



# The Morphoprocess and the Diversity of Evolutionary Mechanisms of Metastable Structures

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## Abstract

This study is a long-overdue attempt to tackle the complexity of evolutionary problems by mutually complementary conceptual approaches rather than from the standpoint of a single dominating evolutionary hypothesis. As a first step, I identify the major problems preventing a clear understanding of evolutionary mechanisms. They are associated with three “uncertainties” accompanying the analysis of evolutionary phenomena: (1) Terminological ambiguity, bordering on a logical inconsistency, in the construction of evolutionary concepts, (2) The uncertainty of direct observation, associated with the difficulties of documenting the evolutionary process and (3) The uncertainty of applicability, arising from the complex multilevel nature of the living matter. Then I outline a fairly substantial approach to the consideration of living systems. The analysis of the uncertainty of applicability suggests that the most productive approach is to apply the notion of an “evolving system” to systems of the organismic rank, understood as an object–process or a morphoprocess. Such systems (highly integrated metastable structures–processes) are dissipative structures with a cyclic character of implementation. Once we have identified the evolving system, we can determine three different conceptual models of transformism of these structures. Importantly, the delimitation is based on a unique set of their characters rather than an affiliation with a particular historic scientific tradition. These models of microevolution are indirect adaptogenesis, direct adaptogenesis and constructional transformism. The logic of each of them has often been used in various evolutionary concepts in the course of the last two centuries. Finally, I present a general outlook on the diversity of mechanisms of transformism. They fall into two groups: combinatory

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mechanisms (transformation through combinations) and transformational mechanisms as such (transformation without combination). It is the transformational mechanisms that are encompassed by the three conceptual models mentioned above. It is becoming evident that the evolutionary process is based on mechanisms described by different models. A time has come for a careful examination of various transformistic possibilities and the identification of prevailing and accessory mechanisms. Different groups of organisms/types of morphoprocesses may be characterized by different leading mechanisms of transformism, which may belong to both “combinational” and “transformational” phenomena. We have to consider a broad kit of potential evolutionary tools and try to comprehend evolutionary phenomena at a new level of conceptual synthesis.

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**Keywords**

Evolutionary concepts · Morphoprocess · Natural selection · Adaptogenesis · Self-organization · Models of microevolution

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**9.1 Introduction**

Pluralism has been making a comeback to evolutionary discussions in the last decades. The single-mindedness of the Modern Synthesis is giving way to the contemplation of the diversity of potential mechanisms of the evolutionary process. One of the reasons is the failure of the Modern Synthesis, with its supremacy of population genetics, to explain many important features of evolution (Lewontin 1974; Gilbert et al. 1996). Another is the pressure of the enormous bulk of information that has recently been obtained in five major directions. Our knowledge of (1) the molecular framework of the living cell has increased dramatically. It is becoming clear that the processes of self-regulation and regular self-assembly of complex intracellular structures prevail over stochastic mechanisms of functioning and morphogenesis. We have looked inside the cell and found not *The Blind Watchmaker* (Dawkins 1996) “but [...] a genetic engineer [...], and she has an impressive toolbox full of sophisticated molecular devices for reorganizing DNA molecules” (Shapiro 1995). Self-organization in the cell is expressed not only in reparation and replication of DNA. This principle pervades the entire cell, from molecules and their complexes to organoids (Misteli 2001; Denton et al. 2003; Kurakin 2005; Carazo-Salas and Nurse 2006; Cortès et al. 2006; Glick 2007; Misteli 2007; Karsenti 2008; Loose et al. 2008; Johnson and Lam 2010 and others).

Our understanding of (2) phenotypic plasticity of multicellular body and transgenerational inheritance (West-Eberhard 2003; Pigliucci 2010; Jablonka and Lamb 2010; Danchin et al. 2011; Kull 2014; Laland et al. 2014) has also expanded. The new information calls for a revision of the relationships between the mechanisms of phenotypic plasticity and those of genotypic adaptations and,

potentially, for a change of the evolutionary paradigm to an “extended evolutionary synthesis”.

A new outlook emerges from the data on (3) a routine exchange of genetic information between organisms from different taxonomic groups, the diversity of non-canonical means of horizontal transfer of hereditary material in different organisms and non-genetic vertical inheritance within a strain of organisms (Ochman et al. 2000; Gladyshev et al. 2008; Gladyshev and Arkhipova 2010; Boschetti et al. 2011; Haegeman et al. 2011; Koonin 2011; Husnik et al. 2013). At the same time, we are beginning to realize the importance and depth of (4) symbiotic relationships in the functioning of biological systems (Kooijman et al. 2003; Gilbert et al. 2015). Finally, (5) paleontological description of the biota’s historical development is now relying on much more complete data (Benton and Pearson 2001; Smith and Ortega-Hernández 2014; Aria et al. 2015; Darroch et al. 2018; Kaufman 2018).

These advances pave the way for a rethink of the relative importance of evolutionary mechanisms: which of them are master mechanisms and which play a subordinate role. Approaches expanding the orthodox Modern Synthesis and laying the ground for a new evolutionary synthesis have already been developed (Kirschner and Gerhart 2010; Müller 2010; Newman 2010; Pigliucci 2010; Jablonka and Lamb 2010; Koonin 2011). Let us not forget that while the Modern Synthesis claimed to possess the gospel-truth about evolution, several dozen comprehensive concepts suggested in the last two hundred years have interpreted the evolutionary process from other vantage points (see for review, Berg 1969; Bowler 1975; Lyubishchev 1982; Gould 2002; Vorontsov 2004; Nazarov 2005; Esposito 2017; Levit and Hoßfeld 2017; Loison and Herring 2017; Kutschera 2017; Popov 2018). These concepts, often branded as “dead ends” or considered as a marginal part of the scientific knowledge, might well turn out, once the rethink has been achieved, to be its solid ground, while their diversity may emphasize the plurality of mechanisms ensuring the general process of evolution of the organic world.

In such a situation, an overview of various concepts and possibly their classification by the key features is long overdue. The need for such an overview is associated not with a historical ordering of the existing knowledge but, crucially, with the development of a heuristic approach to the analysis of the diversity of evolutionary mechanisms. It was exactly such a prudent analysis of the diversity that was advocated by A.A. Lyubishchev in his paper *On the classification of evolutionary theories* (Lyubishchev 1982).

In this work I will give an example of a possible approach to the classification of conceptual approaches to the explanation of evolutionary phenomena. Its substantial part consists of three successive steps or sections. First I will consider the major difficulties arising during interpretation of evolutionary phenomena (Sect. 9.2). Then I will outline a fairly substantial approach to the consideration of living systems (Sect. 9.3), which I will then apply in the third section (Sect. 9.4) dealing with key concepts modelling the mechanisms of the evolutionary process (*Three principal models of the evolutionary process of highly integrated metastable structures*). In

*Conclusion*, I will compare the available models of evolution by their key characteristics.

