

# Philosophy of Evolutionary Biology

A. P. Rasnitsyn\*

*Borisiak Paleontological Institute, Russian Academy of Sciences, Moscow, 117647 Russia*

*\*e-mail: alex.rasnitsyn@gmail.com*

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**Abstract**—Cognition is not a process of mastering truths, i.e., grains of ultimate knowledge. Even in the details, cognition only allows us to get closer to the ultimate truth, not to reach it. Consequently, the real tool of knowledge is not a proof, but a presumption. The latter refers to a certain decision that was successfully established in the past in an appropriate context and therefore can be taken without additional proofs, though only in the absence of serious contradictory evidence. Two paradigms compete within the framework of modern evolutionary biology, i.e., the dominant cladistic paradigm and the often disregarded but indestructible phyletic paradigm, which grew from the traditional view on systematics and evolution. Cladistics corresponds to the genetic (=population-genetic, “synthetic”) theory of evolution, whereas phyletics corresponds to the holistic (=“epigenetic”) one. The cladistic paradigm seemingly offers a strict procedure of objective analysis, but its prerequisites, such as the mandatory dichotomy of a particular phylum combined with the simultaneous disappearance of an ancestor, which disregards the possibility of speciation without divergence, are hardly consistent with the real order of things, and unavoidable sources of subjectivity are also usually ignored. The holistic paradigm does not represent a less clear procedure, but a more complex protocol of analysis, since it not only recognizes the unavoidable elements of subjectivity but also explicitly introduces them into the research protocol as a choice between the conflicting presumptions. Phyletics, as part of the holistic paradigm, provides taxonomic and phylogenetic schemes that are stabler in the long run, and the holistic theory of evolution, together with the adaptive compromise metaphor derived from it, can explain many evolutionary phenomena that are incompatible with the genetic (“synthetic”) theory of evolution, such as the discrete nature of biological diversity, the fundamental nonuniformity of the evolutionary process, and the paradox of the inverse correlation between the evolutionary rate and level of organization, e.g., the highest and lowest rates of the evolution of large mammals and microorganisms, respectively.

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## INTRODUCTION

In this work, I would like to present my vision of the most general problems and tasks of evolutionary biology, which is understood as the study of objects of the organismic level in the context of their evolution and diversification (the formation of biological diversity). Therefore, the reader will not find an overview of the opinions of other researchers here: only what is needed to clarify the author’s standpoint is cited. I see the justification for this approach in the fact that my views are very different from the views characteristic of the majority of colleagues and, judging by the experience of a fairly long life in science, many seem odious. However, I still have not heard any serious arguments against the views that I have formulated. I must also admit in advance that I in no way pretend to be a professional in the field of philosophy: I am sure that many of my statements will seem naive, or even erroneous, to a professional. The justification for my courage may be the fact that I am writing not for philosophers but for biologists. However, it would be very important for me to hear the opinion of a philosopher.

The main questions that life asks us are *what* and *how*, because the no-less important questions—*where*, *when*, *why*, and *wherefore*—are meaningful only when we have decided *what* we want (to know, do, or have) and *how* we intend to achieve it. *What* is the subject of ontology, and *how* is the subject of epistemology (the theory of knowledge). In science with ontology, it is clear in the most general form: we want to *know*. To know what is the real order of things. To know everything and for sure. The problems arise in details, which will be discussed later. The question of *how* we obtain knowledge, how complete and accurate it can be, requires discussion from the very beginning.

## SCIENTIFIC METHODOLOGY

In daily work, a scientist usually does not focus on its methodological foundations. However, when familiar standards and methods begin to fail or simply cease to satisfy us, it is tempting to create something like a scientific revolution (Kuhn, 1970): to discard the routine methods and standards, along with the methodology on which they are based, and to replace all of

it with something else. Revolutions, even scientific ones, rarely pass bloodlessly, in the sense that they discard approaches that are still quite workable, albeit in a slightly different context, and the results that are significant but require rethinking. Therefore, it is preferable to reanalyze the methodological foundations of scientific activity in the hope of identifying and fixing weak points, thereby preserving both the approach itself and the bulk of the results obtained with its use.

Two main approaches—deductive and inductive—have long been distinguished; another hypothetical-deductive method associated with the name of Karl Popper was added to them relatively recently (less than a century ago). Roughly speaking, we can say that, in the case of the deductive approach, the scientist proceeds from some system of postulates that are accepted as true and, in a strictly logical way, deduces the consequences from them, which, for the same reason, are accepted as true. In the case of the inductive approach, the scientist draws conclusions from observations (“facts”) rather than from postulates and, being confident in the truth of these facts, also considers the conclusions to be true, i.e., they describe the actual state of things (what is “in reality”).

This difference does not seem fundamental to me, since the postulates are not a “stab in the dark” but are formulated, albeit from general considerations, such that the results of their application are compatible with experience, with the real order of things. That is, deduction is also observation-oriented and thus relies on induction to various degrees. Conversely, in the case of induction, the results of observations are generalized in the form of inferences about the nature of things, which are already used as postulates in further reflections. This similarity allows the use of the deductive and inductive methods as a unified approach aimed at the comprehension of truth as the purpose of cognition.

The hypothetical-deductive method is just the opposite. It postulates that any conclusions made on whatever basis (observations, postulates, or any other generalizations) remain hypotheses, i.e., inferences that require mandatory testing. A hypothesis in principle cannot be verified, i.e., its fairness (truth) cannot be proven once and for all. As we will see, it cannot be rejected once and for all either; one can only make a decision about its adequacy or inadequacy in terms of the available data, i.e., about the possibility or undesirability of reliance on it for further cognitive or other activities. Thus, the hypothetical-deductive method, which is now recognized as the most appropriate for real cognitive processes, is aimed not at comprehension but at an approach to the truth that uses effective methods of cognition.

In accordance with the hypothetical-deductive method, each step (cycle) of cognition, in my opinion, includes six successive stages.

- Based on previous experience and knowledge, we set a task and plan observations.

- We then conduct observations (and/or perform an experiment) and analyze the results, distinguishing new, not yet understood elements in the resulting pattern.

- Based on general experience and the results of previous knowledge of similar objects, we distinguish the features and elements in the resulting pattern that seem to be the most important. The features and elements that are, we assume, most closely associated with the structure of our pattern allow us to understand and foresee its behavior in different circumstances. For example, when a taxonomist discovers an absolutely new group of insects and begins to classify them (create an internal system of the group), knowledge of the existence and possible differences of sexes and stages of ontogeny will allow the exclusion of characteristics that distinguish males and females, adults and larvae, etc., from the number of taxonomically important characteristics, no matter how profound these differences are themselves.

- This is where the fourth stage begins. We hypothesize about a special similarity between the studied pattern and some class of patterns studied earlier. The hypothesis must be prognostic, i.e., it should point to the particular mechanism responsible for the observed similarity or predict similarity in many other characteristics. This will allow us to make a further assumption about the behavior of our pattern (system, aggregate of objects and phenomena) in various conditions and circumstances. Returning to the previous example, the taxonomist hypothesizes, for example, that structural similarity indicates a higher (say, generic) level of general similarity, whereas coloration belongs to a lower (e.g., species) level. In other words, the taxonomist suggests that such a hypothesis will allow the insect group to be classified in a more natural way than an alternative approach (e.g., one that give more weight to the coloration characteristics).

The four previous stages of cognition strongly depend on the personal experience and intuition of the researcher. Their formal cognitive structure is not yet clear, and I will not discuss them in detail.

- The fifth stage is the testing of the proposed hypotheses for which the longest and most branched chains of consequences are derived from the hypotheses. These consequences (predictions) are compared with the results of observations and experiments (see below for more detail).

- The sixth and final stage is the decision as to whether each of the proposed hypotheses is acceptable based on the test results and whether they should be kept for further testing or should be rejected. Examples and discussion are below.

Since the time of Karl Popper (2005), it has been known that all results of scientific research are nothing more than hypotheses that cannot be finally con-

firmed (verified). One can hope that a hypothesis is open to final refutation (falsification); however, this is also not the case, because the final falsification is at the same time the final verification of an alternative hypothesis that the falsifying result is neither an accident, nor the result of the action of unaccounted factors and circumstances (e.g., Lakatos, 2003, p. 51; Popper, 2005, p. 47). If you postulate that all swans are white and you are presented with a black one, then, before refuting your hypothesis, you should attempt to reject at least two other possibilities: first, that this is not a swan (but, for example, a goose, or a clever fake, or something else like that) and, second, that the swan is not truly black (for example, it has been artificially colored). In my opinion, these alternative possibilities are always evaluated in terms of probability (likelihood) and not as simple “yes” or “no” answer. That is why the sixth stage of cognition is required: the comparison of competing hypotheses and decisions based on the evaluation of alternative falsifying evidence.

According to the proposed interpretation of the hypothetical-deductive method, all of our knowledge is a mountain of hypotheses based on one another, and this mountain is oriented top down, because the basic hypotheses are scanty, whereas the partial ones based on them are an abyss. The trouble is also that our usual analytical tools do not correspond to the material that they are intended to operate on: they are focused on the search for truth rather than on the manipulation of hypotheses. *Proofs* are based on postulates that are regarded true. However, even in mathematics, these basic postulates can be disputed, and they can be not found at all in our biology. *Laws*, as empirical generalizations of a high degree of reliability, are not so reliable, even such fundamental ones as the laws of conservation of matter and energy. And our evolutionary laws, such as those on biogenetic evolution, irreversibility, or a nonspecialized ancestor, are poorly reliable.

*Explanation* is also not the best tool for the penetration of the nature of things. Explanation brings observable phenomena into a general context. However, the way in which a fact is consistently brought into context is not necessarily unique; this also applies to the context itself. It is no coincidence that the same evolutionary phenomena are explained (often with approximately equal success) by selectionists, Lamarckians, and theologians. In fact, Popper developed the falsificationist concept starting from his Freudian experience, when he was convinced that there was no (and, most importantly, it was impossible to imagine) a situation that could not be successfully explained within the framework of psychoanalysis. On this basis, he refused to accept Freudianism, as well as Marxism and Darwinism, as science. Whether his assessment is fair is a separate question. I think Popper was wrong, because, in accordance with his concept of falsificationism, he meant *experimentum crucis*—a decisive experiment that alone must falsify the entire

corresponding system of views and thereby give the final answer to the posed question. However, this is impossible, just as the final falsification of a hypothesis is impossible.

Thus, it turns out that we possess only very unreliable knowledge and inadequate tools for work with it. However, something is clearly wrong in this pessimistic conclusion: if it were true, then science would not have achieved even a hundredth of what it has achieved. In everyday life, truth is even less accessible to us than in science, and the problems faced there require much more responsibility, when the cost of a mistake is one's own life and sometimes the lives of many other people. Nevertheless, we generally solve these problems successfully enough to survive with our negligible reproductive potential.

This means that we still have adequate tools and actively use them, but we are not aware of this, as Monsieur Jourdain did not guess that he was speaking in prose. The lawyers managed to pull the sought-for tool from the subconscious long time ago, but even they did not suspect its universal significance. This tool, in my opinion, is presumption (Rasnitsyn, 1988). Its paradigmatic version (a sample against which all other presumptions can be verified (in our terms, a type specimen)) is, of course, the presumption of innocence: “No matter how heavy the suspicion is, the suspect must be considered innocent as long as and since his guilt is not proven properly.” What is “properly” is a separate and very important question, and we will have to return to it. In all other aspects, all presumptions are structured in the same way: for a certain class of problems, the presumption offers a type solution that should be taken regardless of whether or not there is evidence in its favor, provided that there is no reliable evidence against this decision. An example is reputation: if a person has proven himself well, his words and actions should be treated with trust (if not well, then with distrust), *unless there are serious reasons to estimate them in another way*.

Here are some examples of presumptions from our field. The sequence of deposition layers should be interpreted as a temporal sequence of strata, as long as and since there is no reliable evidence to the contrary. Homotaxal (of similar taxonomic composition) fossil assemblages should be considered geologically synchronous unless there are serious counterarguments for this. Any taxon should be considered monophyletic (descending from the parent taxon in one ancestral lineage) if there is no convincing evidence of its polyphyly. The similarity of organisms should be considered inherited until reliable arguments for its multiple origins are presented. The ontogenetic sequence of changes in the organism should be interpreted as evolutionary unless there is sufficient reason to interpret it in a different way. In general, you should not multiply entities unnecessarily (“Occam’s razor”), i.e., make

the simplest decisions until and since there is no good reason to make more complex ones.

