more frequent and therefore more important. I believe that it is fairly clear that this claim has so far been satisfactorily proven. Erwin maintains that at least in one case it is possible to claim that macroevolution cannot possibly be reduced to microevolutionary processes: »Convincing demonstration have been provided that geographical range is a weakly emergent, heritable trait that cannot be reduced to microevolution.«⁵⁰ I do not believe this hypothesis to be confirmed. First, it is obvious that there is no agreement as for the precise and accurate definition of the term species (an emergent character approach and an emergent fitness approach), upon which the results of empirical evidence highly depend. Second, I believe this discussion to have shown the geographical range to be weakly emergent; however, it has not proved to be heritable at the

⁴⁵ T. GRANTHAM, Is Macroevolution more than successive rounds of macroevolution? *Paleontology*, (2007) 50, 75-85, p. 75.

⁴⁶ D. JABLONSKI and G. HUNT, Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: organismic versus species-level explanations, *American Naturalist*, (2006) 168, 556-564.

⁴⁷ M. R. DIETRICH, 2009, o. c.

⁴⁸ Lieberman and Vrba, 2005, (o. c.) provide a comprehensive table of the changes in meaning of the term species selection.

⁴⁹ M. R. DIETRICH, 2009, o. c.

⁵⁰ D. H. ERWIN, 2009, o. c. p. 190.

species level, therefore »Whereas range size can be emergent without being heritable, true species selection for range would, of course, require heritability«⁵¹. Last, conclusions concerning the originality of species selection on the basis of the emergent fitness approach are possible without verifying that geographical range is itself an emergent character. It would be more acceptable to say that the range size here is proven to be emergent, regardless of heritability. Consequently, I think that it would be more precise to say that there is no strong or convincing evidence as to the existence of empirical proofs of distinct macroevolution processes since these proofs are dependent upon the chosen definition of species selection. Grantham writes: »At present, only a small handful of well-documented cases require hierarchical explanation.«⁵² I believe the hierarchical approach to resemble very much a house of cards: while nature is indeed hierarchically organized, the hierarchical view is based upon diverse definitions of the term species selection. Also, the heritability of geographical range, essential to true species selection for range, and the claims of one of the approaches to the definition of species selection fails to show that the geographical range is itself an emergent character, which would seem to be necessary. In my opinion, it would be sensible to accept the premises of extrapolation view as already confirmed. The hierarchical position brings into question a standard theory, thereby bearing the burden of proof, but still lacking the strength to challenge it completely, or possessing positive empirical proof that would make the existence of a distinct macroevolutionary process plausible.

3. Decision And Evolutionary Synthesis Implications

On one side, the hierarchical view in Erwin's interpretation, claiming that there exists a distinct macroevolutionary process, whereas on the other side there is the extrapolation view, as interpreted by Dietrich, maintaining that no accumulation of evidence is to be expected in favour of either theory. Thus the two views are not contradictory, since Dietrich's interpretation seems to suggest a pluralist approach embracing a number of theories (sub-theories), evaluating and assessing their relative significance. The internal critique that explores the logical consistency of each perspective has established the fact that the set of assumption of the theory of evolution, as interpreted by the extrapolation view and coupled with the classic logic, is inconsistent. Furthermore, a change in logic would seem to render it paraconsistent, i.e. weakly inconsistent. The set of assumptions of the theory of evolution, as proposed by the hierarchical view, seems to implicitly support the existing classic logic of a superordinate theory, which is why the set of assumptions pertaining to the hierarchical view ap-

⁵¹ T. GRANTHAM, 2007, o. c. p. 82.

⁵² T. GRANTHAM, 1995, o. c. p. 318.

pears inconsistent with respect to this logic. As claimed by the hierarchical view, its premises are true: therefore the issue of reducibility of macroevolution to microevolutionary processes would represent an empirical question. The external critique gives an insight into the acceptability of both views in order to check the soundness of their conclusions. Although I am inclined to agree with the set of assumptions of the extrapolation view, assuming that macro-evolution is caused by both micro and macroevolutionary processes: however, microevolutionary processes, occurring far more frequently, seem to be more significant. Conversely, the set of assumptions pertaining to the hierarchical view would appear to lack a generally acceptable definition of species selection (emergent character approach or emergent fitness approach), the degree of acceptability of evidence depending upon the definition choice. Hence »Stricter emergent character definition includes fewer cases and has less potential for future cases«⁵³. Similarly, some of the proposed evidence has been disputed and brought into question from diverse viewpoints⁵⁴.

