

UDC 575+591.3 ONTOGENY AND PHYLOGENY. TO THE PROBLEM OF THE RELATION OF INDIVIDUAL AND HISTORICAL DEVELOPMENT IN ORGANISMS

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Ontogeny and Phylogeny. To the Problem of the Relation of Individual and Historical Development in Organisms. Kovtun, M. F., Sheverdyukova, H. V. — The theory of filembriogenesis is only an introduction to the problem's development of ontogeny' and phylogeny' relation (hereinafter — «relation»). Discussions as to whether ontogeny creates phylogeny, or vice versa, are devoid of meaning. The opinion of O. Hertwig (Hertwig, 1906) that the ontogeny and phylogeny are two parallel and independent developmental processes is valid only in the first part; thesis about independence distorts the essence of «relation.» According to the authors, one of the essential characteristics of the «relation» is that ontogeny gives the material for phylogeny, and phylogeny — its differentiation, that is, creates biodiversity; that ontogeny and phylogeny can exist and function only in conjunction or in parallel, changing places (in terms of priority) in the life evolution.

Key words: ontogeny, phylogeny, relation, evolution.

Онтогенез и Филогенез. К проблеме соотношения индивидуального и исторического развития организмов. Ковтун М. Ф., Шевердюкова А. В. — Теория филоямбриогенезов представляется как введение в разработку сложной проблемы соотношения онтогенеза и филогенеза (далее по тексту — «соотношение»). Дискуссии относительно того — онтогенез творит филогенез или наоборот, лишена смысла. Мнение О. Гертвига (Hertwig, 1906), что онтогенез и филогенез — два параллельных и независимых ряда развития, справедливо лишь в первой части; тезис о независимости искажает сущность «соотношения». По мнению авторов статьи, одной из сущностных характеристик «соотношения» есть то, что онтогенезы нарабатывают материал для филогенезов, филогенезы обновляют онтогенезы, уводя их от инбридинга; что онтогенезы обеспечивают непрерывность жизни, а филогенезы — ее дифференциацию, то есть творят биоразнообразие; что онтогенезы и филогенезы могут существовать и исполнять свои функции только совместно или параллельно, меняясь местами (в плане приоритетности) в процессе эволюции жизни.

Ключевые слова: онтогенез, филогенез, соотношение, эволюция.

Introduction

One of the first, Karl von Baer (1828) was interested in connection between characteristics of developing embryo and adult animals that is known as von Baer's rules. The recapitulation rule was formulated by Fritz Müller (1864). A little later, Ernst Haeckel (1866) transformed the rule of recapitulation in the biogenetic rule, also known as the Haeckel-Müller's rule (cited by Severtsov, 1939). And the scientific foundation for the study of relationship between individual and historical development of organisms was established by Charles Darwin.

Ernst Haeckel stated in the biogenetic rule that ontogeny recapitulates phylogeny, and phylogeny is a mechanical cause of ontogeny. The biogenetic rule, as well as some Haeckel's definitions, was received by scientific community ambiguously: from complete acceptance to harsh criticism and denial. Nevertheless, according to A. N. Severtsov, the rule positively encouraged embryological studies and extensive discussions on Haeckel's generalizations. Debates about the extent of recapitulations, value of coenogeneses had escalated into a general biological problem of the relationship of individual and historical development of organisms, or the development of an individual and species evolution, or connection between ontogeny and phylogeny (surveys and review: Severtsov, 1921, 1939; Mirzoyan, 1963; Raff, Kofmen, 1986). Severtsov, along with criticism, partly exonerates the biogenetic rule, noting that regardless of the incorrectness in a whole number of Haeckel's generalizations (mainly dealing with its phylogenetic component) it has some reasonable ideas. Particularly, some dicta about recapitulations and coenogenesis could not be completely discarded. After analysis of available empirical materials (of comparative anatomy, embryology, paleontology) and critical discussion of different authors' doctrines, Severtsov expounds his vision of the problem of connection between ontogeny and phylogeny (hereinafter is used as a term "relation") and lays down so-called theory ofphylembryogenesis, where, in particular, draws attention to the complexity of the problem of "relation" (Severtsov, 1921).