A more detailed analysis of the system of presumptions used in the field of evolutionary biology called phylogenetics (the study of relationships between groups of organisms) has been given in other studies (Rasnitsyn, 1988, 1996, 2002, 2006; Zherikhin et al., 2008).

I would like to draw your attention here to the fact that a presumption, in fact, is a concentrated experience of successful solutions to specific problems. For example, it is normally more hazardous for the health of society to condemn an innocent person than to leave a criminal free. The normal sequence of geological layers is more common than the reverse. On a geological time scale, migrations are usually instantaneous, and significant asynchrony of fossil complexes similar in composition is rare. Demonstrable polyphyly of a taxon is not a very common situation, especially in higher organisms. The coincidence, as a first approximation, of ontogenetic and paleontological sequences is really striking in many cases, etc. Nevertheless, there are always exceptions, and sometimes there are so many of them that the applicability of presumption is significantly limited. According to G.A. Zavarzin (1987; see also Woese, 1987), the similarity of microorganisms (except for the primary DNA structure) is more often acquired independently than inherited, and the corresponding presumption does not apply to them. In Quaternary paleontology with its fractional chronometry, the demonstrable asynchrony of homotaxal complexes is often explained precisely by migration. Soviet society was organized in such a way that its health was rather supported by the presumption of guilt (i.e., in reality, justice was administered not by the court but by the investigation, the legal instrument of which is the presumption of guilt), etc.

Even for this reason, one should not analyze presumptions in terms of truth or suitability *in general*: one can only say that a given presumption works well in the given context, and its alternative is successfully applied in some other cases. It should also be borne in mind that different presumptions can be applied simultaneously to solve the same problem, and the solutions recommended by them may be incompatible. For example, regarding the evolutionary sequence of changes in a certain structure (which is the problem of the polarization of a characteristic in phylogenetic terminology), important information can be provided by paleontological and ontogenetic sequences, the nature of the distribution of different states of a characteristic in the studied population and beyond, the complexity and degree of the functional perfection of different variants of this structure, the presence of rudiments, etc. Each of these approaches has its own presumptions, and the results of their application to a specific problem often contradict each other. For example, many characteristics of the skull of an adult

human correspond to the embryonic characteristics of apes, whereas in our ontogeny there are no corresponding characteristics of adult apes; i.e., the biogenetic presumption indicates the origin of apes from humans. On the contrary, in the fossil record, skulls of humans appear much later than those of apes, which indicates the opposite course of events.

In this particular example, the solution is quite obvious: the human skull re-acquired embryonic features as a result of a relative slowdown of the corresponding ontogenetic processes; however, such clarity may be absent in other cases. Experience, intuition, and art, in general, are required to answering the question of whether the paleontological sequence is a very serious counterargument that renders a biogenetic presumption unacceptable or, on the contrary, whether the ontogenetic data do not allow one to follow the paleontological presumption.

Of course, this is where presumptions come to one's aid. For example, if there are several independent sources of phylogenetic information that provide conflicting instructions, the indications of the majority of obtained evidence should be followed. Indeed, it is in full agreement with the paleontological presumption that a number of other human organs (primarily, the brain, but also phialine lips, sharply differentiated hair, etc.) have a rather pronounced advanced (apomorphic) character. The primary structure of DNA also brings humans close, not to humanoids in general, but exclusively to chimpanzees. This again contradicts the biogenetic presumption, which assumes that humans are close to the roots of all anthropoids rather than to chimpanzees alone. However, the opinion of the majority cannot always be considered a kind of "voice of God": when the sources of information that have showed themselves to be particularly reliable are in the minority, they must be followed, contrary to the instructions of the majority. If we begin to understand further, we will find more reservations.

It can be easily seen that the use of presumptions is not an easy matter; it always requires experience, intuition, and courage, since the risk of error is never negligible. But life and, furthermore, science is like that and, therefore, I cannot imagine any other means of cognition.

## METHODOLOGY FOR THE SYSTEMATIZATION OF KNOWLEDGE

Cognition is possible only if the acquired knowledge is systematized; otherwise, the cognizing subject will instantly drown in the mass of unsystematized information. Systematization is undoubtedly an obligatory method of cognition, and the nature of the used system (the knowledge systematization algorithm) turns out to be fundamentally important.

Although the methods of knowledge systematization are infinitely diverse, two main approaches (which, of course, do not exclude each other) can be apparently distinguished. We can approach this diversity using a certain a priori logical scheme. For example, using some characteristics that are important for us in some way, we will divide animals into large and small, terrestrial and aquatic, useful and harmful. In contrast, relying as much as possible on a complete set of characteristics, we can also trace the boundaries (hiatuses, gaps) between the groups of objects to be systematized, distinguishing thus outlined groupings as taxa of our system. Wingless kiwis will be considered birds, hairless whales and oviparous platypuses will be considered mammals, saccular sacculin will be considered crayfish, etc., simply because each of them, in terms of the aggregate of characteristics, is closer to the typical representatives of their group. In the first case, we *impose our system* on the existing diversity; in the second case, we attempt to *identify the immanent structure of the group* and reflect it with the resulting system. In the first case, with the *logical division* of diversity, the resulting groups (taxa) will be uniquely defined by the corresponding characteristics and will be called classes. In the second case, *when the boundaries are traced*, taxa are unambiguously determined by hiatuses and correspond to the definition of a continuum (Ponomarenko and Rasnitsyn, 1971; Zherikhin et al., 2008). The first approach is associated with the name of Procrustes, who, as we know, adjusted the size of the guest to the size of his bed using a knife and rope. The second approach is associated with the names of Plato (objects should be separated, i.e., cut along their natural joints) and Linnaeus (the genus determines the characteristic, but the characteristic does not determines the genus; i.e., we first distinguish groups and then look for the characteristics that mark them; for more detail, see Rasnitsyn, 2013a). Although the taxa in reality usually combine the characteristics of class and continuum, the distinction between these terms is fundamentally important.

Taxonomic classification as a cognitive tool organizes our knowledge of biological diversity in such a way as to facilitate our interaction with this diversity. There are many forms of classification created for specific purposes and specific categories of users (e.g., the life-form system or the system of pests, which is based on the characteristics of the harm they cause). They do not pose significant theoretical problems, and here we will only talk about the system that is used as an interdisciplinary language and claims to be of general importance. We will call it the general system of organisms.

Taxa of the general system, in order to perform their functions, must be meaningful associations from the point of view of the widest possible range of users. For example, a bird represents a well-defined concept not only for an ornithologist but also for a hunter, cook, and artist. To meet such a goal, the taxa of the

general system should be maximally homogeneous within themselves and maximally different among themselves in the widest possible range of characteristics. This property allows the system to perform two more important functions. First, it enfolds information about living organisms in an accessible form. For example, our knowledge of the cockroach includes a significant amount of information about itself and about the characteristics of higher taxa. Second, this system makes it possible to predict the properties of insufficiently studied groups. Only an insignificant part of insect species has been studied in any detail, but we have no doubt that they consist of eukaryotic cells of the corresponding structure and function and, with sufficient confidence, we describe many details of the biology of even extinct species. For example, the finding of an incomplete forewing in the Lower Cretaceous sediments of Transbaikalia, which was identified as the wing of a stem sawfly (Cephidae), served as the basis for the prediction that angiosperms, on which only the modern stem sawflies develop, existed already at the beginning of the Cretaceous (Rasnitsyn, 1969). Indeed, angiosperms (leaves of *Dicotylophyllum pusillum* Vakhrameev in Vakhrameev and Kotova, 1977 and pollen of *Asteropolis* and *Tricolpites*) were found in the same sediments and in the same year that this prediction was published (Vakhrameev and Kotova, 1977; see also Krassilov, 1997, p. 105; 2002, p. 377).

Analysis of the methodology of systematics, as already mentioned, reveals a dichotomy. We either *construct* a logical scheme and superimpose it on the diversity, *dividing* it into taxa (Procrustes's method), or we *identify* the preexisting structure of the diversity and explicate the revealed heterogeneity of the diversity in the form of an *empirical* system of taxa (Plato—Linnaeus approach). The choice between these alternatives is determined by the ontology: if the structure (heterogeneity) of the cognizable diversity is expressed well enough to be consistently and reproducibly described by a system of recognizable and, if possible, nonoverlapping taxa, such a system is undoubtedly preferable. It ensures much a more efficient enfolding of information and interaction with reality. If the diversity is poorly structured, then it is difficult to distinguish a system of nonoverlapping taxa. All of the experience of folk and scientific systematization indicates that at least most of the biological diversity is structured enough to make an attempt to use natural structure to systematize biodiversity to be meaningful.

In the biological systematics of the last century, there are three main directions: the already half-forgotten phenetics, the currently dominant cladism, and the traditional, repressed, but ineradicable phyletics ("evolutionary systematics," Ponomarenko and Rasnitsyn, 1971). The differences between them are much deeper than one might assume: they really correspond to different ontologies, different ideas about the structure and origin of biological diversity, and, accordingly, different hypotheses about the evolutionary pro-

cesses that create this diversity. I will outline the ontological aspects of this issue later. Here, I will only attempt to briefly formulate the methodologically most important features of these concepts.

*Phenetics* is ideologically the simplest and most straightforward. If the system is to operate with taxa that are meaningful from the point of view of the widest possible range of users, then these taxa should be maximally homogeneous (similar) within themselves and maximally different from other taxa. This means that it is necessary to find the appropriate characteristics and, to make the result reliable and objective, it is necessary to take many characteristics, to find (create) the correct algorithm (mathematical, to ensure objectivity), and to calculate the structure of the analyzed group. In the third quarter of the 20th century, the phenetic approach was very popular (for review, see Rasnitsyn, 1972), but the expansion of cladism stopped this work.

*Phylogenetics*, in essence, is a refined version of the traditional taxonomy, which, in turn, grew out of folk taxonomy (Rasnitsyn, 2013b). The ideological standpoints of phylogenetics are close to those of phenetics: it also recognizes an ideal (natural) system in which the taxa are maximally homogeneous within themselves and maximally different from other taxa. However, phylogenetics also recognizes the principal incompleteness of the set of characteristics available to us and, accordingly, the necessity of indirect methods to control the naturalness of the system. Of course, the phylogenetic control is at issue, since diversity is formed in the course of evolution; the common history, to various degrees, predetermines the similarity of the descendants of one ancestor. A common origin (monophyly) suggests the probable deep (general) similarity of the members of a monophylum but does not define it unambiguously. Thus, phylogenetics includes phenetics as one of its methods. Indeed, a taxon of the phenetic system can be formally described as a continuum, i.e., as a simple or branching chain of objects, each of which is more similar to its neighbors in the chain than to members of other continua. A phyletic taxon should then ideally be a monophyletic continuum, i.e., it should originate from another continuum via a single, distinguishable root (Ponomarenko and Rasnitsyn, 1971).

Thus, phylogenetics follows the traditional taxonomy, being based on both *similarity* and *relatedness*, whereas phenetics in this heritage has absolutized *similarity*. Cladism, conversely, absolutizes *relatedness*: its taxa, first, are not continua but clades (branches)—tree segments that have a single root (ancestral lineage) and *have no descendants*: no branching allows them to go beyond the clade. Likewise, the clade *has no real ancestor*: only a *hypothetical* ancestor is possible as a collection of apomorphies of the clade. The essence of evolution and biological diversity in cladism is ignored, since the characteristics of organisms (fea-

tures of their organization, development, and behavior) are important only as markers of relatedness, i.e., only as an indication of a divergence event that took or did not take place. Cladistically (to distinguish a clade), only apomorphies are significant, i.e., the characteristics that appeared in the closest common ancestor of the clade. The characteristics of similarity inherited from more distant ancestors (plesiomorphies) are ignored in the analysis of this group, and the characteristics of secondarily acquired similarities (parallelisms, convergences, and reversions) are important only as sources of errors in the reconstruction of the cladogram branching sequence. It is well known that, once acquired, a characteristic can be easily lost (or changed) later, like the legs of a snake, but apomorphy as a marker of a clade (a marker of the emergence of a new branch, a new phyletic lineage) is *indestructible* (a snake is a tetrapod). This means that apomorphy is *not a characteristic*. Apomorphy is a *fact of the history* of a group, the fact of acquiring a certain characteristic by the common ancestor of the clade, and that is why it is indestructible. In reality, of course, apomorphy is always only a hypothesis and not a fact. Here, we use this metaphor only for simplicity.