In accordance with all of the above, I believe that several plausible conclusions are possible in the dispute whether there exists a unique process governing macroevolution. First, it would imply a change in logic enabling the set of assumptions pertaining to the extrapolation view to become paraconsistent, i.e. weakly inconsistent. This would render the extrapolation view logically valid, its premises acceptable, and the argument sound. Second, if we admit the set of assumptions of the hierarchical view to be inconsistent with regard to classic logic of the theory of evolution, thereupon deciding that: (i) the premises have been confirmed while the contemporary synthesis is unacceptable; or (ii) that the premises are unacceptable while the contemporary synthesis is acceptable. Last, it may be assumed that, in order to explain macroevolution, a pluralist approach would be needed: an approach including all the afore-mentioned possibilities, accompanied by revising and reassessing their relative importance for particular areas concerning evolution, in this case macroevolution. Consequently, the hierarchical position questions the extrapolation explanation of macroevolution, but it does not have the strength to challenge it completely nor does it have a positive generally acknowledged or recognized positive empirical proof that would make the existence of a distinct macroevolutionary process plausible. Hereby, the hierarchical position proves the scientific nature of the extrapolation position since it points to the principal falsification of the extrapolation claim, which is a necessary element of scientific criteria (K. Popper in Logik der Forschung), but fails to refute that claim or verify claims (A. J. Ayer in Language, Truth and Logic) that would offer a better explanation of the macroevolution phenomena formation processes. Nevertheless, it is my opinion that the hierarchical position has implications for evolutionary synthesis since

⁵³ M. R. DIETRICH, 2009, o. c. p. 174.

⁵⁴ T. GRANTHAM, 1995, o. c.

it seems to indicate a weaker inconsistency within the set of assumptions in the extrapolation view, coupled with classic logic. This by no means disproves the contemporary synthesis: rather its capacity to explain one area of evolution, macroevolution, is partially weakened. This also opens the hierarchical view a new perspective in its effort towards a more precise theoretical definition of the species selection and empirical evidence, which might eventually clearly prove the existence of distinct macroevolutionary processes, playing a major role in the emergence of macroevolutionary phenomena. It would seem reasonable and rational to embrace the extrapolation view until another sub-theory succeeds in providing a better explanation of the processes underlying and governing macroevolution. The hierarchical view bears in mind the requirement to extend or revise the evolutionary theory. However, it has not yet become topical as a calling for an emergency agenda for its immediate adoption.

Conclusion

Suspecting that macroevolution is guided by a series of successful microevolutionary changes, the hierarchical position questions the extrapolation position on the process that governs macroevolution, simultaneously implying the necessity of revision or extension of evolutionary synthesis which is in line with the extrapolation view. Arguments of the two positions at the internal and external levels indicate that both positions have deficiencies: the set of premises constituting the extrapolation view is acceptable, however, now coupled with classic logic, makes that logic inconsistent and can only be saved by a change in logic, thereby becoming more weakly inconsistent, and its premises not being unambiguously proved. I therefore maintain that the hierarchical view has not succeeded in disproving the extrapolation view, being coherent to contemporary synthesis. However, it seems to have indicated a weakening in the logic coupled with the extrapolation view and evolutionary theory, as well as its inferior power when it comes to the explanation of macroevolution or indeed a hope in the possibility of its claims being proved. The two views do not represent contradictions whose claims could be simply compared because they partially include conceptual differences, requiring a type of interpretation. Here the interpretation has been based upon two critiques, with a conclusion that the hierarchical view does not as yet possess sufficient power or strength to raise questions of revising or extending evolutionary synthesis, making them emergency items on the agenda. I would be inclined to think that this would require more convincing evidence, wherefore it would seem more sensible to give advantage to the extrapolation view and a pluralist approach which derives their capacity of explanation from the authority of a well-corroborated theory, as is the evolution synthesis.

Tonći Kokić

Upravlja li makroevolucijom zaseban evolucijski proces?

Sažetak

Filozofi i biolozi nisu složni oko postojanja zasebnog makroevolucijskog procesa. Suvremeni filozofski stavovi oko ovog pitanja predstavljeni su analizom Dietrichovog i Erwinovog eseja objavljenima u zborniku Contemporary Debates in Philosophy of Biology urednika Ayale i Arpa. Suprotno naslovima eseja (mikroevolucija i makroevolucija su vođene istim procesom i mikroevolucija i makroevolucija nisu vođene istim procesom) koji upućuju na kontradiktorne stavove, razlike dvaju gledišta su fino iznijansirane. Analiza ukazuje na inkonzistentnost Dietrichovog ekstrapolacijskog gledišta koje može biti spašeno samo usklađivanjem pretpostavki standardne teorije evolucije s parakonzistentnom logikom koja ne vodi kolapsu teorije. S druge strane, Erwinovo hijerarhijsko gledište implicitno podupire postojeću logiku nadređene teorije vjerujući da je u barem jednom slučaju moguće dokazati da makroevolucija ne može biti svedena na mikroevolucijski proces. Proučavanje emergencije ukazuje na prihvatljivost tvrdnje da geografska raširenost na razini vrste predstavlja fenomen slabe emergencije koji ne može biti objašnjen svođenjem na mikroevolucijske procese. Slabost ovog tvrdnje je u manjku dovoljno uvjerljivih dokaza pa u konačnici standardno ekstrapolacijsko gledište nije osporeno.

Ključne riječi: ekstrapolacija, fenomen makroevolucije, geografska raširenost, hijerarhijsko gledište, proces makroevolucije.