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## 9.2 Major Problems in Understanding Evolutionary Mechanisms

Two centuries have elapsed since the first holistic evolutionary concept was suggested (Lamarck 1955) but the question about major mechanisms of the evolution of the organic world remains debatable. The reason is associated with three “uncertainties” accompanying the analysis of evolutionary phenomena. To begin with, (1) the subject matter of the notion “evolution” is not formalized strictly enough. This entails a *terminological ambiguity* and even a *logical inconsistency* in the construction of evolutionary concepts. Besides, the evolutionary process is difficult to document experimentally, which may be referred to as (2) an *uncertainty of direct observation*. Finally, a complex multilevel nature of the living matter, represented by a hierarchical series of mutually involved systems of various levels of organization, complicates the choice of the key system, with which the mechanisms of evolutionary process are associated. The latter uncertainty may be referred to as (3) the *uncertainty of applicability*. It is easy to see that the first uncertainty refers predominantly to epistemological problems while the second and the third uncertainties are mostly ontological.

I will deal with these three uncertainties one by one in the three subsequent sections.

### 9.2.1 Epistemological Problem of the Ambiguity of the Notion of Evolution and the Associated Problem of Uncertainty of the Term “Evolution”

The ubiquity of the term “evolution” is in stark contrast with the singularity of attempts at its clear definition. The most profound analysis of the contextual basis of this term can be found in the works of P.J. Bowler and A.A. Lyubishchev (Bowler 1975; Lyubishchev 1982). The former study considered the changes of the meaning of the term “evolution” in historical retrospective, from the denotation of embryological preformism to the denotation of changes of the living systems (transmutation of species) (Ch. Lyell, *Principles of geology* 1832, cited in Bowler 1975) and even nature in general (Spencer 1864). The latter study analysed various semantic meanings of the term “evolution” (Lyubishchev 1982) using the principle of contrapositions.

The most frequent meaning of the term “evolution” is the possibility of transformation of some species into others as opposed to the immutability of species. For a terminological specification of this semantic context—changes of species in time—the term “transformism” was suggested (Berg 1969). Other meanings of the term “evolution” (evolution as preformation; evolution as gradual development;

evolution as ascent, progress; evolution as irrevocable development (Lyubishchev 1982) as well as evolution as the emergence of the new as opposed to combinations) are very important for the definition of the key features of any hypothesis characterizing the evolution of the organic world. Their analysis calls for a special study. Here let us take note that the semantic ambiguity of this term should necessarily be taken into account in studies of evolutionary phenomena.

The choice of parameters is paramount for the comparison of various evolutionary hypotheses by their key characters. Any hypothesis describing the mechanism of evolution answers, directly or by implication, several major questions. Following A.A. Lyubishchev (1982), I will present these questions as contrapositions. Some of them were suggested by Lyubishchev himself in his paper *On the classification of evolutionary theories* (Lyubishchev 1982). Each of the contrapositions presents an evolutionary hypothesis in the continuum of the key semantic character.

- A. An assessment of the degree of finality of evolution in general: TELEOGENESIS (the development of the biota moves towards a certain result, the movement is directed, conforming to laws) VS ATELEOGENESIS (evolution is not directed, there is no movement towards any goal).
- B. An assessment of the formation of correspondence between organisms and their environment: ADAPTOGENESIS (the process of adaptation to the environment [evolutionary adaptation] is directly associated with the impact of evolutionary mechanisms) VS ANADAPTOGENESIS (adaptation of an organism is a side effect of evolution; it is secondary and is not directly associated with the impact of evolutionary mechanisms).
- C. An assessment of predominance of external or internal factors in evolution: ECTOGENESIS (the main driving forces of evolution are entirely associated with the effect of the environment, which forms corresponding evolutionary changes; functionalism sensu Kellogg 1907; Gould 2002) VS AUTOGENESIS (the entire morphogenetic potential is associated with the structural features of organisms; the environment merely triggers internal evolutionary processes of self-assembly and eliminates the organisms that fail to adapt; structuralism sensu Kellogg 1907; Gould 2002).
- D. The assessment of the degree to which evolutionary mechanisms and the processes of formation of taxa are gradual: GRADUALISM (slow and gradual modifications of species; a relative uniformity of the rate of evolution, including the cases of origin of new large taxonomic groups) VS PUNCTUALISM (an abrupt alternation of periods of evolutionary stasis and evolutionary changes; the possibility of fast formation of organisms with new complexes of characters, including those of a high taxonomic rank).
- E. The assessment of the uniqueness and the directionality of evolutionary changes: IRREVERSIBILITY (impossibility to reverse evolution following from Dollo's law (Louis 1893) as well as the uniqueness of the evolutionary emergence of species and taxa of a higher rank) VS REVERSIBILITY and REPEATABILITY (possibility of reversal to the ancestral state in the process of evolution; the possibility of multiple formations of species and higher taxa).

- F. The assessment of the integrity of evolutionary changes: MEROGENESIS (a transforming organism is a set of useful and harmful characters; some characters may change while others may remain intact) VS HOLOGENESIS (the organism is a holistic system; no character can transform by itself; a transformation is always a reconstruction of the entire system).

It goes without saying that this list is not exhaustive and may be extended by additional criteria for comparison. However, even those given above make it possible to compare evolutionary concepts on the basis of their key features rather than their affiliation with vaguely defined directions such as Darwinism or Lamarckism. On closer examination, it turns out that these directions combine several conceptual and logical approaches and are united under one and the same name merely owing to inertia and tradition (see, e.g., Delisle 2017).

### 9.2.2 The Problem of Uncertainty of Direct Observation

The prolonged nature of the evolutionary process means that it is difficult to study experimentally. Our knowledge about its course is mainly derived from the fossil record. Paleontological data, being the only source of information about the direction and features of the macroevolutionary process, are insufficient for any reliable conclusions about potential microevolutionary mechanisms. Attempting an interpretation of the available temporal series of non-ontological data, one encounters a problem of distinguishing evolutionary events as such in the series of dynamic regulatory populational phenomena (Altukhov 2003).

Numerous post hoc conclusions about the mechanisms of microevolution, based on the assessment of the frequencies of alleles/haplotypes in populational groups of the same species or in the distribution of populations of closely related species, actually allow different interpretations of the formation of these changes. Thus, they are also ill-suited for making sound conclusions about the realization of this or that microevolutionary mechanism.

Studies on “experimental evolution” of prokaryotes are probably the closest we can get to direct experimental observation of evolutionary processes (see for review Lenski (2017a, b)). These studies, based on whole-genome sequencing of the same-strain microorganisms separated by thousands of generations, made it possible to identify the key features of the mutation process and to establish the connection between the changes in the genome and the adaptive abilities of the strain. However, even for this remarkable evidence, the question about the prevailing mechanisms of microevolution largely remains open to interpretation.