A theoretical substantiation of cladism (why the system of organisms should strictly reflect consanguinity (be isomorphic to their genealogy)) has not been proposed at all. This is not an axiom (a postulate taken without proof, because it is so fundamental that there simply cannot be proof). However, this is also not a generalization based on observations: what we know about biological diversity and its evolution quite often contradicts the provisions of cladism (see below). Thus, it is nothing but a dogma.

There are two aspects here—cladism as a methodology of phylogenetics (how to find out the relatedness of organisms) and cladism as a methodology of taxonomy (how to take relatedness into account in the construction of a system of organisms). Relatedness is reflected in a cladogram, i.e., a branched graph where nodes correspond to ancestors, edges correspond to evolutionary transitions, and vertices correspond to terminal taxa (operational units of analysis, species in the limit), and clades (branches including a common ancestor, i.e., the basal node and all edges, nodes, and endings above it) correspond to taxa. Within the framework of phylogenetics, cladism implies (in fact, requires) that

- If an evolutionary lineage is divided, then it is divided only in two.
- In this case, each lineage changes so significantly that the ancestral lineage disappears and, accordingly, cannot give rise to the third daughter lineage.
- No evolutionarily significant events occur between divergence events (all such events are bound to divergences).

- There is no fusion of branches (hybridization, symbiosis, and convergence are not taken into account).

- The presence of polytomy in a cladogram (when three or more branches exit a node at once) is always interpreted as a flaw (“unresolved polytomy”).

Cladism as a methodology of taxonomy implies (again requires) that

- The system is isomorphic to the cladogram (the taxon includes only the closest common ancestor and all its descendants).

- Hence, there are no descendant taxa, or, accordingly, ancestral taxa (a node is interpreted as a theoretical construct, i.e. only as a collection of synapomorphies of a taxon).

- Accordingly, only sister relationships between taxa are permissible.

- Phyletic evolution (the emergence of a new taxon without the simultaneous appearance of a sister group) and the budding of taxa (the emergence of new taxa without the extinction of the ancestral lineage) are impossible.

In my opinion, there is no need to prove the contrived nature of the theory of cladism, which does not correspond to the worldview of any practicing taxonomist or biologist dealing with the evolution of organisms. However, it may still be useful to point to a recent study that clearly showed traces of both budding speciation and anagenetic speciation in the evolution of specific groups of organisms: “Our joint analysis of fossil and phylogenetic data provided empirical evidence of budding speciation as the most prevalent process in some clades, but also instances supporting a substantial contribution from anagenetic speciation (while the contribution of bifurcation (a strictly cladistic event, see above (AR)) remains elusive)” (Silvestro et al., 2018, p. 9).

More paradoxical is the general success of cladism and its (usually aggressive) position in modern biology. Of course, there are reasons for this, but, in my opinion, they basically, although not completely, lie outside of evolutionary biology. However, some biological considerations may also support cladism.

The centuries-old experience of taxonomy shows that a system of similarities and differences can rarely be constructed in a single, generally accepted way. However, any phylogenetic lineage has its own evolutionary history, which means that the unique genealogical relationships within it can be reconstructed in only one possible way. In turn, this means that there remains hope for knowledge of the true genealogy and, therefore, it is possible to build the only objective (although not necessarily the best) system of organisms based on this genealogy. Obviously, such a hope, indeed, has a right to exist, but only under one condition: it is necessary to “forget” about the existence of such generally recognized evolutionary phenomena as

(1) budding and phyletic evolution, which cannot be revealed with the cladistic methods; (2) symbiogenesis and hybridogenesis, which lead to the existence of reticular cladograms that are fundamentally incompatible with cladism; and (3) intense parallel evolution, which often radically distorts the true genealogy (Zherikhin et al., 2008).

However, another question is more important: do we need a system in which a human, in fact, turns out to be just a naked ape, forming one taxon with the chimpanzee, as a *general system*, as a basis for an interdisciplinary language (see above)? Thus, the uniqueness of humans does not follow and cannot follow from the cladistic system. Conversely, how can we talk about evolution and, at the same time, refuse to recognize the existence of ancestors? Such an “evolution” is strange enough... How can the existence of real ancestors be ignored in principle if the simplest mathematical calculation shows that the number of terminal branches of a cladogram (i.e., both modern and extinct species that left no descendants) is always approximately equal to the number of ancestral species (in other words, to the number of nodes in the cladogram)? Naturally, the number of final species will be slightly greater than the number of ancestral species if budding predominated in the evolution of a certain clade (and vice versa for the dominance of the phyletic evolution). In any case, paleontological collections always contain a lot of ancestral species, although it is difficult to identify them.

Conversely, it can in no way be denied that even the most primitive cladistic methods, starting with the pen-and-paper cladistics of its founding father Willie Hennig (Hennig, 1950, 1966), can be useful for phylogenetic reconstruction. This, of course, also applies to the subsequent methodological achievements of this field: maximum parsimony and maximum likelihood, Bayesian analysis, and, particularly, phylogenomics. Here, however, a fundamentally important reservation should be made: these are only some of the methods of phylogenetic reconstruction, which means that none of them will reveal the final truth to us but can only give some approximation of it (for more detail, see below). Another fundamentally important reservation is that these are methods of phylogenetics but not taxonomy, because the latter has its own methods and limitations, which do not allow, in particular, to consider humans as just another species of chimpanzee or a similar genus (for more detail, see below and Rasnitsyn, 2002, 2006).

It can be stated that the advantages of cladism as a method of phylogenetic reconstruction allow it to claim the role of no more but one of the useful methodological directions in phylogenetics. However, cladism also claims a more privileged position in a broad philosophical context, emphasizing the objectivity of its methods, the absence of subjectivity, and the minimization of the personal factor. Of course, if clearly

defined protocols and detailed and formalized procedures are indeed followed, this makes it possible to limit the arbitrariness and subjectivity. However, one should not forget, first, that objectivity does not guarantee efficiency, and second, that the objectivity of the result requires total objectivity of the method, which is a serious problems in cladism. The cladistic procedure carefully monitors the use of formalized, standard, and correct calculation methods, and here there are usually no complaints about objectivity. However, the hypertrophied attention to the clarity and correctness of this aspect cast a shadow on those aspects of analysis in which some degree of subjectivity cannot be avoided. This is, in particular, the selection of the specific objects (operational units) of analysis, both basic (ingroups) and especially external (outgroups) objects, which play a fundamental role in the organization of the cladogram (determine the initial state and direction of changes in characteristics in evolution). This refers to the selection of the characteristics used in analysis and often the selection of the calculation parameters. Indeed, if the resulting cladogram does not fit for some reason, the parameters of its calculation can be changed until this cladogram fully satisfies the authors of the study. Such sources of subjectivity and arbitrariness exist everywhere. However, in cladism, with its cult of objectivity, they are not spoken of and, furthermore, are not analyzed, although an open analysis of the sources of arbitrariness could minimize their harmfulness. The problem is swept under the carpet. Mistakes are not criticized, and the methods of the selection of the groups and characteristics for research are not analyzed in a critical light, and, hence, enter the zone of irresponsibility.

It may seem that the objectivity of cladistic methods and, accordingly, the reproducibility of results must promise a high efficiency. Unfortunately, the reproducibility of cladistic results in fact is usually very low, and the scatter of cladograms for the same group is high. Of course, this is a subjective assessment, and it is not easy to make it more objective. My attempt to advance in this direction, published approximately 10 years ago (Rasnitsyn, 2010), was based on the fact that evolution leaves traces not only in the structure of recent organisms but also in the sequence of fossils, and a good correspondence of a particular system to these traces can be regarded as evidence for the adequacy of respective taxonomy methods. It turned out that the traditional methods of taxonomy give a much better correspondence between the system and the fossil record than cladistics. Paradoxically enough, molecular cladistics methods did not reveal any advantage over morphological cladistics. The point, of course, may be that phylogenomics was too young at that time and that now the results could be different, at least in terms of the consistency between the results of molecular and morphological cladistics. Nevertheless, no noticeable advantages of cladistics have been found to date.

It is interesting that, in recent years, cladistic methods (including molecular ones) have made it possible to obtain more definite results that do not give the colossal scatter in the topology of obtained cladograms that occurred before the 2010s. However, in those groups where I feel myself an expert (the system of insects at the order level and the system of hymenopterans at the family level), I am surprised to see that computer cladograms are increasingly closely approaching those that I drew 30–40 years ago with the completely traditional (i.e., intuitive) method (Rasnitsyn, 1969, 1980, 1988; for Hymenoptera, see also Heraty et al., 2011; Sharkey et al., 2012; Klopstein et al., 2013; Payne et al., 2013; Mao et al., 2015; Peters et al., 2017; and for the insect system as a whole, see also Letsch et al., 2012; Misof et al., 2014; Kjer et al., 2016; Wang et al., 2016). Although no consensus was reached, but nothing like that had been previously seen at all, neither in our studies nor in the works of foreign colleagues. The fact that large and well-equipped teams are gradually approaching what has long been done by one person raises serious doubts about the effectiveness of computer cladistics.

Thus, the direct advantages of cladism over the traditional methods of phylogenetics and taxonomy are more than doubtful, the achievements in objectivity are not obvious, and the advantages in the efficiency of phylogenetic reconstructions are still inappreciable. What provided them with this social success? In my opinion, the key word here is “social”, i.e., the sociological aspect in this case was decisive. The cladistic approach, with its denial of the personal factor and emphasis on high technology and clear research protocols that are available even to a student, is extremely democratic: if you work hard, your success will depend only on the equipment and other resources that you have at your disposal. In other words, this success will depend only on the money that you have as a member of a corporation/organization/team, and since money is the equivalent of invested labor, everything is fair and just. In essence, however, this means that primacy in *such* science is guaranteed for rich countries, regardless of the depth of their scientific traditions, accumulated scientific experience, and established scientific schools, especially given the fact that the scientific publishing houses that dictate publication standards are naturally concentrated in such countries. It is well known that a taxonomic and phylogenetic article will not be accepted in a top-rated journal without a cladistic interpretation of results and that foundations award grants only to the projects that promise compliance with the same standards.

Thus, the cladistic method works, among others, in phylogenetics and does not work in taxonomy. What, then, works there? What is an effective practice for the study of biodiversity from a phylogenetic and taxonomic perspective?

My understanding of the basic principles of the study of the relatedness (genealogy) of living organisms, formulated as a method of presumptions, has been described in detail in other works (Rasnitsyn, 1988, 2002, 2006; Zherikhin et al., 2008). To summarize the information described there, two main methods can be distinguished—the analysis of characteristics and the analysis of groups (i.e., direct tracing of relatedness). The analysis of characteristics involves

- the identification of similarities and differences between the compared objects for each character;
- their interpretation as presumable synapomorphies (the similarity acquired by the closest common ancestor of groups similar in this character), symplesiomorphies (the similarity acquired by a more distant ancestor), and homoplasies (the similarity independently acquired by different groups);
- the identification of conflicts between the obtained results, when the presumable synapomorphy of two groups for one characteristic is incompatible with the presumable synapomorphy of one of them with a third group for another character;
- the assessment of the balance of all (including conflicting) data in order to decide which of the incompatible synapomorphies can be accepted as true and which can be considered homoplasies (or symplesiomorphies) and, as a result, to build a diagram of relatedness.

Here, the cladistic methods are naturally used, along with various other methods (for more detail, see the studies cited above).

The direct tracing of relatedness is most clearly carried out in the fossil record, especially if rich, well-preserved fossil material is available, which often occurs with marine skeletal organisms. In these cases, it is possible to trace in detail the transformation of one species into another, then into a third one, etc., as well as bursts of morphogenesis, multiple migrations, extinctions, etc. As an instructive example, I can recommend the works of the school of L.A. Nevesskaja on the mollusks of the Neogene of Eastern Paratethys (Nevesskaja et al., 1986, 2001, 2009; Nevesskaja, 2007; and the publications cited there). However, even a much less complete geological record provides good opportunities to trace relatedness, as, for example, in the case of fossil insects. Xyelidae form a small, relict modern family of Hymenoptera that was previously considered aberrant due to the unusual structure of their antennae. Their fossil record was traced deep into the Mesozoic; it becomes increasingly abundant and diverse until it becomes the only representative of its order in the Triassic. It is demonstrative that, in the more recent Jurassic faunas, most other families of the lower hymenopterans have the same unusual antennae as Xyelidae or bear clear traces of the transformation of xyelid antennae into the normal ones. Taken together, all of the above information indicates that Xyelids were the ancestors of all other hymenopterans and shows

the pathways of the early divergence of the order (Rasnitsyn, 1969, 2002, 2006).

