

The principle of counter-directional morphological evolution and its significance for construction the megasystem of protists and other eukaryotes

Lev N. Seravin

Biological Research Institute of St. Petersburg State University, St. Petersburg, Russia

Summary

Summing up, the following conclusions can be made.

1. Evolution of living systems follows the principle (law) of counter-directional morphological evolution, according to which both gradation and degradation of organisms can take place.
2. Combination of progressive and regressive changes in the structure of living creatures leads to the appearance of new taxa of any rank, including very high one (class, phylum, etc.).
3. In different groups of living organisms progressive and regressive morphological changes or their combination can result in the appearance of very similar but not identical taxa (e.g. sister taxa). The law of irreversibility of evolution should be substituted by a broader and more accurate law. It can be called the law of non-identity of similar structural transformations in different taxa of living organisms.

Key words: morphological evolution, progressive and regressive evolution, Dollo's law

To construct a natural system of protists the role of not only progressive but also regressive morphological changes taking place in the process of those organisms' evolution should be taken into account. The validity of the above statement can be conveniently demonstrated when considering changes upon the megasystem in the works of Cavalier-Smith during the last 15 years. Proceeding from a fairly widely spread point of view that the simpler the living organisms are the more originally primitive they should be, he united the macrotaxa including the flagellates and amoeboid organisms devoid of mitochondria into a single subkingdom Archezoa as a phylogenetically initial state for all the rest of the Protozoa kingdom (Cavalier-Smith, 1983). The investigator included four phyla into this new taxon: Archamoeba (mastigamoebae, entamoebae, *Pelomyxa palustris*), Metamonada, Microsporidia and Parabasalia (trichomonades, hypermastigines). Yet soon, Cavalier-Smith (1987, 1991, 1993) drastically isolated Archezoa from all the other eukaryotes, elevating the rank of this taxon to that of kingdom and even the superkingdom. At the same time he removed the phylum Parabasalia from the Archezoa since its representatives possess hydrogenosomes – microbodies which appear to be related to mitochondria. Besides, the Parabasalia possess dictyosomes which, in Cavalier-

Smith's opinion, are always absent in the true Archezoa. Thus only three phyla remained in this superkingdom: Archamoeba, Metamonada and Microsporidia – unicellular eukaryotes which, in Cavalier-Smith's opinion, are initially devoid of mitochondria, chloroplasts, dictyosomes, and any kind of microbodies. Yet soon, under the influence of convincing biochemical data, Cavalier-Smith (1991, 1993) removes the Entamoebidae from the Archezoa and includes them in the superkingdom Protozoa.

In the 90ies a series of studies on nucleotide sequences and aminoacid sequences of heat shock proteins in a number of archezoan representatives appear, which showed distinctly that the ancestors of those organisms had already possessed mitochondria (Clark and Roger, 1995; Henze et al., 1995; Bui et al., 1996). Cavalier-Smith (1996/1997) excludes the phylum Archamoeba from archezoans. He divides the Protozoa into two subkingdoms, Eozoa and Neozoa. He includes the Percolozoa, Euglenozoa and Trichozoa phyla in the Eozoa, the Parabasalia being included as a subphylum into the Trichozoa. The subphylum Archamoeba (which also contains the class Entamoebae) appeared to be included in the phylum Lobosa, which was distinguished from that of the Rhizopoda by this author. Thus, after all this transformations, only two phyla,

Metamonada and Microsporidia remained in the superkingdom and kingdom Archezoa.

Meanwhile some molecular biological studies have been appearing in which it was shown that microsporidia should be considered as related to higher fungi, simplified owing to intracellular parasitism (Katiar et al., 1995; Keeling and Doolittle, 1996). Therefore Cavalier-Smith (1998) removed the Microsporidia from the Archezoa. It would seem that this taxon should be liquidated. Yet the investigator acted differently. He completely changed the whole Eukaryota megasystem, stopped dividing these organisms into superkingdoms and left only 5 kingdoms: Protozoa, Animalia, Fungi, Chromista and Plantae. All the former innovations were completely given up. The Protozoa kingdom is now divided into two subkingdoms: Archezoa and Neozoa. Cavalier-Smith abolished the Eozoa subkingdom which he had established only half a year before (Cavalier-Smith, 1996/1997). To the archezoans, besides the phylum Metamonada, the Trichozoa were also attributed. The Parabasalia, which some time before had been the first to be removed from the archezoans (Cavalier-Smith, 1987, 1991), were placed as a subphylum into the Trichozoa. In the new system the Archamoeba were reduced in rank to the non-taxonomical group “infraphylum” in the new subphylum Conozoa (within the phylum Amoebozoa). He transfers the Trichozoa phylum (together with the subphylum Parabasalia) from the Archezoa subkingdom into the reestablished Eozoa kingdom (Cavalier-Smith, 1998). Therefore only the metamonades remained within the archezoans.