It is believed that the complexity of the problem of "relations" is primarily based on the fact that it is possible really to observe and explore the only one its component, which presents an individual development or the ontogeny. For the other component (phylogeny) is only the chance to register the results of "activity" of phylogenesis, and to analyze retrospectively on the basis of paleontological records and so-called the hypothetico-deductive method (Popper, 2004). Probably this is the reason that the evolutionary biology has not much succeeded in solving the problem of "relations" since Severtsov, although the problem of the relationship of ontogeny and phylogeny in the development of life is recognized as the fundamental part of the evolutionary theory (Schmalhausen, 1982).

This study aims examination of the problem of ontogeny and phylogeny relationship with some enhancement of information database: to include time factor; evaluate the possible role of substance and energy turnover; judgments of different authors and own about ontogeny evolution; own ideas about phylogeny evolution; renew the discussion on the problem of "relation".

Theory of phylembryogenesis

According to Severtsov, phylembryogenesis are "changes (of organs — MK), related to this or that extent with evolution of adult animals and irrelevant to embryonic adaptations" (Severtsov, 1921, p. 169). In conclusions to that publication he specified: "...the phylogenetic changes in course of embryonal development, that are formed in natural correlation with changes in adult animals and at the same time are not embryonic adaptations directly, we have identified in a special category and designated by the term "phylembryogenesis" (Severtsov, 1921, p. 288). Severtsov contended that "ontogeny is a function of phylogeny".

The theory of phylembryogenesis has been discussed by Russian scientists. The most comprehensive critical and historical analysis is presented, in my opinion, in the monograph of E. N. Mirzoyan (1963) that deals with the history of this issue.

I would like to notice some features of the theory of phylembryogenesis.

First, Severtsov considers only organs (development or "alterations" of organs), but not organisms. Secondly, despite the fact that in his concept, as he stated, the time factor was introduced for the first time, "namely, the period of appearance of new characters in the individual life of animals", the moment of those characters transfer on the species level, i.e. the historical aspect of time is not discussed.

Unlikely somebody would contradict the phylogenetic significance of the embryonal deviations in development of organs, as well as the variability in the development of organs (heterochrony, heterotopy, embryonization) and results of environmental effects. However, though one or other changes in the development of organs, their anlagen, development of fertilized ovum of female of this or that species would result finally in the birth of this species.

Therefore, in my opinion, phylogenetic significance of the embryonal deviations in development of organs, both in the concept of phylembryogenesis and in the publications of other authors (especially in the pre-Severtsov period), is greatly exaggerated. On the role of ever-present mutations is known well, however, if phylogeny relied only on "promising monsters", then it is quite possible that life still was at a level of mollusks or primitive chordates. It should be noted also that focusing on embryonic changes of organs, that result in large-scale phylogeny, is in contradiction with the concept of ontogenetic equifinality (Nazarov, 1984) and the theory of functional systems (Anokhin, 1970, 1973). It seems that other authors do not exaggerate the value of embryonic changes of organs in the phylogeny. For example, M. A. Shishkin assumes that "mutation can not provide a stable effect, because any particular deviation from the normal path of development is a violation of the stability... it (mutation — MK) can not establish anything new" (Shishkin, 1988, p. 457). A. S. Rautian (2006) wrote: "...along with growth in number of getting single or short-term novelties (abrupt change of adaptive norm or trend in progressive specialization) of developing system, there is increase

in probability of stability loss, succession interruption... and destruction of evolving system".

The problem of "relations", as I consider, have to be resolved not only on the basis of when and what deviations in individual development could have a phylogenetic prospects, as well as on the basis of addressing the items of genesis and evolution of ontogeny and phylogeny, as universal and interdependent process of origin and evolution of life, origin of individuality, in particular.

Evolution of ontogeny

Ontogeny and its evolution were the subjects of study, discussions and comprehension of numerous authors. Here are referred only generalized publications and surveys (Mirzoyan, 1963; Kamshylov, 1970, 1979; Korotkova, 1979; Svetlov, 1972; Shishkin, 1981, 1988, 2012; Raff, Kofmen, 1986; Korochkin, 2002; Desnitsky, 2005; Krasilov, 2006). In general, according to cited authors, series of events on the stages of chemical and biochemical evolution of our planet had resulted in emergence of ontogeny. There are many questions and a few answers, and those are hypothetical, in discussion devoted to the evolution of ontogeny. It is likely an axiom only, that ontogeny had to evolve simultaneously with the origin and evolution of life, and to be formed with becoming of individuality.