Paleontological evidence can be very compelling, but, of course, it should not be taken as the ultimate truth. This equally applies to other methods of relatedness tracing, e.g., the use of embryonic similarity (the biogenetic “law” of Mueller–Haeckel and the Baer’s “law” of embryonic similarity). Since a lot has been written about the advantages and disadvantages of this method, there is no need to repeat it here. In addition, phylogenomics is actually involved in relatedness tracing, as are other integral methods for the assessment of the similarity of many groups for many characteristics with a branching diagram, including the “total-evidence cladograms” and any cladograms in general. Since the genealogical schemes obtained in this manner almost always contradict each other in some way and do not coincide in certain areas, they should all be taken into account when they are coordinated in the creation of the “final” cladogram—the current hypothesis of the relatedness of the studied fragment of biodiversity, as far as it can be reconstructed based on the available data. The main question is which instruments should be used for such coordination. I do not know another answer to this question than the erudition, wisdom, and tact of the researcher assessing the weight (i.e., credibility) of each piece of available evidence. In any case, neither the recognition of all of the evidence as equal (a simple calculation of the pros and cons, as in voting), nor the selection of the only option among all options as the final one, seems promising to me.

Finally, there are several more comments on the methodology of taxonomy. Phyletics proceeds from the fact that the organization of living beings is determined not only (and, perhaps, not so much) by the conditions of their existence but by their history. The similarity of history (consanguinity), to a greater or lesser extent, determines the similarity of organization. In order for a phyletic taxon to simultaneously reflect both similarity and relatedness, it must be, first, maximally homogeneous phenetically (i.e., by similarity) and maximally different from other taxa, and second, monophyletic. Monophyly is understood in a broad sense in comparison with cladism, i.e., including holophyly (monophyly in the cladistic sense) and paraphyly. The phylogenetic classification of taxa is determined by the lineages of origin that cross the taxon boundaries. If its lower boundary is crossed by a single lineage (one root of the cladogram), the taxon is called *monophyletic* (in a broad sense), and it is called *polyphyletic* at a higher number of lineages. However, another formulation would be more accurate: *the taxon should be considered monophyletic as long as and since there is no reliable evidence of its polyphyly* (presumption of taxon monophyly). The difference between the phyletic taxon and the cladistic taxon is that the latter determines not only the origin (roots) of the taxon but also its further fate: the

upper boundary of the cladistic taxon cannot be crossed by phyletic lineages; i.e., the taxon cannot have descendants. If its upper boundary is crossed (i.e., the descendants of the taxon still exist), this is already a *paraphyletic taxon* that has no right to exist in cladism.

There is a broader understanding of monophyly as the origin of a taxon with several roots from a common ancestor in the depths of the ancestral taxon (pluriphyly, pachyphyly, or broad monophyly). The difference between this “monophyly” and polyphyly is unclear, because the boundaries of the ancestral taxon cannot be strictly defined within the framework of this definition. It seems to me that the reason for the introduction of the concept of “broad monophyly” is purely emotional: a polyphyletic taxon is traditionally considered unacceptable and, if it cannot be made strictly monophyletic, one still wants to call it something else. This shyness does not contribute to the progress of science: “sweeping the problem of polyphyly under the carpet” will not accelerate the understanding of the reasons for the existence of this phenomenon. However, they are very important, as will be seen in the discussion of the ontology of evolutionary biology. Moreover, since no one has been ever present at the birth of a given taxon, we are unable to rigorously prove the monophyly of the taxon. As always, we can rely only on the above presumption (*the taxon should be considered monophyletic as long as and since there is no reliable evidence of its polyphyly*) and always be ready for the fact that new data may make us doubt it.

One way or another, the study of many taxa may well find that they are polyphyletic in the indicated sense. However, it is difficult to doubt the naturalness of obvious groups such as reptiles, mammals, arthropods, angiosperms, and many other taxa about which such doubts regularly arise. Thus, although it cannot be ruled out that polyphyly may turn out to be the norm in taxonomy, I believe that it is methodologically more correct to proceed from the presumption of monophyly. I can cite two reasons for this approach: first, at the current, very low level of knowledge of most taxa, the discovery of the multiplicity of origin of a particular group would falsify the hypothesis of its naturalness rather than the presumption of monophyly. If the group is, indeed, natural, then additional research provoked by the discovery of polyphyly will only confirm its naturalness and, ultimately, force us to recognize the presumption of monophyly as untrue in this particular case. There is another reason why the rejection of the presumption of monophyly seems to be methodologically dangerous: it would mean the rejection of the use of phylogeny to control the naturalness of a taxon (see below) and, consequently, the transition to the standpoint of pure phenetics. This decision seems to be at least premature.

Now let us get back to the phyletic procedure. The phyletic taxon was defined as a *monophyletic contin-*

*uum* (Ponomarenko and Rasnitsyn, 1971). The definition of monophyly is given above, and the continuum is understood as a continuous linear or branching chain built from subordinate taxa (monophyletic continua of a smaller volume) such that each one is phenetically closer to any of its immediate neighbors in the chain than to members of any other taxa. Thus, the continuum is separated by a hiatus (gap in the continuity of similarity) from all other continua.

It is risky to build a system based on two different criteria (in this case, relatedness and similarity), since it allows arbitrariness in their application, unless the areas of competence of the two criteria are clearly discriminated. Phyletics discriminated them as follows: similarity is used as a criterion specifying a system, and relatedness is used as a criterion controlling its quality. The taxon is distinguished by tracing hiatuses (gaps in similarity) and subsequent testing for common origins.

Thus, phyletics requires that the members of its taxon be sufficiently similar to meet the criterion of the continuum without signs of polyphyly (origination from several ancestral lineages). If the continuum turns out to be polyphyletic, these criteria come into conflict. In this case, the taxonomist is unlikely to discard everything that has been done and start over. The natural reaction will be to attempt to falsify such a result by further studying the relevant group, and such an attempt is usually successful in some sense. For example, a more comprehensive analysis may find that the similarity between polyphyletic groups is superficial. Thus, the order Neuroptera for a long time included groups whose close relationship was not confirmed later. In particular, Sharp (1901) combined under this name not only the neuropterans in the modern sense but also webspinners (Embioptera), termites (Isoptera), booklice (Psocoptera), chewing lice (Mallophaga), dragonflies (Odonata), stoneflies (Plecoptera), mayflies (Ephemeroptera), scorpionflies (Mecoptera), and caddisflies (Trichoptera). The fate of such a group of mammals, the order Pachydermata, was similar: this taxon was used in the 18th and 19th centuries to unite elephants, tapirs, rhinoceroses, hippopotami, and pigs; however, later it was rejected in favor of more natural (monophyletic) orders. In other cases, it was possible to falsify the hypothesis of polyphyly, e.g., for lagomorphs. They used to be classified into the special order Lagomorpha, which is supposedly only convergently similar to rodents (Gidley, 1912). Although the status of the order has been retained for Lagomorphs up to the present time, according to modern concepts, they form a monophyletic group called Glires, together with rodents (Wilson, 1989).

Nevertheless, it is quite possible to imagine a situation when both hypotheses (similarity and polyphyly) turn out to be equally plausible. Most likely, this will mean that our attempt was insufficiently effective and

that we need to attempt to reanalyze the situation to eliminate the conflict. However, it cannot be ruled out that we truly reached the actual plurality of roots of a natural taxon, which we have already repeatedly considered. I do not have a ready-made recipe to distinguish one situation from another. Just in case, it is better to attempt to analyze both the system and the phylogeny of the group once again on a broader basis.

There are also quite obvious cases in which traditional taxonomy (including phyletics) retains clearly polyphyletic taxa that cannot be replaced with monophyletic ones without significant losses. I am referring to various parataxa in areas such as paleontology, parasitology, etc. (see below). The existence of parataxa once again confirms that traditional taxonomy ultimately focuses on similarity and uses relatedness only as a way to indirectly assess the total similarity, which is inaccessible for direct assessment (including allowance for still unexplored characteristics).

In conclusion of the section on the methodology of systematization of knowledge in evolutionary biology, let us turn to the taxonomic nomenclature. Nomenclature (i.e., the set of agreements on how to create and use names of taxa) is usually understood as an area of complicated details and simple basic principles. First, this is not true, since not all of the operating principles of biological nomenclature have been understood and explicitly formulated thus far. Some of them are mentioned in codes (ICBN, 1980; ICZN, 1988, 2000) as subsidiary provisions, and many principles are missing there. Second, some of the basic provisions are not conventions in the narrow sense but reflect different taxonomic concepts or are consequences of certain evolutionary hypotheses. The Linnean principle of binomial nomenclature (in contrast, for example, to the principle of type) is quite conventional and can therefore be easily combined with any taxonomic concept that recognizes the hierarchy of genera and species. In my opinion, there are nine basic principles, six of which are completely conventional and methodologically neutral (taxonomically independent nomenclature principles), and three others are determined by the adopted taxonomic concept (taxonomically dependent principles). Since all of this has already been considered in detail more than once (Rasnitsyn, 1992, 2002, 2006; Zherikhin et al., 2008), here I will focus only on the principle of type, which is most important in the context of the philosophy of evolutionary biology.

The principle of type, which corresponds to the nature of the taxon, is the main achievement of biological nomenclature: it ensures the stability of use and orderliness of changes in the name of a taxon at various changes in its composition (boundaries) and interpretation (change in rank, diagnostic characteristics, etc.). "The nomenclature type serves as an objective standard by which the application of the name is determined regardless of possible changes in the taxon

boundaries" (ICZN, 1988, art. 61a; the formation in ICZN, 2000, art. 61.1 seems less successful). In other words, a taxon cannot be entered into the system in a way other than, ultimately, as a reference to the type with its name. To appreciate the meaning of this statement, let us consider alternative possibilities.

The first thing that comes to mind is the possibility of the introduction of a taxon into the system with reference to its characteristics. This approach means that the characteristics of a taxon perform not only a diagnostic but also a defining function, and the taxon itself corresponds to the concept of "class" (Ghiselin, 1974, 1987). There are various possibilities for such an introduction of a taxon into the system, the simplest of which is a combinatorial system, i.e., a multidimensional matrix, each cell of which corresponds to a certain combination of characteristics and determines the position of the taxon with such a combination. One version of such a matrix is a polytomical table, which is sometimes used by taxonomists. This is a rectangular matrix with rows representing taxa and columns corresponding to characteristics. As a result, each cell reflects the state of one particular characteristic in a particular taxon. This form of the system is really simple and sometimes very useful, but it does not correspond to the tasks of the general system of organisms. It is not flexible: we cannot correct it locally in order, for example, to better match it with the characteristics of a particular taxon, since the introduction of a new characteristic, as well as the redefinition or deletion of an old one, forces us to revise the characteristics of all taxa. For this reason, the combinative system is rarely used, even for identification purposes.

In a more flexible system, taxa are defined by ranked characteristics. In a conventional key to identification, the first used characteristic has the highest rank, because it divides the target aggregate into the largest groups. The characteristics that are introduced next ensure its further division and have a lower rank. Such a system is, indeed, convenient, though not as good as the general system of organisms due to the apparently arbitrary ranking of characteristics. Nevertheless, this approach in a slightly modified form (with the distinguishing of a small number of high-rank characteristics sufficient for the formation of a system) was very popular in the past among taxonomists. For example, in works by Linnaeus (1751), the characteristics of plant fructification played a similar role. This approach was formulated in the clearest form by A.A. Lyubishchev (1923, 1966). Lyubishchev called for the search for a few of the most high-ranking characteristics (parameters) determining the distribution of all other characteristics, just as the nuclear charge determines the properties of atoms and, accordingly, the position of elements in the periodic table. As a result, the construction of a parametric system of organisms was expected; this would make it possible to predict all important properties of the corresponding taxa by these key characteristics (parameters). The

task posed by Lyubishchev seemed hopeless, and he himself failed to solve it. Nevertheless, a solution in a sense was found, but not where he was searching for it. Ironically, this happened in the field that Lyubishchev himself, being a convinced antiselectionist, considered false. The solution turned out to be the cladistic system, with its central statement that the characteristics of the organism and, accordingly, its position in the system are best determined by a single attribute, relatedness. Relatedness turned out to be Lyubishchev's parameter by definition, since it is proposed to introduce a taxon into the system with reference to a certain node of the cladogram, i.e., to the hypothetical ancestor of the clade taxon (Sundberg and Pleijel, 1994; Kluge, 2000; Pleijel and Rouse, 2002). However, we are already convinced of the inadequacy of the cladistic interpretation of the system of organisms and therefore will not further analyze the corresponding alternative to the principle of type.