Studies of the fine structure of *Pelomyxa palustris* (Goodkov and Seravin, 1991, 1995) have shown that this protozoan possesses hydrogenosome-like microbodies and dictyosomes. From the above it follows that *P. palustris* is not an archamoeba. The performed organellologic analysis of those protozoa which Cavalier-Smith had then attributed to the Archezoa suggested that all the Archezoa had sometime originated from ancestor forms which possessed mitochondria, i.e. the present protists devoid of these organelles had lost them secondary, having reverted to the anaerobic or parasitical way of life. On the whole the analysis performed also showed that in the process of evolution protozoans may lose mitochondria, chloroplasts, flagella, dictyosomes, and all these organelles, taken together, in this way approaching the proeukaryotes by their level of organisation. Here it should be reminded that Margulis (1981), when *P. palustris* was held to be devoid not only of mitochondria, but also of all the other main organelles of the eukaryotic cell attributed this amoeboid organism to the forms evolutionary close to the proeukaryotes.

All the above testifies to the fact that regressive evolution may result in fairly significant changes in the protists organisation. Just how it can influence the eukaryotes macrosystems was shown using Cavalier-Smith's publications as an example. Unfortunately there seem to be no summarizing works in which the correlation between pro-

gressive and regressive changes in the process of protists evolution would be considered. At the same time, this problem has long been under study on multicellular animals. Therefore let us turn to these studies.

Acquaintance with the works of A.N. Severtsov (1912, 1914, 1925, 1939), Schmalhausen (1969, 1983) and other authors who studied seriously the problem of the correlation between progressive and regressive evolution did a lot for my understanding of it but still does not give answers to all the questions. One has to support the opinion of those authors (e.g. Fetisenko, 1973 and Georgievsky, 1985) who suggested that this problem is far from being solved, mostly because the problem of regressive evolution is insufficiently worked out. Let us try to clarify the reasons for such a situation and find some new approaches to the analysis of the correlation between progressive and regressive changes in the process of the morphologic evolution of living systems.

The complexity of the structural organization of different living creatures is so different that long before the appearance of the evolutionary idea there appeared a conception of some “ladder of life” or “ladder of creatures” reflecting different levels of the organic world objects' organization. For us this conception is usually associated with the name the Swiss naturalist and philosopher Charles Bonnet (1720–1793). Lamarck (1809, 1935) showed in his “Philosophy of Zoology” that only admission of the existence of consistent plants and animal evolution allows to the understand and explain rationally their gradation, i.e. the existence of different levels of their organization (lat. gradatio – gradual elevation, gradus – step).

Charles Darwin, in chapter IV of his famous book “The Origin of Species”, reports that when natural selection does not work organisms stay practically unchanged for a long time. Under the pressure of selection they evolve, complicating their organization. Yet the opposite process of the simplification of the organism structure may take place. He writes the following: “On the other hand, we can see, bearing in mind that all organic beings are striving to increase at a high ratio and to size on every unoccupied or less well occupied place in the economy of nature, that it is quite possible for nature selection gradually to fit a being to a situation in which several organs would be superfluous or useless: in such cases there would retrogression in the scale of organisation” (Darwin, 1872, p.98).

Following Ch. Darwin, I.I. Schmalhausen (1969) considers reverse evolution possible. I.I. Mechnikov in 1876 (Mechnikov, 1950) calls regressive evolution reverse movement in the development of organisms. It is true that Ch. Darwin (1898) repeatedly emphasized in his “Origin of Species” and other works that evolution of organisms was irreversible. This line was diligently traced by S.A. Orlov (1981). It is quite understandable that such an idea is not quite consistent with the conception of the reverse course of the evolutionary process. Besides, Ch. Darwin, while studying in detail the problems con-

nected with the rudimentation of organs and simplification of the structure of sedentary and parasitic organisms, does not cite any examples which would clearly show that in the process of evolution such regress of living creatures can take place that some species from the above taxa descend to the level of lower positioned taxa, i.e. there may be a real movement down “the ladder of creatures”. In my opinion, it was those two circumstances which determined the existence of contradictions in working out the problem of correlation between progressive and regressive evolution in later investigators.

It is well known that A.N. Severtsov paid much attention to the development of this problem. Of special interest are his books published in 1912, 1914, 1925 and 1939, in which he presents a lot of facts in favour of the conception, developed by him, on the widely spread regress in Metazoa. Thus he writes that “in the animal world regressive changes in the organs and even whole systems of organs are very frequent, and we can presume that we do not know of any group of more or less organized animals, in which one or another quite developed organ did not become reduced wholly or partly (Severtsov, 1939, p.538). At the same time, in all the above mentioned works he emphasizes that progressive and regressive changes are interrelated and occur simultaneously in the same structures, both in aromorphosis and idioadaptation. As early as in his 1914 study A.N. Severtsov claims that “a purely progressive evolution usually occurs only after considerable changes, whereas after greater changes we usually observe that some parts of the evolving organ change progressively, others regressing or becoming atrophied” (p.55). To put it aphoristically, there is no progress without regress. In the scientist’s opinion, a simultaneous combination of two counter-directed morphologic progresses is to be observed even in the course of evolution so regressive that it results in the general degeneration of organisms. A.N. Severtsov (1939) describes this phenomenon as follows: “... The main characteristic of degenerating forms is atrophy of some active organs; it is this character that is the first to leap to the eye of the observer. Yet a more detailed study of the reduction phenomenon suggests that atrophy of active organs in parasites and sedentary forms is not an independent process but only the result of progressive development of a whole number of other organs whose functions replaced those of the above organs and made their very existence superfluous” (p.320). Thus it is possible to say: “there is no regress without progress”. Moreover, it transpires that even under general degeneration of organisms the course of events is “monitored” by progressive morphological changes, whereas regressive ones seem to be playing a secondary part. Therefore A.N. Severtsov never mentions backward or recurring evolution of organisms but only their partial or general degeneration.