### 9.2.3 The Problem of Uncertainty of Applicability

The analysis of evolutionary phenomena, similar to any other study of biological objects, requires a clear definition of the biological systems in question. The

structure of living matter is hierarchical. Studies of various levels of its organization in the context of transformism broadly operate such notions as molecular evolution, the evolution of genomes and other functional systems of organisms, cell evolution, the evolution of tissues and organs of multicellular organisms, the evolution of behaviour, the evolution of populations, communities, etc. All these viewpoints (the angles from which evolution is considered) undoubtedly provide important data characterizing various features of the evolutionary process. All of them are a reflection of the general evolutionary change of the organic world at some level of organization. However, if we are to understand the driving mechanisms of the evolutionary process, we have to identify the level of the living matter organization which makes the decisive contribution into the formation of the evolutionary trajectory. On the other hand, we also have to identify the systems at the levels of which changes are largely a reflection of the operation of the main evolutionary mechanisms.

In the hierarchy of systems, the best integrated and the most individualized (holistic) ones are unitary organisms, which exhibit a high physiological autonomy and complex behaviour as well as a high degree of morphogenetic closedness (Beklemishev 1970; McShea 2001; Levit and Scholz 2002; Granovitch et al. 2010).<sup>1</sup>

The organismic level of individuality may be expressed both at the poly- and at the mono-cellular level. This is the reason why there are two “peaks” of the degree of integration of living systems, characterized by a very different complexity of organization. One of the peaks corresponds to cellular organisms (protists and prokaryotes), while the other corresponds to the meta-cellular level of organization and, correspondingly, to multicellular or, rather, meta-cellular organisms (Metazoa, Metaphyta) (Beklemishev 1970; Granovitch et al. 2010).

Formation and existence of the systems that constitute the elements of a multicellular organism (organelles and their systems, cells, organs, and their systems) are mostly regulated by the organism itself (a highly integrated whole regulates its parts). Systems of the supraorganismic level such as populations and communities are, in their turn, distributive (Serzhantov 1972). Their elements (organisms) have a much greater systemic integrity than the system on the whole. Both biocenoses and populations are characterized by a low degree of physiological and morphogenetic closedness (Beklemishev 1970).

This means that the most significant evolutionary mechanisms should be looked for at the level of systems of the organismic rank: cells-organisms and multicellular organisms. However, even this understanding does not fully clarify the issue of the key objects of the evolutionary process because one needs to account for other essential features of the living matter such as its dynamic nature and temporal changes of the system’s characteristics. For organisms, these features are represented by ontogenetic aspects of their existence. In addition, the life of an organism is

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<sup>1</sup>Not to be confused with a more abstract term “closure” (Mossio and Bich 2017; Kauffman 2019) denoting mutual dependence of flows of energy and matter (causal regime according to the authors) ensuring the existence of biological structures far from thermodynamic equilibrium.

confined to a narrow time frame, while the issues of transformism can only be solved if we consider time frames comparable with a sequence of a series of generations (see Sect. 9.2.1): the required systems should be defined transgenerationally (see Mossio and Bich 2017). All these features of the chosen systems should be taken into account when constructing models of the evolutionary process.

In order to clarify the features of the systems with which evolutionary changes are associated most directly, let us consider a certain outlook on the living systems of the organismic rank. This outlook, which has a long and venerable history, is also promising for the solution of the current problems.

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### 9.3 Conceptualization of the Morphoprocess

The dynamic character of organization of living systems of the organismic rank was understood at the earliest stages of the development of comparative anatomy. Georges Cuvier made an exhaustive characterization of stability of form due to the dynamic nature of its components when he wrote:

[...] the essence of life [...] consists in the ability that certain corporeal combinations have of enduring for a time and in a definite form, incessantly attracting into their composition a part of environmental substances and rendering to the elements portions of their own substance. (Cuvier 1817, 12–13).

V. N. Beklemishev developed this view on the organism and formalized it in the concept of an “object-process” or an “organic morphoprocess” (see Beklemishev 1994; Levit and Scholz 2002; Granovitch et al. 2010; Granovitch 2021). This concept is rooted in the idea that an organism is simultaneously an object and a process (a morphoprocess)—a form enduring in a metabolic flow. The dynamics of the system’s components ensures relatively stable maintenance of its specific features (Beklemishev 1994). However, the form of an organism (as an epiphenomenon of the processes ensuring its existence) is not constant. It undergoes changes in the process of ontogenesis. Thus, the morphoprocess implies an inherent change of the form, which reflects dynamic changes in the functional characters of an object (an individual) in the course of its ontogenesis.

In the late twentieth century, the ideas about organisms as objects–processes found unexpected support in studies of physical and chemical properties of matter. Open systems, which absorb and give up matter and energy into the environment, may exist far from the point of energy equilibrium (that is, the maximum entropy point) for a long time. Under these non-equilibrium conditions the so-called dissipative structures are formed. These are well-ordered complexes, whose dynamic morphofunctional integrity and stability are ensured by their passage through the system of energy flow (Prigogine 1978; Cramer and Prigogine 1993). The concept of dissipative structures describes perfectly the behaviour of certain chemical reactions and physical processes and is also applicable to biological objects and probably even to social phenomena (Artigiani 1987; Cramer and Prigogine 1993; Karsenti 2008).



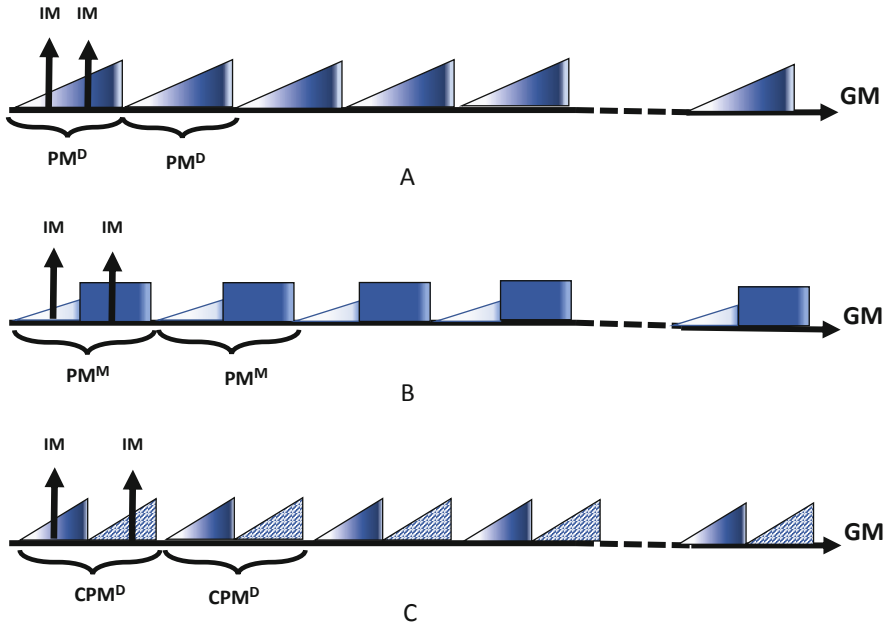
In fact, it is a universal characteristic of behaviour of non-linear open systems under non-equilibrium conditions. At the same time, the formation of order and a regular dynamics of such systems—processes emphatically pose the question about the laws and regularities of self-assembly and self-organization of the living systems (Johnson and Lam 2010; de Paoli et al. 2017; Simunovic and Brivanlou 2017; Werner et al. 2017; Bizzarri et al. 2018; Sazer and Schiessel 2018).