A logical alternative to the class as a group that is defined by its characteristics is the individual, and the suggestion to consider the taxon as an individual (Ghiselin, 1974, 1987, and the references cited there) is quite natural. A taxon possessing the properties of an individual can be introduced into the system ostensibly, i.e., by direct indication (including the reference to its name). For this, its integrity in space and time must be sufficiently high to allow the taxon to be born and die, but not to disintegrate into parts, each of which could claim to inherit the name of the taxon. One can just point a finger—here it is, the taxon—without detailing the part of the taxon to which the name refers. The boundary between the ostensive method and the principle of type lies here: if any part of an individual equally bears its name, special rules for the selection and use of the nomenclature type used to introduce the taxon into the system are superfluous.

A taxon, undoubtedly, is neither a typical individual nor a typical class but possesses the characteristics of both these extremes. As a class, it possesses characteristics, as evidenced by the presence of a diagnosis, and members (representatives). As an individual, a taxon has parts (populations in relation to a species) and, more importantly, the ability to develop (evolve) without losing its individuality. While evolving, the taxon retains its integrity in time, in the multidimensional space of characteristics, and, to varying degrees, in the geographic space. This integrity allows the taxon to be identified as an individual, i.e., by its name. As a result, the taxon fills the logical space between these concepts and turns the class and the individual into two poles of a single spectrum. The taxon is sufficiently holistic to retain its name as a means of identification in the course of changes but is not sufficiently holistic for a simple “here it is” to be sufficient for its identification. A taxon is a continuum, a concentration of points, a cloud in a multidimensional space of characteristics. This cloud may evolve, i.e., change its

size and position in the space of characteristics; it may disappear (die out), or, conversely, split in half or bud off a new cloud, etc. The continuum is characterized both by a hiatus (discontinuity) between it and other cloud-continua and by its diagnostic characteristics. Both of these criteria do not show rigidity and easily change, both in the course of evolution and with an accumulation of knowledge about the taxon. At any time, these criteria may fail to clearly identify and separate taxa.

The possibility of identifying a continuum, in contrast to an individual, is determined by similarity. However, in contrast to a class, we speak of a relationship (general similarity) rather than of a similarity in certain characteristics. Therefore, “pointing the finger” fails to address either the cloud in general or its certain characteristics. It should be addressed to a specific point in this cloud, its nomenclature type. What ever happens to a taxon-cloud in the course of its evolution or when our ideas about it change, the name assigned to the nomenclature type, like a label behind a museum specimen, will always show us what it is about, of course, if the type exists (or at least is described sufficiently completely). The foregoing makes it clear that the nomenclature type is a natural attribute of the traditional (i.e., phyletic) system.

The same result can be reached with a different, shorter, way of reasoning. The purpose of any classification is to cover with taxa the entire diversity to be classified, completely and without overlapping the taxonomic boundaries. If we accept that the taxa themselves, as natural groupings, and the system formed by them really exist in nature and are not invented by taxonomists, then the main purpose of classification is dual. First, it includes the tracing of natural discontinuities in the classified space (dismemberment of nature by its articulations, according to Plato). Second, we fix and rank the identified hiatuses as taxonomic boundaries (rather than impose these boundaries according to Procrustes, in accordance with some external principles).

There are situations in which we must deliberately violate the principle of type and some other related nomenclature principles due to the need to work with inferior material (morphologically or ontogenetically incomplete), which, for various reasons, is important for study (especially often in paleontology). Much has been written about this, too, including studies by the author (Rasnitsyn, 1986a, 2002; Zherikhin et al., 2008).

## ONTOLOGY OF EVOLUTIONARY BIOLOGY

Ontology attempts to answer the question “what really is.” In our case, it is primarily “what biological evolution is.” In its most general form, the answer to this question is more or less clear: biological evolution is the process of the emergence of the new (moreover,

a fitted, expedient new). Of course, it is possible and necessary to discuss and clarify what is accepted as new and what as expedient. However, in most cases, this is clear without a strict definition. In my opinion, it is preferable to fix the boundaries of concepts when the need arises, when there is a risk of loss of mutual understanding without this. Therefore, we will not multiply entities without need and refine ourselves in the accuracy of definitions until an obvious need arises.

Thus, the basic problem in evolutionary biology is the emergence of expedient novelty. The new easily arises by chance, at least as a new combination of old elements. The situation with expediency is more difficult. An expedient novelty can be constructed based on knowledge, which is easily and constantly done by humans. However, humans and, more broadly, the human-type intellect cannot be responsible for evolution—humans are its product but not the creator. In theory, some other intellect may be responsible for evolution; however, another *natural* intellect apparently does not exist and did not exist on Earth (at least, I have not heard of any reliable evidence of it). One may think of an extranatural intellect, which in the broadest sense can be regarded as divine. This cannot be ruled out in any way, since, as is known, the existence of God is irrefutable and incontestable (i.e., unknowable): it is wholly and entirely a matter of faith. All the more incomprehensible is the providence of God. However, an appeal to the a priori unknowable is inadmissible for science: a scientist may believe in God but cannot appeal in constructions to God or to his actions, which change the natural course of events. Otherwise, it will not be science. Therefore, concepts that include the immanent ability for expedient innovations, in my opinion, are not scientific. I primarily refer to the views of Lamarck and Berg. Moreover, the inheritance of acquired characteristics according to Lamarck and the natural characteristic (nomogeneticity) of evolution according to Berg, which are respectable scientific hypotheses per se, do not belong here, in contrast to the immanent (not implying scientific analysis and substantiation) ability of the evolutionary process to create expedient novelty.

The only known source of expedient novelty, besides intellect, is selection, i.e., the memorization and reproduction of a successful choice, which is random only in the sense that it is not known in advance which of the options presented to the choice will turn out to be successful in the near and, moreover, in the distant future. Therefore, the only scientific basis for evolutionary theory at present is selectionism.

There are two main competing approaches in the theory of selectogenesis. They are usually referred to as synthetic and epigenetic. The synthetic theory of evolution, which is better known to our [former Soviet] biologists, can be characterized as a reductionistic one, which reduces effects at the level of the whole to

phenomena at the level of its elements (primarily, the elementary genetic factors and their frequencies in populations). Therefore, quite often (and rightly), it is referred to as the genetic theory of evolution. The opposing epigenetic theory can be referred to as a holistic one, since its adherents attempt to understand the properties of the evolutionary process proceeding from some properties of the whole organism (primarily, its ontogeny). This term goes back to the concept of holistic evolution, which was developed (however, rather speculatively) by Smuts (Smuts, 1926 (cited from Smuts, 1987)). I propose to use it instead of the term “epigenetic evolution,” since the terms “epigenesis” and “epigenetic” are widely used by modern genetics in a completely different sense. It will be already impossible to restore the priority interpretation of the term, which was proposed by M.A. Shishkin (1984), and the parallel use of two different interpretations of the same term in related areas only leads to confusion and misunderstanding, which I already constantly feel.

The relationship between two evolutionary hypotheses—synthetic and holistic (epigenetic)—was specially considered by M.A. Shishkin (1987, 1988a, 2006, 2010) and D.L. Grodnitskii (2000, 2002). Based on their results, I will attempt to present my view of this problem.

## SYNTHETIC THEORY OF EVOLUTION

The synthetic, or more precisely, the population-genetic theory of evolution (since synthesis there is more proclaimed than achieved) considers heredity (i.e., the ability to sustainably reproduce a phenotype and its features in successive generations) as a property of special elementary carriers, genes, which are now identified with regions (loci) of chromosomes and further with DNA regions (cistrons, etc.). Accordingly, the evolutionary process is presented as the dynamics of allele frequencies in populations, which is controlled by selection (differential reproduction of phenotypes). Phenotypic characteristics arise and change as a result of mutations and recombinations of genes, as well as various epigenetic and intergenic interactions. Since all of these changes do not possess the property of initial expediency, it is selection that forms the composition of populations and the properties of organisms, and it does this with an accuracy that is limited only by stochastic (probabilistic) factors. In addition to the factor of chance, the only obstacle to the full compliance of the organization of living beings with the requirements of selection is the exchange of genes, which unifies the structure of populations at a level that corresponds to averaged, rather than local, characteristics of selection.

In accordance with these views, the organization of living beings seems to be soft clay in the hands of selection, i.e., a set of characteristics that are freely shuffled by selection. Accordingly, from this point of view, the

evolutionary process turns out to be uniform (at least to the same extent to which the variations in the environment and selection are uniform). The uniformity of evolution is steadily disturbed only by divergences and extinctions, which in the considered system of views represent the only natural basis for the construction of a system of organisms.

The synthetic theory, of course, recognizes both the pleiotropy of genes (the influence of one gene on several characteristics) and the polygenicity of characteristics (multiple genetic determinations of an individual character); as a result, each characteristic actually depends on the entire genome. However, these admissions are, in fact, declarative, since the total interdependence of the elements of the structure and functions of the organism and, accordingly, *the absence of any permanent contribution of the gene to fitness* makes it impossible to reduce the evolutionary process to elementary genetic or, furthermore, molecular genetic events.

These simplifications are not innocuous: they lead to inconsistencies between theoretical predictions and observational results. Here are examples of these inconsistencies. First, let us consider the rates of the evolutionary process, which are assessed by the rates of the emergence and extinction of taxa of various ranks. The taxon is the only concept for which the very meaning of existence is an attempt at an integrated assessment of the similarities and differences of organisms (see the meaning of taxonomy given above). Of course, the comparability of taxa of the same rank in different groups is not ensured by anything but the intuition of taxonomists. Therefore, this method for the assessment of the rate of evolution is imperfect, but we simply have no other ways to compare the rates of evolution of organisms. No matter how imperfect (subjective) the assessment of differences in taxonomic ranks is, it is more informative than a more objective assessment of differences with the use of characteristics. It is well known that seemingly identical differences can be achieved in quite different ways and turn out to be manifestations of such different-scale organizational transformations that the assessment of the rates of evolution with their use will only be misleading. This conclusion is especially illustratively confirmed by the materials on evolution under insular conditions and at the early stages of the evolution of taxa (the phenomenon of archaic diversity). Here, grotesque forms with an unbalanced organization emerge quickly and easily. They often differ in the characteristics that normally (in stabilized groups) characterize taxa of a much higher rank (see below for more detail). At the same time, a paleontological assessment of the rates of taxonomic evolution gives results and reveals trends that can hardly be attributed to the incomparability of taxa of the same rank in different groups (Rasnitsyn, 1987, 2012; Rasnitsyn et al., 2013, 2015, 2016).

According to the synthetic theory, the evolutionary process is governed mostly by the same factors and mechanisms that operate in the genetics of populations. However, the rate of macroevolution should then obey the same laws as the rate of changes in gene frequencies in population genetics. This rate, in turn, is determined by the power of the flow of adaptively competent genetic variations (changes that are significant for selection) that flow through the evolving population. Therefore, the rate should increase with an increase in the frequency of mutations, the rate of generational change, the population size, and the mobilization reserve of variability.

The paleontological material does not allow direct assessment of the majority of the listed parameters used in population genetics. Some of them can still be estimated indirectly in fossils, insofar as they correlate with other characteristics (such as size, taxonomic affiliation, etc.). In particular, if the genetic approach to evolution is true, then its rate should be minimal in mammals with a relatively slow change of generations and small populations (due to the relatively large size of individuals), maximal in unicellular organisms, and intermediate in invertebrates. In reality, numerous paleontological data show that these relationships are inverse (Rasnitsyn, 1987). Moreover, the differences are very large even at the level of the species, and yet this taxonomic category is considered comparable in different groups. For example, the age of semimodern fauna (fauna in which half of the species are modern and half are extinct) in large mammals (proboscideans and ungulates) is 0.2 million of years (Ma); in small mammals, 0.5 Ma; in birds and fishes, 0.7 Ma; in insects, 3–7 Ma; in mollusks, 3.5–5 Ma; and in diatoms, 15 Ma. The half-extinction time (by analogy with half-life, the time for the extinction of half of the number of species available at a certain time; in our case, this is the age of the fauna that consisted of half of the extinct species and half of the species that have survived to this day) is the smallest in elephants (0.18 Ma); in mammals, it is, on average, 0.54 Ma; in teleost fishes, 3.5 Ma; in graptolites, 1.3 Ma; in echinoderms, 4.2 Ma; in bivalves, 7 Ma; in plankton foraminiferans, 5 Ma; in benthic ones, 18–24 Ma; in diatoms, 5.5 Ma; and in dinoflagellates, 9 Ma. At higher taxonomic levels, intergroup differences are usually similar but often sharper. For example, the age of semimodern fauna for mammalian genera is 4 Ma; birds, 10 Ma; reptiles, 20 Ma; fish, 30–50 Ma; insects, 40 Ma; mollusks, 60 Ma; and foraminiferans, 230 Ma.