V. I. Vernadsky (1967, 1991) supposed that life had existed originally not in the form of organisms, and as a substance of the biosphere. Amongst the trends in biosphere evolution Vernadsky specified: energy accumulation; initiation of new forms of chemical elements migration; that biogenic migration of atoms is tending to maximum; substantial increase of significance of **the living matter** in formation and regulation of the Earth surface layers. Important role he attributed to existing system of the turnover of matter and energy in the biosphere. That turnover, running away from entropy, constantly requires intensification in biogenic migration of atoms that respectively requires new forms of migration and expansion of resources used in the biosphere.

It seems that "new forms of atoms migration" could be realized by the life forms, mainly, that only able to intensify the biogenic migration of atoms (Kovtun, 2006). Of course, the stability of the turnovers (cycles) could be provided by the stable operation of their components. Stability could have components that were able to realize their unique function in the cycles during long time, persistently upgrading it in dynamic environment and the growing requirements of cycles and the biosphere as a whole.

Chemical elements, i. e. components with some "immortality", were components of those cycles on the prebiotic stage of their evolution. They had secured the stability of turnovers. However, this stability was, figuratively speaking, "dead". Attractiveness or, if you prefer, selectiveness in the components of cycles that were becoming biogenic, lied in providing their (cycles) dynamics, the occurrence of new forms of atoms' migration, the capability of steady activity increase of biogenic migration of the atoms (matter and energy), and as a result the speeding-up evolution of turnovers and the biosphere as a whole. However, process of becoming biogenic of the components of cycles unavoidably had disabled their "immortality", characteristic to their precursors. (There are known statements about some "immortality" of single-celled acaryote (Es'kov, 2000)). This implies, that the essential criterion of the process of becoming biogenic of the components of cycles was finding of mechanisms that would ensure the continuity of function in the components of turnovers that were becoming biogenic. That is to "develop" a mechanism of "propagation" with transfer of own unique inherent function in the cycle and the biosphere. That mechanism and was an ontogeny. In such a way could be represented the cause-and-effect relations that accompanied and stimulated initiation of the phenomenon that was called an ontogeny. Its final formation must have taken place with the formation of identity.

Life in a form of biosphere (Vernadsky), coenosis (Korotkov) or ecosystem (Es'kov) had some conceptual character, with a high level of heteromorphic elements that constituted those coenosis (Korotkov, 1979). Heteromorphy implies a certain hetero-functionality of elements, and that is a field of action for natural selection. Naturally to consider that under the high variability of bionts, selection could operate constructively according to some key points (criterions) or objectives. "Criterions", apparently, were specified by the requirements of biotic turnover of matter and energy. Selection had to work, i. e. "for hire" in the cycle, by screening bionts and then individuals for required, at that time, functional and biochemical characters, which were able to satisfy increasing biogenic migration of the atoms and the occurrence of new forms of migration of chemical elements. Realizing the selection of individuals, process of selection simultaneously picked out the mechanisms for transfer of those characters to descendants, by improving them. While reviewing the evolution of ontogeny, I have suggested consider it in two ways: as a phenomenon and as a process (Kovtun, 2013). Ontogeny as a phenomenon was formed under the process of becoming biogenic of the components of turnovers and formation of identity. Further evolution of ontogeny and increasing diversity of ontogenesis were developing through the improvement and modification of its implementing morphogenesis; i. e. that part of the ontogeny, which I entitle the process.

To summarize the evolution of ontogeny, I come to the conclusion, that the matter and energy turnover is one of the leading founders of ontogenesis (as a phenomenon and a process). Natural selection was a tool along with this.

Evolution of phylogeny

The ontogeny evolution is considered in numerous publications and by different authors, while the phylogeny on the contrary is out of attention of evolutionists. (V. A. Krasilov (2006) supposes that such area of investigations is monopolized by molecular phylogeny at present). Paleontologists have formulated over a hundred of so-called laws of evolution in the last half a century (Rautian, 2006). A. S. Rautian (2006; p. 21) observes: "It is difficult to adduce more uncertain area of the theory of evolution than the doctrine of the laws of phylogeny".

Thus it seems logical to raise a question: is it competent to talk about evolution of phylogeny, and if so, what is its nature? It is impossible to avoid also the issue on the genesis of phylogeny.