The term “metastable pattern”, broadly applied to physical and chemical systems—processes, denotes the phenomenon when a system, situated in a certain area of the phase space, may undergo an abrupt transition into another area following a change of the external conditions (Kivelson and Reiss 1999; Alexandrov and Nizovtseva 2014). This pattern is also used to describe the properties of “biological” molecules, e.g., the molecular dynamics of DNA oligomers (Horenko et al. 2008), as well as the organization of chromosomes (Sazer and Schiessel 2018), the organization of cellular systems into tissue constructions (Jakab et al. 2004) and molecular dynamics of cellular processes (“metastable network” processing) (Kurakin 2005, 2007). In general, a more exact term for dissipative structures existing stably far from the maximum entropy point is “metastable processes” (Johnson and Lam 2010). This term emphasizes both their dynamic exchange (absorption/expulsion) of elements with the environment (process) and their ability to maintain form under certain conditions and to shift to an entirely different form of the process under other conditions (metastable).

The application of the term “metastable process” to complex living systems highlights the fact that such dissipative structures are not structures *sensu stricto*. They are a process, that is, a form enduring in the flow of matter and energy exchange with the surrounding world (Johnson and Lam 2010). To note, the term “metastable process” fully conforms to the definition of the morphoprocess given by Beklemishev (1994) when applied to systems of the organismic rank. At the same time, it has a broader scope and may be extended to living systems of any level of organization such as enzymatic reactions, glycolytic cycle, formation of multicellular aggregates in *Dictyostelium discoideum* and self-organization in insect populations (Prigogine and Stengers 1984) as well as to complex non-living systems such as dynamic and stable atmospheric phenomena (Johnson and Lam 2010). Bearing in mind this terminological difference, I will apply the term “morphoprocess” only to organisms.

Developing the ideas about the morphoprocess in an earlier study, we have pointed out the need to specify this term in accordance with the ontogenetic features of organisms and the scheme of the life cycle (Granovitch et al. 2010; Granovitch 2021). As a result, we gave several definitions reflecting various aspects of the morphoprocess (Fig. 9.1).

*Instant morphoprocess* (Fig. 9.1, IM) is an organism in a given time moment. This notion emphasizes the mode of existence of a dynamic form; a living organism exists only in the present; an epiphenomenon of its existence in a vanishing lapse of time is an “instant form”. This notion illustrates the uniqueness of the form reflecting the interaction of structural elements and the flows of energy and information (Granovitch et al. 2010; Granovitch 2021).



**Fig. 9.1** A scheme of the structure of General Morphoprocesses (GM) with arbitrary assessments of Instant Morphoprocesses (IM), Partial Morphoprocesses (PM) and Compound Partial Morphoprocesses (CPM). Partial morphoprocesses: (a) Of organisms with direct development (PM<sup>D</sup>); (b) Of organisms with metamorphosis in the development (PM<sup>M</sup>); (c) Of organisms with direct development and a complex life cycle involving two different generations (CPM<sup>D</sup>)

*Partial morphoprocess* (Fig. 9.1, PM), the “first derivative” of the instant morphoprocess, is the existence of an organism enduring from its origin (the merging of gametes or cell division) to its death or the next division. A partial morphoprocess is the entire sequence of morphofunctional changes of an organism throughout its lifetime, ending with the disintegration of the system due to its death or the division of the cell-organism. Morphofunctional characteristics of a partial morphoprocess are not constant. They are dynamically stable at certain stages (propagation of the form) and change in a regular manner at other stages (Granovitch et al. 2010; Granovitch 2021).

*Compound partial morphoprocess* (Fig. 9.1, CPM) is a sequence of several different partial morphoprocesses in case of a complex life cycle (Granovitch et al. 2010; Granovitch 2021) such as the sequence of medusoid and polypoid generations in Cnidaria, the alternation of parthenogenetic and amphimictic forms in Aphididae, Cynipoidea and Rotifera Monogononta, the alternation of generations in Trematoda, etc.

*General morphoprocess* (Fig. 9.1, GM), the “second derivative” of the instant morphoprocess, is a rhythmic repetition of partial morphoprocess/compound partial morphoprocess at a sufficiently large time scale. General morphoprocess is characterized by a dynamic stability of the form, as is partial morphoprocess, but,

in contrast to the partial and the compound partial morphoprocess, it is also characterized by repeatability (reproducibility, cyclic nature) in a series of ancestor–progeny generations. A cycle of general morphoprocess may consist of a partial (simple) morphoprocess or a regular sequence of two or several partial morphoprocesses (a compound partial morphoprocess) (Granovitch et al. 2010; Granovitch 2021).

In the conceptual field under consideration a partial morphoprocess is an integral of instant morphoprocesses. It is characterized by considerable temporal changes of its morphofunctional characteristics even in the case of the direct development of the organism (Fig. 9.1, PM<sup>D</sup>). Using a multicellular organism as an example, we can describe the succession of these types of changes of a partial morphoprocess. First come changes associated with the dynamics of embryonic and postembryonic development. They are followed by changes associated with the formation of propagative elements (formation of reproductive structures). After that, “necrotic” changes, associated with the organism’s senescence, set in. A partial morphoprocess often consists of two or several “stable” morphofunctional states connected by fast transitions (metastability of a partial morphoprocess). A clear illustration is formed with successive stages of the larva and the imago. The most dramatic reconstructions of a morphoprocess—those that involve fast and vast changes—are called metamorphosis (Fig. 9.1, PM<sup>M</sup>). Vivid examples of such phase transitions of the partial morphoprocess may be found among annelids, molluscs, arthropods, cestodes, acanthocephalans, etc.

General morphoprocess (Fig. 9.1, GM) is a rhythmic repetition of the partial morphoprocess in a series of generations. This means that the characteristics of the partial morphoprocess set the rhythmic basis of the general morphoprocess.

The typology of morphoprocesses is such that these systems can usually be considered within similar groups called species (to be more precise, species morphoprocesses). Organisms with amphimictic reproduction are characterized by an incomplete morphogenetic closedness (Beklemishev 1970) (secludedness *sensu* Levit and Scholz 2002) in relation to each other within these groups. In contrast, species morphoprocesses of agamic species are fully characterized by a morphogenetic closedness. Such species exist as sets of parallel clonally reproducing ancestor–progeny lines. At the same time, however, these morphoprocesses, similarly to those of amphimictic species, are typologically separated from those of other species.

Intraspecific variability of the morphoprocesses is set by the plasticity of the morphoprocess and by the multiple genetic variants of species morphoprocess (genetic heterogeneity). Despite its intraspecific variability, a group of species partial morphoprocesses is characterized by a stable manifestation of a complex of the species characters. In this way, modality—the most stably reproducing complex of characters of the partial morphoprocess of a species—manifests itself. Thus, general morphoprocesses of species, as series of partial morphoprocesses constituting them, rhythmically reproduce the modal characters of a given species.