These figures do not bring into question the genetic predictions. Selection is absolutely automatic: if individuals differing in the degree of fitness appear in a population, they will be steadily selected in full accordance with the provisions of population genetics. The different involvement of individuals in the reproduction of a population will also automatically lead to a change in its hereditary structure, to the extent to which these differences are heritable. Therefore, the

distribution of evolutionary rates predicted by genetic theories must necessarily take place in nature, to the extent to which the power of the *total* flow of genetic variations in the long-term aspect is correlated with the power of the flow of *selected* (highly adaptive) inherited changes. This is confirmed by the well-known differences in the typical breeding rates between domestic animal breeds, plant varieties, and strains of microorganisms. No less illustrative are the occasionally observed maximum rates of insect evolution, when 46 species of longhorn beetles of the genus *Plagithmysus* emerged as a result of 17 introductions (Gressitt, 1978) on the island of Hawaii, which is 0.5 million years old (Rotondo et al., 1981); i.e., at least one event of speciation occurred, on average, over 150–200 thousand years.

However, it is obvious that, in general, the distribution of evolutionary rates at the level of the species and higher in the first approximation is opposite to that predicted by population genetics. This means that the constraints that are critical for population genetics are not critical for the evolutionary process. Roughly speaking, the flow of general genetic variability is evolutionarily redundant, even in populations of large mammals, not to mention other, more numerous and faster reproducing organisms. The rate of changes at the suprapopulation level (i.e., the rate of evolution) should be regulated by some other factors. We will consider the question of what these factors may be later. Here, we can only conclude that the level to which the synthetic theory of evolution attempts to reduce the evolutionary process and, thereby, to explain the latter does not meet the hopes placed on this approach and does not provide the expected explanations (at least with regard to the paradox of evolutionary rates).

There are other groups of data that do not fit into the framework of the synthetic theory of evolution. If the organization of living things is soft clay in the hands of selection or a set of characteristics that are freely shuffled by selection, then its results should be predictable to the extent to which the conditions of evolution are known. Antiselectionists have shown with numerous examples that this is not the case (e.g., Lyubishchev, 1982). Even closely related forms under seemingly similar conditions can behave completely differently. The most paradoxical example of this is the spotted hyena, which is extremely extravagant in the reproductive sphere, and the striped hyena, which is close to it but is quite ordinary in this respect (Glickman et al., 2006).

The widespread, if not universal, discreteness of biological diversity is even less explicable from the synthetic point of view. In this system of views, only one form of discreteness is natural—the discreteness of an amphimictic species under conditions in which the gene exchange is sufficiently intense to unify the composition of populations despite the local variation in

selection. However, there should then be a good correlation between the degree (completeness and antiquity) of isolation, on the one hand, and the degree of divergence, on the other. This is not observed in reality: the inhibitory effect of gene exchange on the rate of divergence (i.e., leveling the differences between the diverging parts of a single population) cannot be confirmed. This conclusion was made, in particular, by S.S. Shvarts (1980), who compared mammalian species with different tendencies to form isolates. The self-evident counterexample of insular speciation actually belongs to a different context (see below).

The discreteness of species in parthenogenetic and asexual organisms, which are devoid of gene exchange, is completely inexplicable from the point of view of the synthetic theory of evolution. Indeed, a comparison of closely related bisexual and parthenogenetic species of rotifers (Mayr, 1974) and weevils (Ivanova, 1978), bisexual and asexual species of protists (Polyanskii, 1957; Poljansky, 1977), lower algae (Polyanskii, 1956), and ferns (Farrer, 1990) showed that unisexual and asexual species are as discrete as bisexual ones.

No less illustrative is the long-term (for millions, tens, and possibly even hundreds of millions of years) evolutionary stasis at the species and generic level, when an *exchange* of hereditary information is out of the question (for examples, see Rasnitsyn, 1987). In particular, persistence for 10–20 Ma is quite common (Zherikhin, 1999). The finds of various Pliocene galls, which are indistinguishable from the galls caused by modern insect species on the same plants, are much more recent (3–5 Ma); however, they are no less important (Zherikhin, 2002). The morphological specificity of the gall is determined by the biochemical effect of the gall-forming insect on the tissues of the host plant. Therefore, the morphological stability of galls proves the biochemical stasis of insects for millions of years. The record holder, however, is *Triops cancriformis* (Schaffer), which has changed little since the Early Triassic (approximately 230 Ma), and even the question of the species independence of Permian populations remains unresolved (Tasch, 1969). This conclusion is confirmed by the molecular clock data for two morphologically almost indistinguishable Japanese populations of another species, *T. longicaudatus* (LeConte): they indicate the divergence of the species approximately 15 million years ago. For other species of this genus, including *T. cancriformis*, the divergences date back 25–45 Ma (Suno-Uchi et al., 1997).

No more understandable in this system of views is the common phenomenon in which less recent taxa are significantly more discrete and demonstrate clearer relationships than species. Indeed, species tend to have diverged relatively recently, have less time to diverge than the higher taxa, and, therefore, should have retained more traces showing how exactly the divergence proceeded (see below for more detail). All

of this is indicative of a discrepancy between the population genetic approach with its derivatives (the synthetic theory of evolution and the biological concept of the species), on the one hand, and the results of observations, on the other.

## HOLISTIC (EPIGENETIC) THEORY OF EVOLUTION

### *Basic Provisions*

In contrast to synthetic theory, the holistic theory considers the evolutionary process primarily as a process of transformation of ontogeny in the course of evolution (Shishkin, 1987, 1988a, 1988b, 2006, 2010; Rautian, 1993). Special attention is given to the integrity of ontogeny in the sense that both the process itself and its result (the structure of the organism at successive stages of development) are much stabler than any individual factors or processes of development. Normal development is equifinal and is capable of relaxing (suppressing, absorbing, leveling) a very wide range of influences and disturbances, both external and internal, including the results of various errors and disturbances of normal development.

Thus, normal ontogeny (reaction norm) in general, rather than individual characteristics, is inherited (steadily reproduced in subsequent generations). In addition to the norm, there are various deviations (aberrations) of development with unstable reproduction, which are rarely realized under normal conditions. Under unfavorable conditions, when the mechanisms of protection of the norm can be disturbed or overcome as a result of a strong external influence or for internal reasons (developmental errors), development proceeds along an aberrant (deviating and unstable) pathway. Since endogenous developmental aberrations easily arise not only during sexual but also during parthenogenetic and asexual reproduction, their occurrence is the realization of the latent heterogeneity of the population rather than the emergence *de novo* of any genetic changes.

The holistic theory regards aberrations as a selection material that is able to create a new adaptive norm on its basis. Such a process can more easily be described in terms of the metaphor of an ontogenetic (initially epigenetic, in Shishkin, and even earlier in Waddington) landscape. Normal ontogeny is a stable (stabilized) sequence of closely related separate ontogenetic processes. More or less isolated segments of this sequence are called creodes. If we imagine a creode in the form of a strongly deepened valley in a certain landscape, along the slope of which the ontogenetic process flows, then the aberrations will be represented by gentle lateral valleys that are raised in the sides of the main valley. The realization of an aberration (i.e., reaching a lateral valley by ontogeny) requires either a strong external effect on the developing organism, which pushes it out to the lateral valley,

or a change in the landscape itself, flattening the valley bottom (additional aberrant change), or both together.

Although aberrations are unstable (“not hereditary”; the most common of them are often called modifications), they are constantly (albeit unpredictably in detail) reproduced in the population, since the ontogenetic landscape with the corresponding lateral valleys is the adaptive norm of the species. Therefore, despite their weak heritability, aberrations serve as the material for selection. If aberration is beneficial, selection will selectively preserve those landscapes that more consistently reproduce it. In other words, the advantage will be given to those in which the corresponding valley is deepened and the level of its bottom at the junction with the main valley is closer to the bottom of the latter. If, at the same time, the main valley also flattens below the fork (i.e., if the stability of the previous norm decreases), the former aberration will have a chance to become a new norm. If the previous norm retains its value, then both norms will be stabilized, and a mechanism will develop for ontogenetic switching between them. When this mechanism uses an environment signal for switching, we obtain typical modification variability. When a genetic signal (e.g., recombination) is used, we obtain a Mendelian form. In this way, Mendelian characteristics arise both in nature (e.g., the conventional sex-determination mechanisms) and in the laboratory (e.g., during the stabilization of pure lineages).

In general, for the holistic theory of evolution, the spectrum of possible developmental pathways (creodes and their aberrations) fixed (“memorized”) in the adaptive norm (i.e., the ontogenetic landscape, its *ontogenotype*) is the essence of a living organism, its ontogenetic potential, which determines the existence of an organism; selection works with it. The purely genetic level (genes and their alleles, the dynamics of their frequencies in the population, mutations, recombination, etc.) lies much deeper and does not determine the specifics of the evolutionary processes.

The genotype–phenotype antinomy is generally incorrect in the light of ontogeny and the functioning of the organism. It is necessary to discriminate between a system of creodes (evolutionarily stabilized systems of morphogenesis forming an ontogenotype) and a system of various switches, timers, and modifiers that combine many creodes into a single system of ontogeny and functioning of the organism, which again is stabilized evolutionarily. Both creodes and modifiers, timers, and switches are influenced by changes in the molecular level (DNA–various RNAs–proteins cascade, as well as epigenetic factors such as methylation, etc.). However, creodes, as more complex stabilized systems, most often either quench molecular and other influences on them or simply fail to function under their influence. For this reason, creodes evolve (acquire evolutionarily new expedient changes) rather slowly. Much simpler coupling mech-

anisms change much more easily. It is not surprising that they evolve much faster, which is reflected in the ideas that the phenotype is relatively stable (especially when it comes to the “wild type”) and that the genotype evolves faster than the phenotype (“The population retains its normal “wild” phenotype, despite the continuous mutagenesis, which is accompanied precisely by the accumulation of mutations and, consequently, the continuous rearrangement of its genotype” (Schmalhausen, 1968, p. 113)).

Ontogenetic processes in the aspect of inheritance were considered in greater detail by M.A. Shishkin (1987, 1988a, 2006, 2010). For us, another aspect of the problem of the evolution of ontogeny is more important.

### *Adaptive Compromise*

The integrity of the organization of living beings has a significant effect on the nature of their evolution. At the morphogenetic level, this effect is manifested in the fact that creodes become highly stabilized due to the deep interdependence between changes in different creodes (and, as a consequence, between changes in different properties and characteristics of the organism). They are very difficult to “push” out of the normal intraspecific variability, which itself is already stabilized by the selection of previous generations. Therefore, *evolution* (i.e., successful escape beyond the normal, stabilized ontogenotype (ontogenetic landscape)) proceeds with difficulty, infrequently, and with poorly predictable results.

In other words, in the hands of selection, the organization of living beings turns out to be a fragile, capricious material; evolutionary transformations are more or less abrupt, and the resulting biodiversity is more or less discrete. This discreteness is not absolute. Even where it exists, we do not always manage to find it easily (because of the overlapping of the limits of the stabilized variability of organization options, see below). Nevertheless, it exists and is so widespread that biologists and especially taxonomists prefer not to think about it too often, focusing on exceptions and difficult cases. The existence of exceptions is quite natural. A stabilized ontogenotype (adaptive norm) includes a certain, more or less wide, range of variability that arose as a result of the selection of previous generations. The spectra of normal variability of closely related species may overlap, creating problems for taxonomists, even if the landscapes themselves (ontogenotypes) differ discretely.

An unexpectedly strong confirmation of the discreteness of biodiversity has recently been provided by an analysis of the ample accumulated barcoding data (the sequence of the bases of one of the fragments of mitochondrial genes). These sequences, which were studied on 5 million individuals of 100 000 animal species, turned out to be discrete (not overlapping) in

more than 90% of cases. This is why they so often allow the confident identification of species (Stoeckle and Thaler, 2018).