Arrangement of events related to biological changes of components involved in turnovers of matter and energy, formation of individuality that are presented briefly above, provides the priority to ontogeny, in terms of the time of genesis. However it is assumed theoretically that those phenomena should appear and develop simultaneously. (I dare say that phylogeny, like ontogeny, should also be regarded as a phenomenon and as a process).

In general, reproduction of kin could not be unlimited because nature abhors a vacuum as well as uniformity. Competitive relationships in homogeneous environment (of organisms) sooner or later result in the differentiation of uniformity, and if it does not occur, — to its elimination (inbreeding). Differentiation of uniformity and is the start of the phenomenon, named phylogeny (the terms "phylogeny" and "ontogeny" were introduced by Ernst Haeckel).

Some traces or antecedent of the phylogeny start, as well as the ontogeny, can be found in probiotic and pre-individual period of life development. Formalizing concepts we proceed from the assumption that the phylogeny can be identified as division, split, branching of something much bigger or complex onto less bigger or complex, and that take place by operation of physical-chemical laws. For example, the same coacervate drops, having enlarged the mass and the size to critical level, are splitting into several drops. The latter ones, in turn, increase their mass (pass the way of parent drop) and then split. There is an analogy: mass increasing is an ontogeny; fission and splitting are a phylogeny.

If we accept the thesis that the differentiation of uniformity is the main characteristic and objective of phylogeny, then we can unambiguously define the evolutionary trends for this phenomenon, — those are seeking, development and enhancement of methods or mechanisms for differentiation. Most probably in evolution the phylogeny has developed two basic mechanisms of differentiation: divergence and adaptive radiation (the term of Henry Osborn).

Nevertheless, unambiguously to judge about the evolution of phylogeny is impossible. Phylogeny as a phenomenon originated under the pressure and control of environmental factors, known nature laws and phenomena: the trend to increase the number of organisms; and as a result — growth of competition for food, refuges, territory, etc.; variability is the universal

attribute of nature; existence of potentially unoccupied ecological niches; inherent tendency of organisms to relocations (migrations), and also nature abhors a homogeny. Mechanisms of differentiation have started at the same time with the phylogeny and under the same factors. In this sense the terms "phylogeny" and "differentiation" can be equated and interpreted as synonyms, per se. Possible also to assume that evolution of the phylogeny was realized through enhancement (evolution) of differentiation mechanisms in parent groups of animals onto several sister's groups, with isolation and with prospects of speciation, and such "mechanisms" were, originally, divergence, and then adaptive radiation. However, there are not any persuasive arguments and facts for the discussion on further evolution of the mechanisms of branching or differentiation, and therefore, on evolution of the phylogeny as a phenomenon. It seems they had become optimized, at least in the Paleozoic period, that concurred with the activation of speciation and the leap forward of biodiversity (Shklovsky, 1987).

To summarize this section, we conclude that the main result of the evolution of phylogeny was finding a method and a mechanism of branching or phylogenetic divergence, and processes known as "adaptive radiation." If the main objective of the ontogeny is reproduction, the main objective of the phylogeny is biodiversity through adaptive radiation of the products of ontogeny.

Some aspects of ontogeny and phylogeny relations

Contemporaries of Haeckel and Severtsov had different opinions on meaning of ontogeny and phylogeny interaction: from formulation of ontogeny as recapitulation of phylogeny (Haeckel and his followers), up to opposite views that ontogeny does not recapitulate phylogeny, but alternatively induce it (Garstang, 1922). Besides there were other concepts: according to O. Hertwig (1906) ontogeny and phylogeny are two parallel and independent types of development; D. Sobolev (1924) considered that ontogeny did not recapitulate phylogeny, though, ontogeny and phylogeny (both) followed the same laws (cited by Mirzoyan, 1963). It seems to me that despite the difference of opinions and definitions, each of them has some element of truth.

According to the above, a component of the complex problem of "relations" can be formulated.

Ontogeny produces initial material and constitutes framework for phylogeny; phylogeny renews ontogeny. Such a periodicity in "relations" is maintained during the whole evolution of life.

Why was applied the definition "phylogeny renews ontogeny"? It was because phylogeny did not set up ontogeny. It has been already provided by nature (evolution) during the process of becoming biogenic of the components involved in the turnover of matter and energy. And it is not evolved (as a result of differentiation-phylogeny) in each new group of organisms, and it might be renewed or modified according established morphogenesis (heterochrony, heterotopy; alteration, reduction or extension of stages; coenogenesis and phylembryogenesis, etc.).