Francisco AYALA and Robert ARP (eds.), *Contemporary Debates in Philosophy of Biology*, Malden, MA, Blackwell Publishing Ltd., 2009.

--- Are Macroevolution and Microevolution Governed by the same Processes? Introduction, in: Francisco AYALA and Robert ARP (eds.), *Contemporary Debates in Philosophy of Biology*, Malden, MA, Blackwell Publishing Ltd., 2009b, 165-167.

Kevin DE QUEIROZ and Michael J. DONOGHUE, Phylogenetic Systematics and the Species Problem, in: David HULL and Michael RUSE (eds.), *The Philosophy of Biology*, Oxford, Oxford University Press, 1998, 319-348.

Michael R. DIETRICH, Microevolution and Macroevolution are Governed by the Same Processes, in: Francisco AYALA and Robert ARP (eds.), *Contemporary Debates in Philosophy of Biology*, Malden, MA, USA: Blackwell Publishing Ltd, 2009, 169-179.

Theodosius DOBZHANSKY, *Genetics and the origin of species*, New York, Columbia University Press, 1937.

Douglas H. ERWIN, 2009. Microevolution and Macroevolution are Not Governed by the Same Processes, in: Francisco AYALA and Robert ARP (eds.), *Contemporary Debates in Philosophy of Biology*, Malden, MA, Blackwell Publishing Ltd, 2009, 180-193.

Douglas H. ERWIN and Robert L. ANSTEY, Speciation in the fossil record, in: Mark RIDLEY (ed), *Evolution*, New York, NY, Oxford University Press, 2004, 185-197.

Michael T. GHISELIN, A radical solution to the species problem, *Systematic Zoology*, (1974) 23, 536–544.

Richard GOLDSCHMIDT, *The Material Basis of Evolution*, New Haven CT, Yale University Press, 1940.

Stephen J. GOULD, *The Structure of Evolutionary Theory. Cambridge*, MA, Belknap Press of Harvard University Press, 2002.

--- *Punctuated Equilibrium*, Cambridge, MA, Belknap Press of Harvard University Press, 2007.

Todd GRANTHAM, Is Macroevolution more than successive rounds of macroevolution? *Paleontology*, (2007) 50, 75-85.

--- Hierarchical Approaches to Macroevolution: Recent Work on Species selection and the 'Effect Hypothesis', *Annual Review of Ecology and Systematics*, (1995) 26, 301-321.

David L. HULL, Individuality and selection, *Annual Review of Ecology and Systematics*, (1980) 11, 311–332.

--- A Matter of Individuality, in: Marc ERESHEFSKY (ed.), *The Units of Evolution*, Cambridge, MA, A Bradford Book, 1992, 293-317.

David JABLONSKI and Gene HUNT, Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: organismic versus species-level explanations, *American Naturalist*, (2006) 168, 556-564.

Bruce S. LIEBERMAN and Elisabeth S. VRBA, Stephen Jay Gould on species selection: 30 years of insight, *Paleobiology* (2005) 31 (2, Supplement) 113-121.

Jason S. ROBERT, Evo-devo, in: Michael Ruse (ed.), *The Oxford Handbook of Philosophy of Biology*, New York, NY, Oxford University Press, 2008, 291-310.

Gemma ROBBLES, Weak consistency and strong paraconsistency, *Open Access Journal for a Global Sustainable Information Society* (2009) 7, 185-193.

--- Extensions of the Basic Constructive Logic for Weak Consistency B_{Kcl} Defined with a Falsity Constant, *Logic and Logical Philosophy*, (2007) 16, 311-332.

David SEPKOSKI, *Rereading the Fosssil Record: The Growth of Paleontology as an Evolutionary Discipline*, Chicago, The University of Chicago Press, 2012.

--- Macroevolution, in: Michael RUSE (ed.), *The Oxford Handbook of Philosophy of Biology*, New York, NY, Oxford University Press, 2008, 211-237.

Maynard J. SMITH and Eörs SZATHAMÁRY, *The major transitions in evolution*, New York, NY, W. H. Freeman, 1995.

Elliott SOBER, Philosophy of Biology, Boulder, Westview Press, 2000.

Steven M. STANLEY, A theory of evolution above the species level, *Proceedings* of the National Academy of Sciences (USA), (1975) 72, 646-650.

--- Macroevolution: Pattern and process, W. H. Freeman, San Francisco, 1979.

Koji TANAKA, Francesco BERTO, Edwin MARES and Francesco PAOLI, Paraconsistency: Introduction, in: Koji TANAKA, Francesco BERTO, Edwin MARES and Francesco PAOLI (eds.), *Paraconsistency: Logic and Applications*, Dordrecht, Springer, 2013, 1-15.

Joseph TRAVIS and David N. REZNICK, Adaptation, in: Michael RUSE and Joseph TRAVIS (eds.), *Evolution: The First Four Billion Years*, Cambridge, MA, The Belknap Press of Harvard University Press, 2009, 105-131.