The above conceptual scheme allows a more concrete discussion of evolutionary phenomena because, overcoming the “uncertainty of applicability” (see above, Sect. 9.3), it points to the category of living systems promising for the evolutionary

analysis. It becomes clear that *the object of evolution is a concrete general morphoprocess*, in other words, the ancestor–progeny line, considered as an object–process. From this viewpoint, an evolutionary phenomenon is a stable modification of a general morphoprocess in the process of its cyclic realization.

Having identified a potential evolving system and having defined an elementary evolutionary phenomenon, we should turn to mechanisms ensuring the modification of the general morphoprocesses, in other words, the mechanisms of evolutionary changes. It is clear that they should operate at the level of the partial/compound partial morphoprocess. There are many diverse ideas on this topic, and the leading role may be attributed to different mechanisms depending on the preferred scheme of the evolutionary process. Nevertheless, all the schemes may be boiled down to three conceptual models of microevolution. They will be discussed in the next section.

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## 9.4 Three Conceptual Models of Microevolution of Highly Integrated Metastable Structures–Processes

### 9.4.1 The Model of Indirect Adaptogenesis (Granovitch 2018, 2021)

Indirect adaptogenesis is currently the most popular model within the framework of transformistic interpretations of evolution. It includes selection-based notions and postulates natural selection as the main evolutionary force. Its correspondence to empirical facts is frequently taken for granted, and other models are ignored. Indirect adaptogenesis is based on the assumption that information about changes in the environment is reflected in the general morphoprocess not through a specific direct impact but through a generalized “signal” of the magnitude corresponding to the degree of reproduction of the partial morphoprocess. At the same time, the external signal causing the transformation does not result in adequate changes of the partial morphoprocess transferred to the general morphoprocess but regulates the arrangement of partial morphoprocesses in the population. This, rather than anything else, consistently results in the change of the modality of morphofunctional characteristics of the general morphoprocesses of a given population. Hence, the name of the model—indirect adaptogenesis or indirect impact of the environment on the modality of the general morphoprocess. The model in general is logically based on *tychogenetic* and *selectogenetic* ideas. It assumes that the mechanism of evolutionary change is selectogenesis (*selectogenesis*, term—Berg 1922, cit. ex (Berg 1969; Lyubishchev 1982)), from the Latin *selectio*—choice, selection), that is, a differential contribution of partial morphoprocesses into the modality of the totality of general ones. The material making the selection possible is, it would seem, a random distribution of minute hereditary deviations of the species morphoprocess (*tychogenesis*). *Tychogenesis* (term—Osborn (1929); from the Greek *týche*—chance) assumes that small hereditary deviations are the basis of further evolutionary changes. The key aspect of the tychogenetic approach is the assumption that initial hereditary deviations are random, that is, (a) variation, accumulation of small

mutations is unlimited and non-directional and (b) the primary act of variation is independent of the need for it and the character of the need for it.

The acknowledgement of tangible differences in the effectiveness of reproduction of the carriers of such deviations introduces into play the action of the environment (*ectogenesis*). Its effect on the morphoprocess, however, is not direct but mediated by selection. On the one hand, it is postulated that organisms are different in respect of their reproductive characters and that these differences are random, independent of the environment (whose impact may only be reflected in a non-specific increase of the frequency of deviations). On the other hand, it is postulated that the input of individuals into the next generations is, correspondingly, different. These two postulates are crucial for the choice of the major mechanism of transformation within the model of indirect adaptogenesis—it is the selection of “the fittest”, or natural selection.

In general, indirect adaptogenesis is a change of the modality of the general morphoprocess *without a corresponding change* of the partial morphoprocess. The change of the modality is based on the choice of the totality of partial morphoprocesses available in the variation set of a population. Transformism is modelled as *ectogenesis* meaning that the environment is its initiating and directing force. The model is a variant of *adaptogenesis* since its mechanism is associated with the multiplication of the most successful partial morphoprocesses in the general morphoprocess and the maintenance of a “correspondence” between the modality of the general morphoprocess and the environment.

Consistently applying the model of indirect adaptogenesis, one has to assume that evolution is gradual and divergent, that the evolutionary process is undirected and that every act of speciation is unique, creating a new species, which is unique genetically, ecologically and physiologically. The stochasticity of the model’s mechanisms betrays its idiographic character: each transformation phenomenon is the result of a unique combination of the impact of factors and the work of essentially stochastic mechanisms of tychogenesis and selectogenesis. This means that the evolutionary process, in general, is also thought of as undirected—a superimposing succession of unique events. The only system in which the mechanisms of indirect adaptogenesis may operate is the totality of partial morphoprocesses. Hence, the assumption that *the population is the smallest unit of evolutionary transformations* and the promotion of the so-called populational thinking.

#### **9.4.2 The Model of Direct Adaptogenesis (Granovitch 2018, 2021)**

The model of direct adaptogenesis presents other potential mechanisms of the transformation of the morphoprocess than those described in Sect. 9.4.1. It is based on the assumption that changes conforming to the external impact, which occur during the implementation of a partial morphoprocess, can be imparted to the general morphoprocess. Changes in the environment result in corresponding fine-tunings of the implementation of a partial morphoprocess, which are specifically (that is, in conformance with the impact of the environment and in accordance with

the internal systemic organization of the object) reflected in the morphoprocess. It was this directed specific impact (as distinguished from the indirect input of differing individuals into the next generation or, in other words, of partial morphoprocesses into general ones, see Sect. 9.3) that gave the model of direct adaptogenesis its name. This logical scheme is characteristic of all the hypotheses implying the mechanism of inheritance of characters acquired by the organism during its lifetime. Direct adaptogenesis is the conceptual basis of various groups of “Lamarckian” evolutionary theories (see for review, Gould 2002; Vorontsov 2004; Nazarov 2005; Bowler 2017; Esposito 2017; Loison and Herring 2017).

In the light of this model, transformism is a constant modification of the partial morphoprocess, ongoing under the influence of the changing external conditions and accumulated, in the series of its cyclic implementation, in the general morphoprocess. Information about the changes in the environment is imparted to the general morphoprocess in a direct manner rather than as a generalized signal of the degree of reproduction. If so, it is the partial morphoprocess (not the population, which is the combination thereof!) that is the key object of potential evolutionary changes.