Ontogeny also does not set up phylogeny. This phenomenon is also the product of nature (nature abhors a vacuum and uniformity), though based on ontogeny results and the laws of nature. Above judgment is semantically close to the concepts of Hertwig and Sobolev.

It is worth attention the other definition of Haeckel, noticed by Severtsov (1939): phylogeny is a mechanical factor of ontogeny. At the same time from my point of view, the phylogeny is rather more a "mechanical" consequence of ontogeny.

Division is a fundamental and general mechanism of ontogeny and phylogeny, at least on the initial stages. The embryonic fission (cleavage) differs from the division in phylogeny (branching), however, they are similar inherently, as both resulted in differentiation of: cells in the first case and groups of organisms in the second case. Results of the first one are individuals, results of the second one are populations, subspecies, species.

Some other similarities and distinctions. Embryonic fission starts from zygote in prenatal ontogeny; resulted in multiply of the number of cells, their differentiation, concentration, migration, specialization, gastrulation, germinal layers formation, organogenesis... in the organism. The engine is morphogenesis.

Organisms are objects of phylogeny, more correctly, groups of organisms (females and males), i. e. results (products) of ontogeny. The engine is branching of larger groups (parental) into several smaller ones (sister) with maintenance of genotypes.

Preparedness for ovicell cleavage is determined by its maturation and fertilization; preparedness for branching in a group of organisms is probably stipulated by reaching a certain critical abundance of individuals or their biomass on a certain territory. Further on everything follows according to established laws. Abundance, to a considerable extent, depends on the efficiency or productivity of reproduction of individuals that inhabit the territory. In other words, it depends on productivity of ontogenesis (ontogeny) in the community. Quite possible presence of correlation between productivity of ontogeny and the rate of differentiation of groups (phylogeny): the greater the abundance of reproduced individuals (progenies) for some period (season, several seasons, some years or centuries...) on a limited territory occupied by a given population or species, the more likely a requirement for differentiation of community and the higher rate of expansion; the more different life conditions in the sister phyla and criteria for isolation appear, the faster speciation. Hence follows another component of the problem of "relations": phylogeny depends on the progress and productivity of ontogeny; in turn it supports productivity by renewal of ontogeny. Such "renewal" might ultimately result in a divergence of ontogeny that enhances productivity of ontogeny and expands the field of activity of phylogeny.

However, relationship of ontogeny and phylogeny does not always run so smoothly. It might be a species differentiation of terrestrial and aquatic organisms, and more specific the imbalance in species abundance of land and ocean inhabitants on the one hand, and their biomass on the other hand. Thus, from the total number of species of animals and microorganisms that inhabit the planet Earth, 93 % of species are terrestrial and 7 % of species are aquatic; regarding biomass (dry matter) the share percentage of terrestrial organisms is barely only 0.8 %, whereas the share of marine organisms is 93.7 % (cited by Kartashov, 1975; Shklovsky, 1987). It looks like phylogeny makes no progress (by the species abundance) in the aquatic environment, while ontogeny is functioning successfully (by the biomass). Does this not contradict the stated above, and specifically the thesis that phylogeny renews ontogeny? If rely on fish species with high reproductive potential, regardless some specific detals of differentiation, the basics of the "relations" are preserved: the differentiation is active but up to the level of populations. Vast areas of oceans, which surface is twice as much as the surface of earth, support the expansion; and certain uniformity of the aquatic environment (by comparison with earth) is unfavourable for the reproductive (and other types) isolation, and hence for active speciation. At the same time in reproductive period, populations congregate in huge flocks, where the exchange of gene pool occurs, and therefore ontogeny renews. Thus, coordination of ontogeny and phylogeny is preserved, but in terms of speciation and "relations", it takes place the manifestation of environmental factors and their variability. Those factors are much more diverse and variable on the continents.

It should be specified one more factor that corrects "relations", and it is an ethological lability of organisms and their level of organization. As far back as M. M. Kamshylov (1972) has noted that the loss of simplicity in organization increases the efficiency of information reception from environment and "competence" in its application. Therefore, it should be added activity and "mentality" of figurants involved in the process by themselves, among other factors that have an impact on "relations" and differentiation of species in particular. Members of the order of rodents are an example: out of 3.5 thousand species of mammals 2.5 thousand (78.2 %) are rodents.