We do not yet know how to see, outline, and measure the ontogenetic landscape itself, not just its external manifestations. Although the ontogenotype is inaccessible with direct observations, it is almost as reliably deduced from the available data as an atom or a neutrino. The ontogenotype is inaccessible to direct observations, because it is a very complex system of interconnections and interactions. Similarly to an atomic charge, the ontogenotype essentially determines the properties and behavior of its incarnations—individuals, species, or other taxa. Therefore, it can even be defined as the materialized essence of all these incarnations, which is, in a sense, a return to essentialism, but to an essentialism of a substantially different sense than Plato’s, since the essence is recognized here as material and knowable as the essence of the atom (the charge of its nucleus).

However, let us go back to the evolution of the evolutionary landscape. It is convenient to analyze its high coherence and the buffering of its evolutionary changes within the framework of yet another metaphor—the adaptive compromise metaphor (Rasnitsyn, 1987). Indeed, the stability of a balanced landscape can be viewed as one of the consequences of the systems theory, in particular, its postulate that no system can be optimized simultaneously in more than one parameter. It is no coincidence that the swift cannot run and swim, the penguin cannot run and fly, and the ostrich does not fly and can hardly swim well.

The optimization of real systems is possible only as the finding of a compromise between the conflicting requirements for the optimization of various parameters. For living beings, whose organization is full of various correlations and interdependencies, the compromise between different adaptive functions must be especially tense. Therefore, a stable ontogenotype should be organized according to the principle of a well-worked compromise between the conflicting needs of the maximal optimization of all adaptive functions.

The consideration of a living being as an adaptive compromise is not something new. E. Mayr, apparently, had a similar phenomenon in mind when he wrote that the epigenotype of a species, its system of canalization of development and feedback (i.e., our ontogenotype), is often integrated so well that it resists changes with remarkable persistence (Mayr, 1974, p. 353). Much earlier, similar ideas of the struggle (competition) of parts of the body were expressed by V. Ru and A. Weismann (Weismann, 1905) and, before them, in the form of the principle of compensation or balancing, by I.V. Goethe and J. Saint-Hilaire (Darwin, 1859). Apparently, before anyone else, back in the 4th century BC, such thoughts (in the form of

the principle of economy) were formulated by Aristotle (cited from Aristotle, 1937).

The adaptive compromise metaphor is important in that a wide range of relatively easily testable consequences can be derived from it. The most common of them is the difficulty of changing a well-balanced organization. Of course, this difficulty is not absolute, and the loss of the adaptive meaning of any function will lead to a reduction in the systems that support it to the extent to which these changes are feasible. The loss of an adaptation that lost its significance, which can naturally be explained by the reduction or disintegration of obsolescent systems, makes it possible to further optimize other systems that have retained their adaptability.

For us, the very difficulty of the rearrangement of a once-formed compromise (i.e., the existence of barriers to changes to the existing organization) is still more essential. Apparently, the evolutionary landscape should not be represented as it is usually drawn: in the form of adaptive peaks separated by valleys of reduced fitness and connected by ridges, along which the evolving group can gradually move in the direction from the disappeared peak to the retained one. Schram's model (Schram, 1983)—a system of holes separated by barriers of adaptive instability—seems more plausible.

The difficulty of overcoming the stability of a once-achieved successful compromise predetermines many important properties of the evolutionary process: the already mentioned unevenness and retardation (buffering) of evolution, the discreteness of living beings, and the low evolutionary efficiency of elimination. Many of the questions that synthetic theory cannot answer intelligibly, such as the unevenness of evolution, the wide spread of evolutionary stasis, the lack of a visible influence of population-genetic factors on the rate of the evolutionary process—all of these effects turn out to be natural and expected when the process is considered from the standpoint of an adaptive compromise. However, as expected, they are replaced by other problems that are no less difficult to solve.

Evolution is going on, despite all the barriers, but at the cost of the extinction of many groups that have not been able to successfully overcome these barriers. Let us try to understand the conditions under which this occurs and how it happens, how a balanced ontogenotype can be transformed into another, also balanced, one. The conventionally postulated mechanisms of the evolutionary process, which are based on the interaction of intra- and interpopulation polymorphism with isolation, do not give an answer to this question. It was convincingly shown that reproductive isolation not only is unnecessary for evolution but often does not even stimulate it (Gritsenko et al., 1983, Ch. 7). According to all laws of population genetics, the universality of intra- and interpopulation polymorphism, combined with the monstrous pressure of normal

elimination (see below), should lead to constant and rapid evolution with a characteristic distribution of rates (high for lower organisms and low for higher ones, see above), which is also not observed.

I can draw only one conclusion from the considered contradiction: under normal conditions, intraspecific polymorphism does not contain evolutionarily competent characteristics. Simply speaking, none of the ontogenotype variants that are regularly realized in the populations of a species has an evolutionarily significant advantage over other variants under normal conditions. In other words, "all animals are equal, and there are no more equal among them." How can this be true if polymorphism sometimes affects seemingly vital organs and structures? The answer, apparently, is still the same: all of the available variants exist, because they are consistent with the existing epigenetic system, i.e., they do not destabilize it. However, they are unable to create new stability (some other, not necessarily the best, but a different stabilized system). In other words, intraspecific polymorphism, together with modification variability at its supraorganismal level, performs the same function of system stabilization in an unpredictably variable environment, which is performed by ontogenetic regulation, physiological reactions, and behavior at the organismal level.

Since the analysis of individual factors does not give an answer to the question of the specific mechanism that ensures the evolutionary process, we will attempt to solve this problem from the other side: we will analyze the conditions in which evolution actually proceeds, and this happens relatively quickly. Although reproductive isolation, as already mentioned, is not an important evolutionary factor under normal conditions; it is well known that, in the conditions of isolated islands, water bodies, etc., evolution proceeds especially rapidly and often leads to the formation of strongly altered, even grotesque, forms. S.S. Shvarts (1980), who specially analyzed this paradox, came to the conclusion that the reason lies in the reduced tension of competitive relations in poor, unfilled (on an evolutionary time scale) island biocenoses. Specifically, the evolutionary role of the unfilling of cenoses, according to Shvarts, is that a weakened competition enables a rapid, unilateral specialization. This interpretation is very attractive for the adaptive-compromise concept: an ancestral species, moving from the mainland to a depleted island biocenosis, finds itself in conditions that are softened in many parameters and allow additional optimization of those functions that remained under tight environmental control at the expense of others functions that are not controlled so strictly by selection. In fact, as we will see, the matter is more complicated and by no means can be reduced to weakened selection. However, for now we will use this lax term.

*Evolution Trigger*

The above model of evolution on islands is also interesting, because it corresponds to the concept of inadaptable evolution proposed by V.O. Kovalevskii (Rasnitsyn, 1986b). However, more importantly, it demonstrates a fairly real mechanism that can overcome the stability of a well-balanced adaptive compromise that slows evolution. Naturally, the question arises as to whether such a mechanism can operate not only when islands are populated but also in some other situations.

To answer this question, let us consider some other cases of the transition of a group to similar conditions—whether an acceleration of evolution and its similarity to inadaptation (i.e., an increase in the scope of changes in combination with their unilateralism and imbalance) will also be observed there. The transition to a relatively free, unfilled ecological space, which stimulates morphogenesis, is characteristic of the early stages of evolution of many taxa. This phenomenon is described by the “law of archaic diversity” (Mamkaev, 1968), which indicates a sharply increased variability of organization at the early stages of taxonomic evolution. This is why species and genera at this time may differ in characteristics that later characterize families and orders. No less characteristic of the stage of archaic diversity is the low evolutionary stability of the early members of the taxon, which is reflected in the large number of short basal branches on almost any phylogenetic scheme based on rich paleontological material (e.g., Rasnitsyn and Quicke, 2002, Fig. 1, 179, 266, 278, 306, 331, 393, 408). The acceleration of evolution in the early stages of the history of the taxon more specifically demonstrates the fact of the approximate coincidence of the age of the genus and many of its species (Shvarts, 1980). This shows that a significant part of divergence occurs at the earliest stages of evolution of the emerged taxon.

All of the above indicates that the transition of the group to the conditions of a depleted biocenosis and an unfilled ecological niche, indeed, provokes evolution (usually inadaptable). In this case, the formation of euadaptive groups (i.e. harmonious, adapted to filled biocenoses and tense competitive relationships) may be associated with the subsequent tightening of conditions and the intense extinction of the majority of the newly emerged groups (those that were unable to rapidly turn from inadaptable to euadaptive ones).

The question of soft/harsh/catastrophic conditions is not as simple as it often seems. The equilibrium population density corresponds to those values at which mortality balances the reproductive potential of the population. This means that, of all of the offspring of each female, on average, only one of her daughters manages to leave their own offspring (Beketov's law, Beketov, 1860). One year earlier, C. Darwin wrote about the same issue (Darwin, 1859). For this reason, elimination in populations (with the exception of brief

and more or less balancing episodes of fluctuations in abundance) is normally almost equal to fertility, i.e., close to the maximum. However, if the almost complete elimination of offspring is the norm for the population existence, if the chances of leaving offspring for each individual are always minimal, if the extinction of entire populations is a common phenomenon even on an ecological time scale, then what do we mean when we talk about worsening living conditions?

It seems that there is no hardening of conditions at the population level in nature at all. It is difficult to talk about it, even in application to the specific and supraspecific level. Here, the deterioration of conditions can only mean a trivial (on an evolutionary time scale) extinction of species, the effect of which on evolution will be manifested only as an emptying of the ecological space and, accordingly, a softening of conditions. However, nature abhors a vacuum, especially an ecological space, and the surviving species will immediately fill the void. They intensify the reproduction process of the remaining populations and thereby nullify the short-term softening of the conditions of their existence. The fact that fluctuations in population density with periodic softening of conditions are the most common phenomenon and, at the same time, cases of irreversible evolutionary change generated by it have not yet been described proves that a direct decrease in mortality, as well as its increase, is not a factor of evolution. What, then, can overcome the stability of the ontogenotype and successfully lead the organization of a living being beyond the historically conditioned norm?

The cause for the stability of the ontogenotype is the once-reached compromise between the conflicting needs of the optimization of various adaptive functions of the organism. These needs are contradictory in the sense that, due to the complex interweaving of morphogenetic and functional relationships among all parts and characteristics of the organism, the adaptive enhancement of one function must entail a loss of effectiveness for others. Of course, the weakening of the integrity of ontogeny, which facilitates the independent transformations of individual systems, is not only possible but also takes place in nature. However, this direction (simplification of organization and general degeneration) is quite specific, requires appropriate conditions, and is neither typical nor particularly widespread. After all, in order to lose the height of organization, one must first acquire it. The weakening of integrity as a mechanism of evolution exists, but it is clearly insufficient to explain the evolutionary process.

Thus, we need to reconstruct the conditions in which a change in organization occurs under conditions of constant or increasing integrity, or rather, when a temporary decline in integrity is rapidly replenished. For this purpose, we will attempt to refine the adaptive-compromise metaphor. The main problem for evolution is, as we have seen, the contradictory

nature of the relationship between adaptive functions in the course of their optimization. The contradiction is created by tight ontogenetic and functional ties between the systems that ensure these functions, on the one hand, and by the strict control over the proper performance of functions, on the other. We have seen that a loosening of ties is possible but not sufficient to explain evolution. A general weakening of the selective control of the proper performance of adaptive functions, as we have seen, is also impossible: on an evolutionary time scale, elimination is always close to the maximum possible values. Where is the way out?

### *Destabilization and the Cradle Effect*

The situations that provoke rapid evolution, which were discussed above, can serve as a clue for the solution of this issue. What they have in common is that the population enters new, unusual conditions (primarily, impoverished, unbalanced communities of the island type and new (sparsely populated) adaptive zones). Under such conditions, the cenotic control over the performance of certain functions (e.g., protection from predators and specialized parasites, which are often in shortage in such unbalanced communities) can be reduced by strengthening control in other directions. In the end, these conditions are called new precisely because the situation with the selective requirements differed from the previous situation (in particular, some functions were controlled much more stringently than under the previous conditions). If the population survived under these conditions, this means that the total elimination did not consistently exceed its reproductive potential and, therefore, the selective control of other functions was reduced.

Thus, evolution is apparently provoked only by a unilateral softening of the environmental control of the organization, when only some of the adaptive functions remain under strict monitoring by selection. An obvious consequence of such unilateral control is an imbalance and destabilization of the existing organization, and it actually does manifest itself in such cases (Zherikhin in: *Deyatel'nost' ...*, 1967; Belyaev, 1974; Shishkin, 1984, 1987; McCune, 1990; etc.).