Very many investigators adhere to the motto “there is no regress without progress” (Davitashvili, 1956, 1973;

Erlich and Holm, 1966; Schmalhausen, 1969, 1983; Grant, 1980; Georgievsky, 1985; Berdnikov, 1990; etc.). Yet at the same time they usually forget another motto: “there is no progress without regress”. This usually results in underestimation or neglect of regressive evolution. Let us quote some authors to illustrate this.

I.I. Schmalhausen (1969) writes in his book “The Problems of Darwinism”: “It is the process of elevating organization that is the general characteristic of evolution as a whole... Alongside progressive development there is sometimes a certain stagnation in the evolution to be observed, and even backward movement – general regress” (p. 406).

L.Sh. Davitashvili (1956) makes an emotional statement: “... we think it expedient to emphasize that contrary to the tendency of some scientists it is absolutely impossible to hold regressive movement as something directly opposite to progress in the development of living nature. Some biologists are wrong in believing that regress phenomena are as significant in the history of organic world as progress phenomena; progress reigns supreme in the historical development of living nature, development from the lower to the higher” (p. 92).

N.V. Timofeev-Resovsky and co-authors (1969) hold that “the conception of arogenesis should be extended to the phenomena of group regress which some investigators (Severtsov, 1939; Schmalhausen, 1969; etc.) distinguish as an independent type of evolutionary progress (catogenesis, degradation). While regress in the development of the group is generally relative, the type of the evolutionary process in this case remains the same as that during morphological progress, the group’s transition into another adaptive zone” (p. 228). Thus these authors deny regressive changes as a special trend in morphological evolution. Therefore it is not surprising that Rezanov (1987) summarizes opinions of different authors who studied the problems of the correlation between progressive and regressive evolution as follows: “In modern natural science, especially biology, evolution is understood as the forward movements of life consisting in creating more complicated organisms” (p. 77).

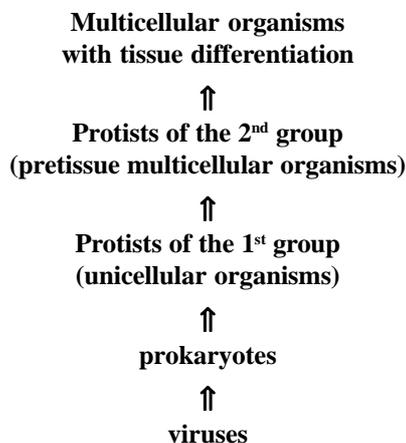
In general, regressive evolution can be seen to “disappear”, only progressive one remains. It may not be worth while to specially emphasize that all the above authors are adherents of Dollo’s law.

It seems to be time some new approaches were found which would help investigate the problem of the correlation between progressive and regressive changes taking place in the process of morphological evolution. In my opinion, the following steps should be taken. First, the exact meanings of the words “progress” and “regress”, so important for us, should be defined. Second, distinct levels should be distinguished of the living systems organization (a modern “ladder of creatures” should be created), which would allow to see clearly whether, in the course of evolution, living creatures are able or unable to move down from

the “ladder of creatures”. Third, all the main types and forms of morphological regress should be accounted for. Fourth, it is necessary to prove that regressive changes may play a considerable part in the appearance of taxa of the highest rank (the level of classes, phyla, kingdoms). Five, a thorough penetration into the meaning of Dollo’s law which is usually referred to as the law of the irreversibility of evolution.

Let us try to use all these approaches. And first of all, let us turn to the dictionaries (Dvoretzky, 1976; Komarova, 1992). Two main meanings appear to correspond to the word “progress”, i.e. it conveys at least two different notions. The first means development from the lower to the higher, which in our case means moving up the “ladder of creatures”. The second means forward movement, perfection; in other words, horizontal movement. It is not difficult to see that these two meanings correspond to two different types of progressive evolution: arogenesis and allogeneses (see Timofeev-Resovsky et al., 1969).

The word “regress” also harbors two words: a) passing over from the more complex to the lower forms, and b) moving backward. In the first case this corresponds to moving down the “ladder of creatures”, in the second, reduction of organisms in the course of “horizontal evolution (during idioadaptations). Correspondingly, to avoid contradictions two forms of correlations between progressive and regressive evolution should be distinguished. If it is possible to bring out distinctly the movement of organisms up and down, the “ladder of creatures” one should speak using the terminology of Lamarck (1809) and Huxley (1957, 1963), of gradation and degradation of living organisms respectively. Yet if the level of their organisation does not change significantly, in spite of their structure becoming simpler, i.e. during horizontal evolution, one could speak of regressive changes in one or another structural formation or of underdevelopment of the whole organism (e.g. in case of neoteny). A clearcut morphologic gradation (the modern ladder of animals) can be judged about if we position different groups of animals into the following vertical row:



If the level of organization of living creatures can “shift” downwards this imagined ladder, it can be stated that degradation as an evolutionary event does exist.