Impossible to ignore that in a certain historical period of life evolution (before venturing onto land in the Cambrian period, 550 million years ago) speciation in the aquatic environment was intensive. According to paleontology data, there were more than a thousand species only of trilobites (extinct at present); ocean waters teemed with the Cambrian echinoderms and mollusks, appeared vertebrates, there were more than 500 species of fish. Appreciable differentiation of the species on land was observed in the Mesozoic era, simultaneously with decrease of this process in the hydrosphere (Kamshylov, 1975). What are the factors of decrease of the differentiating function of phylogeny in aquatic environment and high activity on land?

It seems that resources of phylogeny are limited (according to the conservation law in original, Lomonosov's interpretation: if in one place occurs decrease, then in another one it would increase).

There is not much sedition (controversy) in such supposition; in fact almost all is limited in nature. Scales of variability, diversity, evolutionary pathways, reproduction are limited, i. e. factors and phenomena about the same rank with the phylogeny.

However, this problem is too controversial and requires a special study and discussion.

Conclusions

Interrelationship and interdependence of individual and historical development of organisms can not be in question, as the fact that in some historical periods of the life evolution, crises could have arisen in those relations. But if such situations occurred, the life (its evolution) surmounted them, though through larger or lesser losses, revitalized and more stable. All of those events could not take place spontaneously. The question arose about controlling and regulating authority. It seems that such authority was biotic turnover of matter and energy flows, and simultaneously being formed biosphere. Formation of the biosphere and biotic turnover, according to I. S. Shklovsky refers to the Proterozoic era (2600–1600 Ma), when the life becomes a cosmic factor. However, only in the Paleozoic era (550–250 Ma) is registered a rapid development of life and its diversity (Shklovsky, 1987). Thus, more than a billion years was required for evolution, grinding, relative stability and dynamics in relations between individual development and evolution of species (ontogeny and phylogeny).

As have been mentioned, the scientific foundation of the problem of relationship between individual and historical development of organisms was established by Darwin, and Haeckel drew to it worldwide attention. Severtsov stated and published fundamentals of thephylembryogenesis theory in 1912, and after 9 years of work he had understood the extreme complexity of the problem of "relations": "...I do not suppose that issue of relations between ontogeny and evolution is limited to those facts and reasons, which are outlined in the study: it is much more complex, and its investigations just are launched "(Severtsov, 1921, p. 291). It seems to me that the problem of "relations" is much more difficult than has been presented by Severtsov, and that "phylembryogenesis" are only one of the components of the whole problem.

Summing the presented arguments, it is worth to consider other inferences that to some extent reflect various aspects of "relations".

Phenomena of ontogeny and phylogeny are so close and correlated that it is impossible to set a preference to one of them: without ontogeny would not be phylogeny and ontogeny would exhaust (inbreeding) without phylogeny.

Origin and evolution of ontogeny and phylogeny are inherently linked with origin and evolution of the biosphere and with the process of becoming biogenic of the components of matter and energy turnover.

Ontogeny is accumulating initial material for phylogeny, and phylogeny renews ontogeny, leading it away from inbreeding.

Phylogenetic differentiation or branching of maternal group of organisms onto sister groups depends on the productivity of ontogeny; each sister group of organisms also has renewal of ontogeny.

The main result of the phylogeny evolution is the acquisition of the method or mechanism of differentiation in homogeneous groups of organisms on the sister groups (branches) by means of phylogenetic divergence or by adaptive radiation.

Ontogeny is mainly governed by morphogenetic factors, and phylogeny is governed by epigenetic ones.

Aromorphic groups are mainly going upon the path of adaptive radiation according to Severtsov, and one of the sisterly branches might become aromorphic as a result of adaptive radiation.

Concepts of the succession in development, induction, ontogenetic equifinality... call for restraint in assessing the phylogenetic potential and prospects of deviations in the development of organs in embryogenesis (but not denial!), as well as possibilities of largescale change of the process of embryogenesis.

If the main objective or function of ontogeny is reproduction (propagation), the main objective of phylogeny is an establishment of biodiversity by means of adaptive radiation of the products of ontogeny.

All stated above adduce to the main conclusion that one of the essential characteristics of the relationship between individual and historical development (development of individuals and species evolution; ontogeny and phylogeny) is that ontogeny provides the continuity of life, and phylogeny supports its differentiation or diversity (biodiversity) and renewal of ontogeny. Both phenomena could not exist one without the other, as life and its evolution would have been impossible.