In the light of modern knowledge, the mechanisms of direct adaptogenesis seem to be quite diverse. They are united by one feature: a possible “trans-generational” transition of adaptive modification responses of the organism/partial morphoprocess. In other words, these responses can be reproduced in successive partial morphoprocesses. These are mechanisms of adaptive long-term modifications with subsequent genetic assimilation (Schmalhausen 1982; West-Eberhard 2003; Levis and Pfennig 2016; Levis et al. 2017), paramutation phenomena associated with epigenetic regulation of an allele under the influence of another allele (Chandler 2010; Suter and Martin 2010; Hollick 2017), various other instances of epigenetic and structural inheritance (Jablonka and Lamb 2010; Goldberg et al. 2007; Danchin et al. 2011; Rissman and Adli 2014; Tikhodeyev 2018), phenomena associated with the canalization of development and the genetic basis of phenotypic plasticity (Kirschner and Gerhart 2010; Newman 2010; Pigliucci 2010), mechanisms determining the resistance of bacteria to phages based on CRISPR-CAS system (Koonin and Wolf 2009; Deveau et al. 2010; Horvath and Barrangou 2010; Chylinski et al. 2014). An important contribution to our understanding of the potential importance of mechanisms of direct adaptogenesis is an immense bulk of data describing mechanisms of cell reparation and mechanisms of induced mutagenesis including site-specific mutagenesis under the impact of specific factors (Ponder et al. 2005; Galhardo et al. 2007; Lynch 2010) and ideas about structural limitations and dynamic nature of the genome, including those associated with environmental factors (Capy et al. 2000; Shapiro 2009, 2016; Koonin and Wolf 2010; Laos et al. 2014).

An important aspect of the model of direct adaptogenesis is its ectogenetic nature. It assumes the possibility of transformation under the impact of external factors, that is, ectogenesis. If we speak about understanding the course of evolution in general, the model is also idiographic: each act of transformation is considered unique, being

determined by the impact of a unique combination of environmental conditions. In this regard, the model lacks the prerequisites for understanding evolution as a vector process with a regular character.<sup>2</sup>

### 9.4.3 The Model of Constructional Transformism (Granovitch 2018, 2021), syn. Orthogenesis (Term—Haacke 1893, cit. ex. Popov 2018), from the Greek ὀρθός—Straight)

Within the framework of this model, the driving force of transformation are internal regularities of morphofunctional organization of living systems. The logic of the model may be characterized as self-assembly (not selection!) of increasingly more complex systems. This means that it is the only model that consistently assumes *autogenesis*, the change based on internal structural–functional laws of the morphoprocess, rather than ectogenesis. Based on this feature, this model may be defined as “constructional transformism”. It was used in numerous evolutionary concepts, from Galton’s polyhedron to the nomogenesis of L. Berg (1922), the typrostrophism of O. Schindewolf (1993) and the organicism of A. Vandel (1964) (cit. ex. Popov 2018). Variation of organisms is recognized to be not random but strictly directed. The model is *nomothetic*, being aimed at the search for strict laws of evolutionary transformations and implying the possibility of predictive interpretations. On the whole, the model recognizes the internal directivity of the evolutionary process, i.e. orthogenesis. The main problem of orthogenetic evolutionary interpretations is the seeming lack of a logical explanation of the formation of adaptations of organisms in the course of evolution, that is, their conformity to the environment (Lyubishchev 1982; Gould 2002).

The explanation of evolutionary changes with the help of constructional transformism is based on an enormous body of evidence from three major subject domains: (1) Evidence of a limited character of variation, its non-homogenous character, (2) Evidence of a regular and correlated character of morphogenetic processes in multicellular organisms and (3) Evidence of self-assembly of molecular and cellular structures. It would be futile to try to analyse all this evidence within the framework of this paper. So I will simply list the main information units providing argumentation in these three domains.

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<sup>2</sup>Significantly, it is this feature (understood or intuited) of direct adaptogenesis that made scientists look for additional macroevolutionary mechanisms when constructing holistic concepts based on this logical scheme. These additional conditions were necessary to impart directivity to the evolutionary process, to represent it as a progressive advance. Such were the “gradation principle” of Lamarck (1955), the “principle of perfection” of morphological characters of C. Nägeli (1884, cit. ex. Nazarov 2005) and the “batmism” of E. Cope (1904).

#### **9.4.3.1 Evidence of a Limited and “Non-homogenous” Character of Variation Has Been Analysed Before (Granovitch 2018, 2021), the Main Points Being as Follows**

- Fossil record indicates that morphogenesis has a limited character and that there are numerous parallelisms in the evolution of large taxonomic groups (Rozanov 1973, 2005; Tatarinov 1976; Ponomarenko 2005, 2008; Markov 2010).
- “Non-homogenous” character of variation of extant and extinct species is confirmed by the methodology of construction of potentially possible (mathematically calculated) spaces of certain characters (D’Arcy Thompson 1961; Raup 1966, 1967; Raup and Stanley 1978; Thomas and Reif 1993; Ubukata 2005; McGhee 2007; Meyen 2007; Brakefield 2010).
- The manifestation of variability range and separate characters is rather conservative in species from the same genus and even family (Vavilov 1987).
- Broad occurrence of agamic, autogamic and parthenogenetic species among protists and multicellular organisms (Hausmann et al. 2003; Ruppert et al. 2004; Grebel’ny 2008).
- The existence of numerous cryptic species (see for review, Hausmann et al. 2003; Trontelj and Fišer 2009), that is, genetically distinct groups that have all the prerequisites for a morphofunctional divergence based on genetic isolation (Bickford et al. 2006) but remain within the same typological framework.
- Canalized nature and regular character of variation of characters early in the ontogenesis (Kovalenko 1996a, b; Kovalenko and Danilov 2006).
- Ideas about systemic organization of genomes, coordinated functioning of systems of reparation of matrix processes, regulation of the level of mutational variation, directed transposition of mobile genetic elements in the genome of different species (Radman 1974; Echols 1981; Khesin 1984; Gierl 1990; Fedoroff et al. 1995; Golubovskii 2000; Ponder et al. 2005; Shapiro and von Sternberg 2005; Galhardo et al. 2007; Karpen and Hawley 2007; Asis et al. 2008; Koonin and Wolf 2009; Koonin 2010).
- An essentially non-stochastic functioning of epigenetic systems reflecting interactions based on the feedback of the genome sensu stricto (a set of species-specific sequences of DNA nucleotides) and other molecular components of the cell associated with the regulation of functioning of protein-synthesizing apparatus, dynamic structure of chromatin, the laws of “protein” heredity, the functioning of the system of “small RNA” (see a series of reviews, Allis et al. 2007; Tikhodeyev 2018).

#### **9.4.3.2 Evidence of a Regular and Correlated Character of the Morphogenetic Processes in Multicellular Organisms**

Ideas about a regular and correlated character of morphogenetic processes in multicellular organisms were first developed by Waddington (1957) and Schmalhausen (1982). These authors, aiming at a better understanding of the nature of an organism (a morphoprocess), emphasize its representation as a system of dynamic correlations. The ontogenetic development of a multicellular organism follows a stable trajectory owing to the internal correlations and the regular character of the



major processes, a phenomenon referred to as the canalization of development (Waddington 1957; Scharloo 1991). Evo-devo, currently a flourishing research direction, focuses on the following mechanisms of self-organization, autonomous development and regulation of morphogenesis.