Two basic types of morphological regress should be discerned: **reduction**, i.e. incomplete development or simplification, and **segregation** – a separation of a part or division into parts. Two forms of reduction are well known – **rudimentation** and **neoteny** (Severtsov, 1939; Schmalhausen, 1969, 1983; Terekhin, 1975; Matthews, 1983; Takhtadjan, 1983; Dzwillo, 1984; Borkhsenius and Chernova, 1989; Wasser, 1989; Seravin, 1992, 1995). Rudimentation in metazoans leads to an essential lessening, embrionization and in utmost cases to complete disappearance of the whole systems of organs, separate organs or tissues, and in protists – of organelles and other subcellular structures.

A great reduction was undergone by morphological systems of sedentary and parasitic Metazoa. It can be shown on the example of the phyla Pogonophora, Bryozoa, Phoronida, classes Ascidia (phylum Chordata), and also the classes Trematoda and Cestoda from the phylum Plathelminthes and others. In all these animals, alongside with the disappearance of some organs, new formations, progressive morphological changes appear, which compensate to some extent the functions of the structures lost in evolution. Because of that these taxa did not descend to a lower level of organisation. For example, trematods and cestods are flatworms, as well as their ancestors. Pogonophors are in no way inferior to annelids (the phylum Annelida), from which they are now reliably known to have originated (see McHugh, 1997). At the same time, were it not for regress, phyla and classes mentioned above could not have appeared at all.

However regressive evolution can lead to other results, as demonstrated by a parasitic phylum Mesozoa. The very name of this taxon shows that zoologists think these animals to be intermediate between protists and metazoans. An egg of mesozoans of the class Orthonectida gives rise to a larva; its body is covered by ciliated epithelium and inside there are cells of single type. After penetration into its host the larva loses the outer cell layer, and the remaining inner cells merge to form a multinuclear plasmodium, i.e. a real protist. Later some of the nuclei with the surrounding cytoplasm separate as cells. Many of these cells develop into rather simple males and females: they lack digestive apparatus, a general nervous and excretory system (Malakhov, 1990). Zoologists justly consider Mesozoa which do not possess tissue organization to have originated from some more complicated free-living Metazoa – cnidarians or flatworms – by means of deep degradation connected with parasitic way of life. However it should be noted that recent investigations of fine structure of orthonectide females have shown that mesozoans are more complicatedly organized than thought before (Slusarev, 1994).

Phylum Myxozoa (myxosporidians) embracing fish parasites with few cells has always been attributed and is attributed now to protists. However some authors have long been falling to a conclusion that these animals appeared in the process of regressive evolution of some Cnidaria or Mesozoa (Weil, 1938; Gottschalk, 1957; Lom, 1977). This is not a chance opinion: though myxosporidian trophozoite is a multinuclear plasmodium, its spores usually consist of five cells of three different types, i.e. cellular differentiation is present, which is atypical for protists. Two cells form surficial valves of the capsule, two form lasso cells, and one is a binuclear amoeboid embryo.

Recently Siddall's group (Siddall et al., 1995) has performed a detailed study of the fine structure of pansporoblast (a spore in the process of formation) of myxosporidian *Thelohanellus nikolskii* and has found a number of morphological features characteristic of Metazoa. There are cytoplasmic bridges with longitudinal microtubules between the cells of the developing spore, which is similar to the i-cells of cnidarians. There are well-pronounced septal cellular contacts and desmosomes between capsulegenic cells, which is characteristic of epidermal cells of most Metazoa. Such contacts are absent not only in multicellular protists but even in sponges. Lasso cells formation in pansporoblast takes place according to the same scenario (up to the same details) as that of similar capsules in cnidarians. Finally, thin collagenous fibres are excreted around the spores. Presence of collagen is characteristic of all representatives of Metazoa without any exceptions. At the same time, it has never been found in either uni- or multicellular protists. Thus, taking into consideration cell differentiation in myxosporidian spores, it can be concluded that these organisms are now known to possess five characters typical for or widespread in Metazoa but unknown for protists.

Siddall et al. (1995) have performed an investigation of nucleotide sequences of 18S rRNA in myxosporidian *Henneguya doori* and in parasitic narcomedusa *Polypodium hydriformis*, establishing that they are closely related, sister species. Comparison of similar molecular-biological data obtained from studying 18S rRNA in other myxosporidians and cnidarians, has supplemented the conclusion on the origin of Myxozoa from Cnidaria by means of degradation. The researchers are coming to an opinion that phylum Myxozoa should be annulled and myxosporidians should be introduced into phylum Cnidaria as a taxon of lower rank.

Metazoan nature of myxosporidians is also supported by other authors (Smothers et al., 1994; Schlegel et al., 1996; Andree et al., 1997). Cavalier-Smith who in 1993 insisted that Myxosporidia were and would always remain protists, two years later (Cavalier-Smith, 1995) transferred them together with Mesozoa into Animalia (=Metazoa) kingdom, still, however, calling these groups of organisms protists.

Thus, though Myxozoa are pre-tissue multicellular protists by their structural organization, on molecular and subcellular levels they bear visible traces of their metazoan origin.