Since the adaptability of the system inevitably decreases during destabilization, rearrangement can hardly occur under normal conditions. Therefore, an evolving group can hardly penetrate an already occupied niche and displace its owner. It is more plausible that it will either occupy a niche vacated as a result of the extinction of its previous inhabitant or will be able to create (open) a new niche. This is probably why we know a lot of plausible examples of the recent emergence of new taxa under island conditions, as well as due to anthropogenic introduction. Especially striking are helminthological examples (cited in the discussion based on the report by Rausch, 1982, p. 184) of two successive speciation events over 300 years (in the

house-mouse parasite imported to North America) and the divergence of two species of human tapeworms no more than 16000 years ago. An equally striking example is the emergence of a new cryptic species in the complex of apple fruit flies *Rhagoletis pomonella* (Tephritidae) on the apple tree, which was introduced to North America, and, moreover, a new parasite in the *Diachasma alloeum* (Braconidae) complex on it within no more than 150 years (Feder and Forbes, 2010). However, such examples around us are quite scarce, even though both biodiversity and the degree of knowledge of it under normal conditions are usually much higher, and, accordingly, the probability of the detection of cases of natural speciation is higher.

The foregoing suggests that evolution (especially at the supraspecific level) is possible only as a result of a change in conditions in which the selection affecting the population becomes substantially unilateral. Only such selection seems to be able to overcome the stability of the previous well-balanced adaptive compromise. Meyen (1987) had this in mind when he said that selection sometimes condones evolutionarily dubious innovations. It is even possible to formulate the general principle of the “cradle effect,” according to which evolutionary innovations arise in the “cradle,” i.e., under special conditions (though not always particularly mild by human standards). In particular, the traditional Russian cradle, in which the baby lay tightly swaddled, indeed, can hardly be called a comfortable place.

### *Evolutionary Triad: Inadaptation—Euadaptation—Stasis*

One way or another, the newly emerged group, which has undergone destabilization in the “cradle” and has lost its former balance, must undergo strict, all-around control under the influence of selection for all adaptive functions and, thus, restore its stability. In other words, an evolutionary change must go through two stages—initial destabilization and subsequent stabilization of the changed ontogenotype.

As already mentioned, the results of these events can be identified, respectively, with inadaptive and euadaptive changes in organization. In other words, in the course of evolution, the organization of living beings goes through three successive stages: inadaptation, euadaptation, and stasis (of course, if extinction does not occur, which is possible at any stage, although the highest risk in this regard is, naturally, the process of euadaptation, and the calmest is stasis). The first two stages, as the most vulnerable ones, should be short-term by necessity, whereas stasis may last for an indefinitely long time. Coming out of stasis can hardly be spontaneous and should be caused by a change in conditions. If such a change causes such an increase in the *total* elimination that exceeds the limits of reproductive potential, the population will inevitably become extinct. If this process continues for a lon-

ger time, this will entail extinction of the whole species and even higher taxa. If the conditions of existence change such that the control of the organization becomes unilateral, it cannot be ruled out that the population will be able to enter the process of inadapative transformation of its ontogenotype. Whether or not it will be able to successfully pass it and, moreover, go through the extremely risky process of euadaptation, is already a matter of chance (and a very rare chance).

Another important feature of our model that should be noted here is its autoregulation. No matter how high the stability (i.e. buffering) of the ontogenotype of even a noticeable part of the inhabitants of our planet has risen, cataclysms are unlikely to seriously threaten the diversity of life on Earth (of course, if we mean evolutionarily significant periods of time). Even if a considerable part of biodiversity “stagnates” in the perfection and, therefore, rigidity of its ontogenotypes and turns out to be significantly “thinned” by the next catastrophe (subglobal glaciation, asteroid/nuclear winter, or a similar apocalypse), nothing terrible will happen to the biosphere. The surviving species will enter a situation of incomplete communities with significantly weakened competitive relationships. This will provoke a rapid, inadapative evolution, the rapidity of which increases with the extent of the “weeding.” As communities fill up, many of those that “pulled the winning ticket” will lose it. However, the greater the proportion of losers is, the more chances will be had by those who manage to hold out a little longer. Thus, the newly formed vacancy will definitely be filled. However, the new communities may be little similar to the previous ones. Examples of such events are known (Rasnitsyn, 2012), but, of course, they require confirmation and further analysis.

Another important feature of our evolution model is the relatively low predictability of the results of its action (i.e., a very incomplete correspondence between the conditions of evolution and its results), which is due to the great complexity of the evolving system and, accordingly, the impossibility of simple, predictable solutions. This, of course, is a distressing property of the model, but it reflects the reality (in contrast to synthetic theory, from which the predictability of evolution may seem to necessarily follow but is not observed in reality).

Another important pattern of evolution that cannot be generalized from synthetic theory can be brought into conformity with the *selectionist paradigm* (“evolution is the process of the interaction of selection with the existing organization, i.e., with the product of the selection of previous generations”) if we consider adaptation as a compromise. I refer here to the unevenness of the evolutionary process, which so irrefutably arising from the paleontological data. The three-term cycle “Inadaptation—Euadaptation—Stasis,” in which the two first stages are very rapid and are

followed by a long period of evolutionary stability, easily finds parallels with the models proposed by paleontologists (Simpson, 1948; Krasilov, 1969; Eldredge and Gould, 1972; Stanley, 1975; Gould and Eldredge, 1977; Zherikhin and Rasnitsyn, 1980; Zherikhin, 1987; Shvarts, 2004) and geneticists (Carson, 1975) with the aim to introduce unevenness into synthetic theory. This similarity is undeniable but should not be overestimated. Only the phenomenology is similar, and the various mechanisms of the unevenness of the evolutionary process assumed by these models are far from being always realistic.

This does not mean that the supporters of synthetic theory have never considered the idea of ontogenotype stability. This is exactly what E. Mayr (1974; see above: balanced epigenotype) and other authors (e.g., Valen, 1982; Laurin and Bruno, 1988) wrote about. The problem is that this idea comes from a completely different paradigm, not the synthetic—holistic one.

### *Some Results*

Thus, it can be concluded that many of the observed features of the evolutionary process are in good agreement with the predictions of the holistic theory of evolution (particularly, the adaptive-compromise metaphor). However, problems also remain. The riddle of significant differences in the evolutionary rates between large groups of living organisms, which are so obviously opposite the predictions of the synthetic theory, still cannot be flawlessly explained with the holistic theory, although it does not irreparably contradict the latter. Indeed, if the main factor that slows evolution is the difficulty of changing a balanced ontogenotype (and this difficulty will only increase with its complication), then the evolution of more complex forms of life should be hampered especially strongly; however, in fact, it proceeds generally faster. At least in part, this contradiction is removed by the fact that more complex forms have larger sizes. Accordingly, they are more vulnerable when conditions change due to the obvious problems with the search for less changed habitats (refugia). This is indicated, for example, by the much longer existence of small mammals as compared to the large ones (Rasnitsyn, 1987), despite the quite comparable level of complexity of their organization. There are many other factors that accelerate the extinction and, accordingly, the diversification of more complex organisms, which was described in more detail in the already cited works (Rasnitsyn, 1987, 2002; Zherikhin et al., 2008). Of course, the discussed contradiction is still far from being resolved. However, the prospects of its successful resolution obviously exist; even now, it can hardly be doubted that the holistic concept of evolution is much more consistent with the observed evolutionary processes than the alternative approaches.

To complete the discussion of the ontology of the evolutionary process, we can conclude that the holis-

tic theory of evolution is generally in good agreement not only with the results of observations and experiments in the field of the implementation and transformation of ontogeny but also with the paleontological data. The experience of recent decades shows that a huge body of evidence can be confidently interpreted, and this gives hope that the remaining problems and issues will also be successfully resolved later.

Now let us briefly return to methodology, more precisely, to the dependence of the methodology of evolutionary biology on its ontology. We have seen that the population-genetic (“synthetic”) concept of evolution represents the evolutionary process as the dynamics of alleles in populations, which is controlled by selection and stochastic processes. Selection forms the population composition and the properties of organisms, and it does this with an accuracy that is limited only by stochastic factors and gene exchange, which unifies the structure of populations at a level that corresponds to averaged, rather than local, characteristics of selection. The organization of living beings is represented here as a set of characteristics that are freely shuffled by selection, and the evolutionary process is uniform to the extent to which the variations in selection determined by the environment are uniform. This uniformity is disturbed only by divergences and extinctions; however, only they can be used to build a natural system of organisms. In other words, a natural system that is consistent with the population-genetic theory of evolution can only be strictly genealogical, with the boundaries between taxa drawn along the points of divergence (i.e., cladogram nodes). Taxa are distinguished in accordance with the reconstructed facts of their history, rather than on the basis of their current properties, which are important only as historical evidence. This is an accurate description of the cladistic system as a strictly hierarchical system excluding paraphyletic (i.e., ancestral) taxa.

The holistic theory of evolution, on the contrary, considers the evolutionary process primarily as a process of evolutionary transformation of ontogeny, as the evolution of creodes (i.e., stabilized (selected in a series of generations) ontogenetic processes and their ensembles). Mutations and alleles serve here as *switches* between alternative trajectories of development, rather than as *creators* of structures, properties, and characteristics. The strong interdependence between the ontogenetic processes and, accordingly, between the properties and characteristics makes the optimization of the whole organism a very difficult task, the product of a tense compromise. Once successfully reached, a compromise is firmly stabilized (buffered), since a balanced complex system of the organism is very difficult to change beyond the normal intraspecific variability (which itself is already stabilized by the selection of previous generations). Therefore, evolution is significantly complicated, since a prerequisite for it is a successful escape outside the stabilized ontogeny. Moreover, such evolution is not

very predictable and is more or less abrupt, and the resulting biodiversity is more or less discrete. Discreteness is used by phylogenetics as a material for the construction of a system of organisms via the identification and tracing of hiatuses (discontinuities in biodiversity).

## CONCLUSIONS

The problems of the evolutionary wing of modern biology, which includes the sections that study the history and current state of biological diversity, including the theory and methodology of the above sections, are associated primarily with the search for a paradigm. The dispute between two approaches—the elementary (“reductionist”) and holistic paradigms—has lasted for more than a century. Surprisingly, the delimitation of these such different approaches did not occur in an explicit form; thus, the products of each of them continue to coexist in the minds of scientists, as well as in their published products. The population-genetic (synthetic) theory of evolution, which represents the evolutionary process as the dynamics of the frequencies of discrete hereditary determinants (genes) in populations under the influence of selection, corresponds to the elementary paradigm, which reduces the studied system to its elements. The observed evolutionary process is perceived as a reflection of this dynamics, and its specifics affects the features of both the genetic level of organization and selection per se. The evolutionary process is more or less uniform, and divergence and extinction are the only regular sources of discreteness that make it possible to split the result of evolution (i.e., the observed biodiversity) into taxa. This paradigm is consistent with the taxonomic concept of cladism, in which a taxon arises in the course of evolution as a product of divergence and is introduced into the system precisely on this basis, and the sequence of divergences is determined with synapomorphies.

The alternative, holistic paradigm reduces the evolving system to the whole (in particular, to the ontogenotype), i.e., to the system for the construction of a living organism in ontogeny. In the mirror of the ontogenetic theory of evolution, a complex living system, permeated with intertwining interconnections and interactions, appears as a tense compromise of conflicting requirements for the optimization of various adaptive functions. Changes to such a system are significantly difficult, hardly predictable, and more or less abrupt, and the specificity of the evolutionary process is determined primarily by the characteristics of the ontogenotype and, to a much lesser extent, by selection. Due to the abruptness of evolutionary changes, the biological diversity arising in the course of such evolution is discrete and broken by hiatuses into natural separate entities, which should be used as taxa of the general system. Accordingly, the meaning of taxonomy, which is adequate to the ontogenetic concept and the holistic paradigm, consists of the

identification of objectively existing discreteness and the tracing of hiatuses.

The available data allow us to conclude that the structure of biological diversity more likely corresponds to the ontogenetic rather than the population-genetic concept. However, the very attempt to discriminate between the concepts and methodologies used in the analysis of the evolutionary process and its results, going back to one of two competing paradigms, seems to be more important. A strict discrimination between the two paradigms and their consequences may allow us not only (and not even so much) to make a meaningful choice between them but also to eliminate the simultaneous use of mutually incompatible principles and approaches.

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#### COMPLIANCE WITH ETHICAL STANDARDS

*Conflict of interests.* The authors declare that they have no conflicts of interest.

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