- Self-organization of cellular aggregates into regular multicellular structures, including canalized development of embryos at the early stages of embryogenesis (van den Brink et al. 2014; Baillie-Johnson et al. 2015; Bedzhov et al. 2015; Ozone et al. 2016; Turner et al. 2016; Simunovic and Brivanlou 2017; Bizzarri et al. 2018).
- Formation of specific architectonics of organs using interaction of differentiating cells, including the formation of complex organ-like aggregates from pluripotent iPS cells (Taguchi et al. 2014; Dye et al. 2015; Sakaguchi et al. 2015; Takasato et al. 2015; Guye et al. 2016; Koehler et al. 2017; McCauley and Wells 2017).
- Autonomous patterning of repeated structures based on the physical–chemical reaction–diffusion model (Turing model, Turing 1952) (Cooke and Zeeman 1976; Sheth et al. 2012; Tsiairis and Aulehla 2016; Liao and Oates 2017).
- Processes of self-organization, autonomous coordination of different cell types during the formation of tissues and complex systems of organs of a multicellular organism (Sheth et al. 2012; Raspopovic et al. 2014; Onimaru et al. 2016; Walton et al. 2016).
- Systems switching the development to new stable trajectories based on dynamic modules (Newman 2010).
- Potential mechanisms responsible for the emergence of evolutionary novelties (West-Eberhard 2003; Müller 2010).

#### **9.4.3.3 Evidence of Self-Assembly of Molecular and Cellular Structures**

A plethora of data accumulated in the last decades indicates that self-assembly and self-organization of molecular and cellular structures are often due only to their constructional features and are not directly connected with the genetic apparatus of the cell. Both self-assembly and self-organization processes are of interest to us. The distinction between them is traditionally based on energy dependence (Gerhart and Kirschner 1997; Halley and Winkler 2008; Werner et al. 2017). Processes considered as self-assembly are characterized by the minimization of energy in the system, which has approached the state of thermodynamic equilibrium. Correspondingly, these processes do not need an energy supply. On the contrary, self-organization implies the formation of elaborate complexes in a system that is far from the zone of thermodynamic equilibrium. Stable existence and increasing complexity of such systems are possible only under conditions of constant energy flows through them (Prigogine and Stengers 1984). It is noteworthy that processes of both types also contribute to the canalized development of a multicellular organism (see above Sect. 9.4.3.2).

There is ample evidence of self-assembly and self-organization of molecular complexes and organoids of the cell. Leaving aside self-organization and replication of the genetic apparatus, which are quite well studied, I would like to note that almost

all major structures and functions of the cell operate based on these physical and chemical principles. There are data about the self-assembly of membranes, locomotor systems ensuring motility of cellular elements, the self-assembly of organoids, the assembly of cell division apparatus, the formation of vacuoles and, finally, the spatial organization of chromosome material (Palade 1983; Attardi and Schatz 1988; Mitchison 1992; Warren and Wickner 1996; Nédélec et al. 2003; Denton et al. 2003; Carazo-Salas and Nurse 2006; Cortès et al. 2006; Misteli 2007; Papanikou and Glick 2009; Svetina 2009; Inagaki and Katsuno 2017; Sazer and Schiessel 2018). Considering these data, we begin to intuit that the entire morphofunctional organization of the cell is a totality of coordinated processes of self-organization (Misteli 2001; Kurakin 2005; Kholodenko 2006; Karsenti 2008; Johnson and Lam 2010). Hence, we may characterize the cell as a morphoprocess implemented regularly under given physical conditions.

Concluding the third section, I would like to remind the reader that the three models explaining the mechanisms of microevolutionary process (transformism) are far from being new. The first model had underlain the ideas about natural selection in the classical Darwinism and Modern Synthesis (but see Delisle 2017, 2021 to emphasize the differences of the concepts). It incorporated the ideas of Weismann about the continuity of germplasm, assimilated views on heredity, was reborn as Modern Evolutionary Synthesis and underwent numerous modifications under the pressure of new data (Gould 2002; West-Eberhard 2003; Newman 2010; Müller 2010; Pigliucci 2010; Jablonka and Lamb 2010). The second model is rooted in the ideas of Lamarck and Saint-Hilaire, which have been repeatedly reborn as Neo-Lamarckism. The third model also has a venerable history in its numerous guises of ortho-Lamarckian/orthogenetic evolutionary concepts. A comparative characteristic of the three logical schemes presenting potential evolutionary mechanisms transforming the morphoprocess is given in Table 9.1.

These three mechanisms, as well as a group of mechanisms based on a combination of different morphoprocesses (transformation through combinations), are presented in Fig. 9.2, which is discussed in more detail in Conclusion.

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## 9.5 Conclusion

In the three main sections of this work, we specified what exactly we wanted to know about living systems by singling out transformism as the central meaning in the polysemantic notion of “evolution”. Then we identified morphoprocesses as the systems to which this notion can be applied most productively. Finally, we concluded that most of the explanations of the mechanisms of transformism ever suggested can be arranged into three logical models describing the transformation of the modality of the general morphoprocess.

Let us now present the differences between the models (and, strangely enough, their similarities too) as a “cladogram of similarities and dissimilarities”. In order not to mislead the reader, who might be used to phylogenetic constructions, I specifically state that this scheme bears no relation to the historical outlook on the development

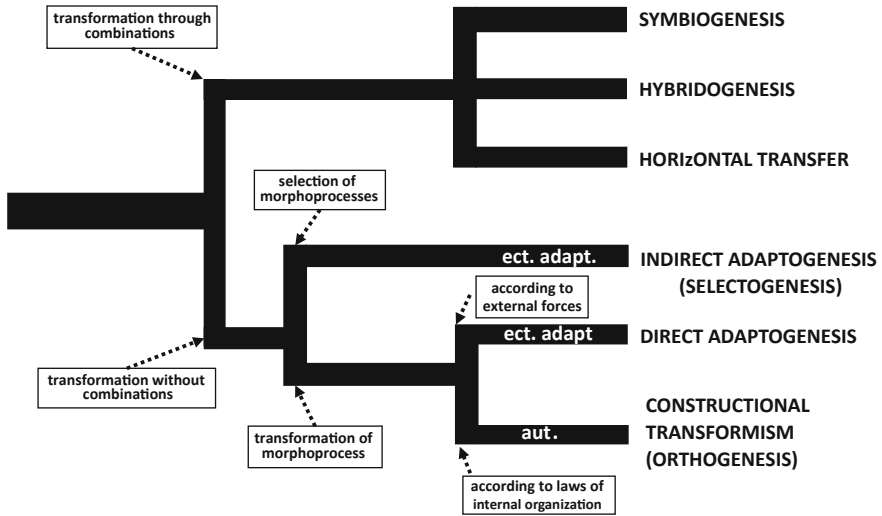
**Table 9.1** A comparative characteristics of the three major logical models of transformism