Neoteny, usually followed by evolution by means of arogenesis is well known to give rise to new macrotaxa. According to A.L. Takhtadjan (1954, 1983), the appearance of vascular plants higher taxa, including phylum and class, took place on the basis of neoteny. It is established that the origin of appendicularians (class Appendicularia) is connected with neoteny of ascidians (Garstand, 1922; Ivanova-Kazas, 1995). There are good reasons to believe that the origin of some other classes and even types of invertebrates was also connected with this form of reduction (Ewer, 1960; Gould, 1977). However we could find no reliable cases of essential degradation of organisms on the basis of neoteny.

Now let us dwell on the consequences of regress of segregation type. It should be noted from the very beginning that it is widespread in ontogenetic morphogeneses. Let us give some examples. Miracidia – free-living larvae of parasitic flatworms – trematods swim in water by means of epidermal cilia. After penetration into the organism of transitory host they usually lose all the surficial cell layer. As a result, a small number (9–12) of the same cells is left, which form, by means of division and differentiation, a complex multicellular sporocyst (Dobrovolsky et al., 1983). The females of a louse fly *Ascodipteron speisereianum*, after penetration under the skin of the host (a bat), loses (segregates) its wings and all legs. The larvae of parasitic crustaceans from order Copepoda have the structure of typical nauplii, which, however, after their transition to endoparasitism, lose their limbs and even body segmentation. Quite numerous examples of segregation of structures or body parts in embryos, larvae or adults can be found in the "General parasitology" by V.A. Dogiel (1962) and in the monographs of O.M. Ivanova-Kazas (1975, 1977) "Comparative anatomy of invertebrates".

A number of filamentous, i.e. multicellular algae make a transition from water to land. Such aerophilic species inhabit stones, tree trunks or the surface of soil and snow. In the process of evolution they are transformed into unicellular forms by means of segregation of filaments (Masyuk, 1993). It is especially clearly demonstrated by green algae of the order Ulotrichales. In different families of this taxon species originate independently, in which filaments which have already been formed fall apart into fragments with few cells in each. In some species they are segregated into pairs of cells, in others – into single cells. Finally, there are species which are always (secondary) unicellular (Moshkova and Gollerbach, 1986).

Morphological, biochemical and molecular-biological investigations have proved that yeast (unicellular) higher fungi have originated inside the phyla Ascomycetes and Basidiomycetes independently of micelium (multicel-

lular) forms (Kreisel, 1983; Novak, 1987; Hendriks et al., 1989; Kreisel and Schawer, 1989).

It is well known that some parasitic eubacteria – micoplasm, rickettsia and chlamidia – in the process of evolution have undergone a great reduction which decreased their genome volume and resulted in the loss of important structures and some biochemical systems. Already Green (Green, 1935) supposed that viruses originated from such prokaryotes by means of further regress. This point of view was supported and developed by some other authors (Matthews, 1983; Syurin et al., 1984). However, for a number of viruses groups (e.g. for retroviruses) another idea, supported by molecular-biological investigations, is just as true – that these organisms could have originated by means of transposons' – mobile elements' – isolation from genomes in prokaryotes, protists or metazoan cells. Therefore, such viruses originate by means of segregation. R.B.Khesin (1984) – the author of the brilliant book "Genome Instability" – justly considers viruses to be polyphyletic by their nature and admits both hypotheses of their origin – by means of reduction and by means of segregation – to be true. Thus, by means of reduction and/or segregation a whole kingdom, or even empire (according to O.G.Kusakin and A.L.Drozdov, 1994), or still better, a domain Vira originates, comprising the most primitive creatures which parasitise on the genetical apparatus of pro- and eukaryotes. The appearance of such unique, tiny parasites as viruses is impossible to comprehend without taking into consideration the importance of regressive evolution. The diversity of organic world would be much more limited, were it not for regress being so widespread and important in it.

Generalizing the ideas of Ch.Darwin, A.N.Severtsov and many researchers, and also using new data, including molecular-biological ones, we can confidently state that morphological evolution of living creatures is a counter-directional process. Combination of progressive and regressive changes in the organisms structure in the process of evolution results in the appearance of new taxa and even macrotaxa, and the level of their organization can be higher (if progressive changes dominate) or remain the same or become lower (if progressive and regressive changes are more or less equal). In the cases when regress dominated essentially over progress, taxa appear which come back to a lower level of organization, really descending the "ladder of creatures". Therefore, in a certain sense, evolution is reversible. But then, what about Dollo's law? In 1893 he wrote about the irreversibility of evolution like this: "An organism cannot come back, even partially, to a previous state, which has already been realised in the series of its ancestors" (Dollo, 1893, p. 165). Later, however, under the influence of criticism of other investigators and the appearance of new data Dollo (Dollo, 1905) changed his original generalization essentially; he wrote like this: "An organism never comes back exactly to its previous

state due to indestructible nature of the past it always retains some trace of the transitional stages passed by it" (p. 443). This definition is repeated word by word in his subsequent works (see, e.g., Dollo, 1912, p. 107). It can be seen that in the new variant not the reversibility of evolution, but the possibility of exact repetition of evolutionary ways is rejected. That the essence of Dollo's law is not irreversibility of evolution but its incomplete repetition follows also from the commentaries on this law of many of its followers (Shishkin, 1968; Gabunia, 1974; Schmalhausen, 1983; and others).