References

- Anokhin, P. K. 1970. The theory of functional systems. *Advancements of Physiological Science*, **1** (1), 19–54 [In Russian].
- Anokhin, P. K. 1973. Fundamental issues of the general theory of functional systems. *Principles of the system organization functions*. Nauka, Moscow, 5–61 [In Russian].
- Desnitsky, A. G. 2005. Evolutionary transformations of sea urchins ontogeny. Ontogeny, **36** (3), 182–189 [In Russian].
- Es'kov, K. Yu. 2000. History of the Earth and life on it. MIROS, Moscow, 1-351 [In Russian].
- Kamshylov, M. M. 1970. Biotic cycle. Nauka, Moscow, 1-160 [In Russian].
- Kamshylov, M. M. 1979. Evolution of Biosphere. Nauka, Moscow, 1-256 [In Russian].
- Korotkova, G. P. 1979. Origin and evolution of ontogeny. Izdatelstvo Leningradskogo universiteta, Leningrad, 1–282 [In Russian].
- Korochkin, L. I. 2002. Ontogeny, evolution and genes. Nature, 7, 1-12 [In Russian].
- Kovtun, M. F. 2006. Causes and Factors of Evolution from the Positions of the System Approach (Biosphere as an Arena of Evolutionary Processes). *Vestnik Zoologii*, **40** (6), 483–495 [In Russian].
- Kovtun, M. F. 2013. Ontogeny: the phenomenon and the process (to the problem of ontogeny evolution). *Vestnik Zoologii*, **47** (3), 195–204.
- Krasilov, V. A. 2006. Paleontology and paradigms of modern natural history. *In: Evolution of Biosphere and Biodiversity*. KMK, Moscow, 7–19 [In Russian].
- Mirzoyan, E. N. 1963. *Individual development (ontogeny) and evolution*. Academy of Sciences of the USSR, Moscow, 1–302 [In Russian].
- Nazarov, V. I. 1984. Finalism in modern evolutionary theory. Nauka, Moscow, 1-285 [In Russian].
- Popper, K. R. 2004. Logic of scientific research. Respublika, Moscow, 1–447 [In Russian].
- Raff, R., Kofmen, T. 1986. Embryos, genes and evolution. Mir, Moscow, 1-402 [In Russian].
- Rautian, A. S. 2006. The assemblage (bouquet) of evolution laws. *In: Evolution of the biosphere and biodiversity*. KMK, Moscow, 20–38 [In Russian].
- Schmalhausen, I. I. 1982, Selected Publications. Nauka, Moscow, 1-382 [In Russian].
- Schmalhausen, I. I. 1983. Selected Publications. Nauka, Moscow, 1–360 [In Russian].
- Severtsov, A. N. 1921. *Studies on the theory of evolution: Individual development and evolution.* State publishing house of the RSFSR, Berlin, 1–312 p. [In Russian].
- Severtsov, A. N. 1939. *Morphological patterns of evolution*. Academy of Sciences of the USSR, Moscow, Leningrad, 1–610 [In Russian].
- Shishkin, M. A. 1981. Patterns of ontogeny evolution. Journal of General Biology, 42 (1), 38-54 [In Russian].
- Shishkin, M.A. 1988. Evolution as epigenetic process. *In*: Menner, V. V., Macridin, V. P., eds. *Modern Paleontology*. Nedra Press, Moscow, vol. 2, 142–169 [In Russian].
- Shishkin M. A. 1988. Regularities in evolution of ontogeny. *In*: Menner, V. V., Macridin, V. P., eds. *Modern Paleontology*. Nedra Press, Moscow, vol. 2, 169–209 [In Russian].
- Shishkin, M. A. 2012. System-defined morphogenesis and its display in the fossil record. *Paleontological Journal*, **4**, 3–15 [In Russian].
- Shklovsky, I. S. 1987. Universe, life, intellect. Nauka, Moscow, 1-320 [In Russian].
- Svetlov, P. G. 1972. Ontogeny as a vectored (teleonomic) process. *Archive of Anatomy, Histology, Embryology*, **36** (8), 5–16 [In Russian].
- Vernadsky, V. I. 1967. The Biosphere. Nauka, Moscow, 1-376 [In Russian].
- Vernadsky, V. I. 1991. Scientific thought as a planetary phenomenon. Nauka, Moscow, 1–271 [In Russian].
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