	Indirect adaptogenesis	Direct adaptogenesis	Constructional transformism
Degree of finalism of evolution in general	Ateleogenesis (micro- and macroevolution)	Ateleogenesis (microevolution) Teleogenesis (macroevolution)	Teleogenesis (micro- and macroevolution)
Relationship between the formation of adaptations and the mechanism of microevolution	Adaptogenesis	Adaptogenesis	Anadaptogenesis
Prevalence of internal or external evolutionary forces	Ectogenesis	Ectogenesis	Autogenesis
Degree of gradualness of microevolution	Gradualism	Gradualism	Punctualism
Degree of irreversibility of evolution	Irreversibility	Irreversibility	Reversibility and repeatability
Degree of autonomy of separate features of an organism	Merogenesis	Hologenesis or merogenesis	Hologenesis
Nomothetic or idiographic character	Idiographic	Idiographic (microevolution) nomothetic (macroevolution)	Nomothetic
The unit of microevolution	Population/set of several general morphoprocesses	Single general morphoprocess	Single general morphoprocess

of ideas. Its only purpose is to illustrate the differences in the logic of the models in the order of their similarities and dissimilarities (Fig. 9.2).<sup>3</sup>

Thus, evolutionary changes in the sense of a stable transformation of the modality of the general morphoprocess may occur in two essentially different ways. The first way is the possibility of a combination of characters of partial morphoprocesses of different modalities owing to their incomplete physiological and morphogenetic closedness of organization (see Beklemishev 1970). This category embraces hybridogenesis, symbiogenesis and horizontal transfer of hereditary material—phenomena whose importance for the evolutionary process, in general, have been actively discussed in recent years. Suffice it to say that the symbiogenetic hypothesis is currently considered as the best suited for explaining the origin of various structural types of the eukaryotic cells (Margulis and Fester 1991; Chapman and Margulis 1998; Antonelli et al. 2003; Kozo-Polyanskii and Raven 2010). Horizontal

<sup>3</sup>Let us note, nevertheless, that all “phylogenetic schemes”, seemingly reconstructing evolutionary events and based on any character basis, are, strictly speaking, simply diagrams of “similarities and differences”. On the contrary, the means of their evolutionary interpretation (evolutionary hypothesis for a given group of organisms as such) would be radically different depending on the assumed model of transformism.



**Fig. 9.2** A scheme showing relationships of different models of transformism in the form of a hierarchical tree. Brief comments on the semantic dichotomies of different concepts are given in brackets. *Ect.* ectogenesis; *adapt.* adaptogenesis; *aut.* autogenesis

transfer of genetic material is already assumed to be a leading evolutionary mechanism in prokaryotes (Koonin 2011), while the body of evidence indicating its importance for multicellular eukaryotic organisms is also growing (Gladyshev et al. 2008; Boschetti et al. 2011; Fussmann 2011; Haegeman et al. 2011; Husnik et al. 2013).

In this work, I focussed on other means of transformation, those that do not imply the above combinatory phenomena. The basis of their diversity is the principle of “transformation without combination”, that is, without the combination of partial morphoprocesses belonging to different “species” (see Fig. 9.1). In this case, we deal with a situation when the transformation of the general morphoprocess should be ensured only by its own properties under the influence of environmental factors.

The most important dichotomy associated with this idea results in two different interpretations of the leading mechanisms of the evolutionary process. The first interpretation assumes the leading role of two coupled phenomena, tychogenesis and selectogenesis. It is based on the idea that the modality of the general morphoprocess changes using a selection of partial ones (See Sect. 9.4.1; indirect adaptogenesis). The recognition of such a model as the only correct one necessarily leads to the recognition of the stochastic character of evolution in general and the idiographic nature of our ideas about it. The directivity of the evolutionary process is then a moot question.

Non-fulfilment of the conditions of tychogenesis entails the admission that the mechanism of indirect adaptogenesis is secondary. In this case, the leading role among the mechanisms of transformism should be given to non-selective phenomena, shown in the scheme in the second branch as “transformation of partial

morphoprocesses”. In this case, we assume a change of the modality of the general morphoprocess using transformation of partial morphoprocesses successively implemented within it. This interpretation, in turn, implies two different emphases on the prevailing mechanisms of transformation.

The first emphasis is on the recognition of the possibility and the leading role of the changes of the partial morphoprocess commensurate with the environment, which are imparted to the general morphoprocess (Sect. 9.4.2, direct adaptogenesis). To note, in this case, too, the ideas about microevolution are idiographic, being based on the direct fixation of stochastic fluctuations of the environmental impact in the general morphoprocess. The second possible emphasis is on the primacy of structural–functional features of the partial morphoprocess for its further modification and the recognition of the environmental impacts as a potential trigger of such modifications (Sect. 9.3.3, constructional transformism). Only these ideas can be the basis of an outlook representing evolution as a regular, directed process and promoting a nomothetic understanding of evolutionary phenomena.

In two out of the three concepts of “transformation without combinations” (indirect and direct adaptogenesis), the adaptation of the morphoprocess to the conditions of the environment and the formation of adaptations are a direct consequence of the operation of the mechanisms of transformism (selectogenesis in the former case and direct, hereditarily fixed reaction in the latter case; adapt. on the scheme). In the case of constructional transformism, an adaptive character of evolution is not evident and calls for additional explanations. I have suggested a possible explanation of the formation of multilevel adaptations within the framework of this model in earlier work (Granovitch 2018).

In the same two concepts (indirect and direct adaptogenesis) transformism appears as an ectogenetic process (ect. in the scheme). In both cases, evolution is triggered, directed and fully determined by the impact of the environment. In contrast, constructional transformism is an autogenetic process (aut.). The emphasis in the explanation of the transformation of the morphoprocess is shifted to internal constructional features of the living matter, the environmental impact being at best a trigger.

In one of the models (indirect adaptogenesis), the leading role in the transformation of the modality of the general morphoprocess is ascribed to natural selection (the mechanism of selectogenesis). In direct adaptogenesis and constructional transformism, the role of the selective principle and hence natural selection is downplayed to an accessory mechanism altogether lacking morphogenetic significance.

In conclusion, I would like to note that, on the one hand, each of the three conceptual models of transformism has its own internal logic. On the other hand, however, these concepts cannot and should not be considered mutually exclusive. The reign of a single concept—indirect adaptogenesis embodied by the Modern Synthesis—is over. A time has come for a careful examination of various transformistic possibilities and the identification of prevailing and accessory mechanisms. Different groups of organisms/types of morphoprocesses may be characterized by different leading mechanisms of transformism, which may belong

to both “combinational” and “transformational” phenomena (Fig. 9.2). A vivid example is the recognition of the horizontal transfer of genetic material as one of the leading evolutionary mechanisms in prokaryotes (Koonin 2011). What we currently need most is a balanced assessment of the contribution of different mechanisms characteristic of a given group of organisms/types of the morphoprocesses and the identification of the leading ones. In the age of “postmodernism in the understanding of evolutionary phenomena” (Koonin 2011), we have to consider a broad kit of potential evolutionary tools and try to comprehend evolutionary phenomena at a new level of conceptual synthesis, “Transformism 2.0”, based on the input from all conceptual approaches.

**Acknowledgments** I am eternally grateful to Natalia Lentsman for her creative, thoughtful, generally invaluable contribution to the English translation of the manuscript. This study was supported by a grant from the Russian Science Foundation (RSF) no. 19-14-00321-П.

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