Still we cannot call Dollo's law the law of "irrepeatability of evolution", because for many characters, organs (organelles) and even systems of organs evolution can be repeated. For example, in different evolutionary lines of flatworms intestine appears several times (Ivanov and Mamkaev, 1973). In the main branches of Metazoa nervous systems are formed independently (Minichev, 1994). The same tissues appear repeatedly in different groups of invertebrates (Zavarzin, 1986). Nowadays a lot of parallelisms in the morphological evolution of living creatures are known (Seravin, 1987; Tatarinov, 1987; Severtsov, 1990; and others); this phenomenon is widespread both among pro- and eukaryotes. The structures of living systems thus originating are often very similar but never identical.

Summing up, the following conclusions can be made.

1. Evolution of living systems follows the principle (law) of counter-directional morphological evolution, according to which both gradation and degradation of organisms can take place.

2. Combination of progressive and regressive changes in the structure of living creatures leads to the appearance of new taxa of any rank, including very high one (class, phylum, etc.).

3. In different groups of living organisms progressive and regressive morphological changes or their combination can result in the appearance of very similar but not identical taxa (e.g. sister taxa). The law of irreversibility of evolution should be substituted by a broader and more accurate law. It can be called the law of non-identity of similar structural transformations in different taxa of living organisms.

To build a correct megasystem of protists (as well as Eukaryota) it is necessary to take into consideration the principle of counter-directional morphological evolution.

References

- Andree K.B., Gresoviac J. and Hedrick R.P. 1997. Small subunit ribosomal sequences unite alternat actinosporean and myxosporean of *Myxobolus cerebralis* the causative agent of whirling disease in salmonid fish. J. Euk. Microbiol. 44, 208–215.

- Berdnikov V.A. 1990. The main factors of evolution. Nauka, Novosibirsk (in Russian).
- Borkhsenius S.N. and Chernova O.A. 1989. Micoplasmas. Nauka, Leningrad (in Russian).
- Bui E.T., Bradley P.J. and Johnson P.J. 1996. A common evolutionary origin for mitochondria and hydrogenosomes. Proc. Natl. Acad. Sci. USA, 93, 9651–9656.
- Clark C.G. and Roger A.J. 1995. Direct evidence for secondary loss of mitochondria in *Entamoeba histolytica*. Proc. Natl. Acad. Sci. USA, 92, 6518–6521.
- Cavalier-Smith T. 1983. A 6-kingdom classification and a unified phylogeny. In: Endocytobiology II (Eds. W.Schwemmler and H.E.A.Schenk). Walter de Gruyter, Berlin; N.Y. pp. 1027–1034.
- Cavalier-Smith T. 1987. Eukaryotes with no mitochondria. Nature. 326, 332–333.
- Cavalier-Smith T. 1991. Archamoebae: the ancestral eukaryotes? BioSystems. 25, 25–38.
- Cavalier-Smith T. 1993. Kingdom Protozoa and its 18 phyla. Microbiol. Rev. 57, 953–994.
- Cavalier-Smith T. 1996/1997. Amoeboflagellates and mitochondrial cristae in eukaryote evolution: megasystematics of the new subkingdoms Eozoa and Neozoa. Arch. Protistenk. 147, 237–258.
- Cavalier-Smith T. 1998. A revised six-kingdom system of life. Biol. Rev. 73, 203–266.
- Darwin Ch. 1872. The origin of species by means of natural selection. Murray, London.
- Darwin Ch. 1898. The origin of species by means of natural selection. Vol. 1. O.N.Popova Publishing House, St.Petersburg (in Russian).
- Davitashvili L.Sh. 1956. Essays on the history of the teaching of the evolutionary progress. Academy of Sciences of the USSR, Moscow (in Russian).
- Davitashvili L.Sh. 1973. The teaching of the evolutionary progress (aromorphosis theory). Metsnierba, Tbilisi (in Russian).
- Dobrovolsky A.A., Galaktionov K.V., Mukhamedov G.K., Sinkha B.K. and Tikhomirov I.A. 1983. Maternal sporocyst. In: Parthenogenetic trematod generations. Proceedings of the Leningrad Society of Naturalists. 82, 4, 11–51 (in Russian).
- Dogiel V.A. 1962. General Parasitology. Leningrad University Publishing House, Leningrad (in Russian).
- Dollo L. 1893. Les lois de l'évolution. Bull. Soc. Belge Géol. Paléontol. et Hydrol. 7, 164–166.
- Dollo L. 1905. Les Dinosauriens adapté à la vie quadripède secondaire. Bull. Soc. Belge Géol., Paléontol. et Hydrol. 19, 441–448.
- Dvoretzky I.Kh. 1976. Latin-Russian Dictionary. Russkiy Yazyk, Moscow.
- Dzwillo M. 1984. Regressive Evolution in der Phylogenese des Tierreichs. Z. zool. Syst. und Evolution. 22, 115–126.
- Erlich P. and Holm R. 1966. The process of evolution. Mir, Moscow (in Russian).
- Ewer R. 1960. Natural selection and neoteny. Acta Biotheoretica. 13, 161–184.
- Fetisenko B.A. 1973. The elaboration of the problem of regressive evolution in the works of A.N.Severtsov and I.I.Schmalhausen. In: History and theory of evolutionary teaching. Leningrad. pp. 121–128 (in Russian).
- Gabunia L.K. 1974. On the history of the discovery of the law of evolution irreversibility. Proceedings of the XII International Congress on the history of science. Section IX. History of biological sciences. Nauka, Moscow. pp. 118–121 (in Russian).
- Garstand W. 1922. The theory of recapitulation. A critical restatement of the biogenetic law. J. Linn. Soc. 35, 117–131.
- Georgievsky A.B. 1985. Darwinism. Prosvescheniye, Moscow (in Russian).
- Goodkov A.V. and Seravin L.N. 1991. New ideas on the nature of the 'giant amoeba' *Pelomyxa palustris*; the position of this organism in the system of lower eukaryotes (Peloflagellata classis n.). Zool. Zh. 70. 5–16 (in Russian with English summary).
- Goodkov A.V. and Seravin L.N. 1995. *Pelomyxa palustris*: amoeba, caryoblastean, archezoan, or peloflagellatan? Tsitologiya. 37, 1053–1063.
- Gottschalk C. 1957. Die Amoebosporidien. Eine vergleichende Betrachtung ihrer sistematischen Stellung in Tierreich. Zeitschr. Wissen. Zool. 160, 1–38.
- Gould J. 1977. Ontogeny and phylogeny. Harvard Univ. Press, Cambridge, Mass.
- Grant V. 1980. Evolution of organisms. Mir, Moscow (in Russian).
- Green R. G. 1935. On the nature of filterable virus. Science. 82, 443–445.
- Hendriks L., Goris A., Neefs J.-M., Van de Peer Y., Hennebert G. and Wachter R. 1989. The nucleotide sequence of the small ribosomal subunit RNA of the yeast *Candida albicans* and the evolutionary position of the Fungi among the Eukaryotes. System. Appl. Microbiol. 12, 223–229.
- Henze K., Badr A., Wettern M., Cerff R. and Martin W. 1995. A nuclear gene of eubacterial origin in *Euglena gracilis* reflects cryptic endosymbioses during protist evolution. Proc. Natl. Acad. Sci. USA. 92, 9122–9126.
- Huxley J. S. 1957. The three types of evolutionary process. Nature. 180, 454–455.
- Huxley J. S. 1963. Evolution, the modern synthesis. Rev. ed. Harper, N. Y.
- Ivanov A.V. and Mamkaev Yu.V. 1973. Turbellarian worms (Turbellaria), their origin and evolution. Nauka, Leningrad (in Russian).
- Ivanova-Kazas O.M. 1975. Comparative anatomy of invertebrates. Protists and lower metazoans. Nauka, Novosibirsk (in Russian).

- Ivanova-Kazas O.M. 1977. Comparative anatomy of invertebrates. Trochophors, tentaculates, chaetognates, pogonophores. Nauka, Moscow (in Russian).
- Ivanova-Kazas O.M. 1995. Essays on the phylogeny of lower chordates. St.Petersburg University Publishing House, St-Petersburg (in Russian).
- Katiar S.K., Visvesvara G.S. and Edlind T.D. 1995. Comparison of ribosomal sequences from amitochondrial protozoa: implications for processing, mRNA binding paromomycin susceptibility. *Gene*. 152, 27–33.
- Keeling P.J. and Doolittle W.E. 1996. Alpha-tubulin from early-diverging eukaryotic lineages and the evolution of the tubulin family. *Mol. Biol. Evol.* 13, 1297–1305.
- Khesin R.B. 1984. Genome instability. Nauka, Moscow (in Russian).
- Komarova L.N. (Ed.) 1992. A modern dictionary of foreign words. Russkiy Yazyk, Moscow.
- Kreisel H. 1983. Teliomycetes – Ustomycetes – Basidiomycetes: Gedanken zur Klassifizierung der höheren Pilze. *Sydowia*. 46, 154–166.
- Kreisel H. and Schauer F. 1989. Dimorphism in System der Pilze-Grauzone der Taxonomie? *ZBL Microbiol.* 144, 219–229.
- Kusakin O.G. and Drozdov A.L. 1994. Phyleme of organic world. Part 1. Prolegomenes to the phyleme construction. St.Petersburg (in Russian).
- Lamarck J.-B. 1809. Philosophie Zoologique. I, II. Dentu, Paris.
- Lamarck J.-B. 1935. Philosophy of zoology. Biomedgiz, Moscow, Leningrad (in Russian).
- Lom J. 1977. Myxosporidian ultrastructure, an attempt at a synthesis. In: Progress in protozoology. Clermont-Ferrand. p.254.
- Malakhov V.V. 1990. Mysterious groups of marine invertebrates. Moscow State Univ. Press, Moscow (in Russian).
- Margulis L. 1981. Symbiosis in cell evolution. Life and its environment on the early Earth. W.H.Freeman and Co., San Francisco.
- Masyuk N.P. 1993. Evolutionary aspects of eukaryotic algae morphology. *Naukova Dumka*, Kiev (in Russian).
- Matthews R.E. F. 1983. The origin of viruses from cells. *Int. Rev. Cytol. Suppl.* 3, 245–280.
- McHugh D. 1997. Molecular evidence that echiurans and pogonophorans are derived annelids. *Proc. Nat. Acad. Sci. USA*. 94, 8006–8009.
- Mechnikov I.I. 1950. An essays on the problem of the origin of species. In: Selected works on biology. Publishing House of the Academy of Sciences of the USSR. Moscow (in Russian).
- Minichev Yu.S. 1994. Neurophylogenesis regularities. In: Mechanisms of structural plasticity of neurons and nervous system phylogeny. Nauka, St.Petersburg. pp. 160–215.
- Moshkova N.A. and Gollerbach M.M. 1986. Green Algae. Class Ulotrichales. 1. In: Identification guide to the freshwater algae of the USSR Iss. 10 (1). Nauka, Leningrad (in Russian).
- Novak E. K. 1987. Az élesztők helyl a gombákárendszerebená. *Mikol. közl.* 2–3, 81–82.
- Orlov S.A. 1981. The positing of the problem of evolution irreversibility in the works of Ch. Darwin. In: The problems of the latest history of evolutionary teaching. Nauka, Leningrad. pp. 148–155 (in Russian).
- Rezanov I.A. 1987. The history of geotectonic ideas. Nauka, Moscow (in Russian).
- Schlegel M., Lom J., Stechman A., Bernard D., Leipe D., Dykova J. and Sogin M.L. 1966. Phylogenetic analysis of complete small subunit ribosomal RNA coding region of *Myxidium lieberuehni*: evidence that Myxozoa are Metazoa and related to the Bilateria. *Arch. Protistenk.* 147, 1–9.
- Schmalhausen I.I. 1969. The problems of darwinism. Nauka, Leningrad (in Russian).
- Schmalhausen I.I. 1983. Ways and regularities of evolutionary process. Nauka, Moscow (in Russian).
- Shishkin M.A. 1968. Irreversibility of evolution and factors of morphogenesis. *Paleontological J.* 3, 3–11 (in Russian).
- Seravin L.N. 1987. On the parallelisms on subcellular level of living systems. *Vestnik LGU.* 1, 3, 3–10 (in Russian).
- Seravin L.N. 1992. Eukaryotes lacking the most important cell organelles (flagella, Golgi complex, mitochondria) and the main task of organellology. *Tsitologiya*. 34, 3–33 (in Russian with English summary)..
- Seravin L.N. 1995. The main ways of protists evolution. *Vestnik SPbGU.* 3, 2, 3–17 (in Russian).
- Severtsov A.N. 1912. Essays on evolutionary theory (individual development and evolution). Kiev University Publishing House, Kiev (in Russian).
- Severtsov A.N. 1914. Modern problems of evolutionary theory. Nauka, Moscow (in Russian).
- Severtsov A.N. 1925. The main directions of evolutionary process (progress, regress, adaptation). *Dumnov*, Moscow (in Russian).
- Severtsov A.N. 1939. Morphological regularities of evolution. Publishing House of the Academy of Sciences of the USSR, Moscow, Leningrad (in Russian).
- Severtsov A.N. 1990. Directions of evolution. Moscow State Univ. Publ., Moscow (in Russian).
- Siddall M.E., Martin D.S., Bridge D., Desser S.S. and Cone D.K. 1995. The demise of a phylum of protists: ppylogeny of Myxozoa and other parasitic Cnidaria. *J. Parasitol.* 8, 961–967.
- Slusarev G.S. 1994. Fine structure of the female *Intoshia variable* Alexandrov and Slusarev (Mesozoa, Orthonectida). *Acta Zool.* 75, 311–321.
- Smothers J.F., Dohlen C.D., Smith L.H. and Spall R.D. 1994. Molecular evidence that the myxozoan protists are metazoans. *Science*. 265, 1719–1721.

- Syurin V.N., Belousova R.V. and Fomina N.V. 1984. Veterinary virusology. Kolos, Moscow (in Russian).
- Takhtadjan A.L. 1954. The problems of plant evolutionary morphology. Leningrad State Univ. Publ., Leningrad (in Russian).
- Takhtadjan A.L. 1983. Macroevolutionary processes in the history of plant world. Botanical J. 68, 1593–1603 (in Russian with English summary).
- Tatarinov L.P. 1987. Essays on evolutionary theory. Mir, Moscow (in Russian).
- Terekhin A.S. 1975. On the means and evolutionary significance of the reduction of biological structures. Botanical J. 60, 1401–1412 (in Russian with English summary).
- Timofeev-Resovsky N.V., Vorontsov N.N. and Yablokov A.V. 1969. A short essay on evolutionary theory. Nauka, Moscow (in Russian).
- Wasser S.P. (Ed.) 1989. Algae. A reference book.. Naukova Dumka, Kiev (in Russian).
- Weill R. 1938. L'interprétation des cnidosporidies et la valeur taxonomique de leur cnidomes. Leur cycle compare à la phase larvaire des narcomeduses cuninides. Wimereux. 5, 727–744.
- Zavarzin A.A. 1986. Transactions on parallelism theory and evolutionary dynamics of tissues. Nauka, Leningrad (in Russian).