THE PROBLEM OF CONSTRAINTS ON VARIATION, FROM DARWIN TO THE PRESENT

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ABSTRACT. The real number of variations is lesser than expected one. There are no blue-eyed Drosophila, no viviparous birds or turtles, no hexapod mammals, etc. Such observations provoke non-Darwinian evolutionary concepts. Darwin tried rather unsuccessfully to solve the problem of the contradictions between his model of random variability and the existence of constraints. He tried to hide this complication citing abundant facts on other phenomena. The authors of the modern versions of Darwinism followed this strategy, allowing the question to persist.

KEY WORDS. constraints, variation, evolution, parallelisms, selection, orthogenesis, Darwinism, adaptation, heresies, evolution

The discussion concerning evolutionary constraints still continues in modern biology; it is evident that some restrictions on variation, and correspondingly on evolution, exist. However, the significance of this fact for evolutionary biology is questionable. The statements on constraints were often opposed to Darwinism since the beginning of its existence. The modern interest in this phenomenon raises this question: do the data on constraints contradict the traditional Darwinian view on evolution or just add some corrections? To answer this question, I will focus on the arguments over constraints from a historical perspective. Darwin himself tried to solve the contradictions between his model of random variability and the existence of constraints. In what follows, numerous evolutionists discussed this problem. The historical analysis will contribute to solve this question: is evolution wandering through the vast space of adaptation or is it moving "on rails" created by constraints on variation?

DARWIN ON CONSTRAINTS

The critics of the adaptationist program ("Panglossian paradigm") R. Lewontin and S. Gould pointed out the "pluralism" of Darwin, referring

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to the fact that he made some concessions concerning Lamarckian mechanisms and that sometimes he did not consider natural selection the exclusive force of evolution (Gould, Lewontin 1979). Nonetheless, it is not the whole story. The Lamarckian viewpoint on the sources of variability was not a concession but an integral part of Darwin's theory. He believed that before the action of selection, any variation arises due to the action of the environment or the use and disuse of organs. He was informed well on the phenomenon, which was called later "mutation," and he explained it by the action of external conditions upon the organism or its ancestors. Regarding other evolutionary mechanisms, Darwin allowed a lesser pluralism; he discussed carefully all possible objections to his theory and always succeeded in removing them. In the most difficult cases he certainly recognized some other mechanisms besides selection, but he could argue convincingly that these were so unessential as to be negligible.

Darwin tried to prove that variability is practically unlimited, that it can always supply natural selection with some kind of resources. He based this claim, first of all, on the human practice of selection. He collected abundant examples of the successful creation of new domestic races. "It would seem as if they had chalked out upon a wall a form perfect in itself, and then had given it existence"—Darwin shared this opinion about sheep-breeders expressed by Lord Somerville (Darwin 1987, reprint of the first edition 1859, p. 90). However, he was forced to admit some cases where creating anything humans may wish for was impossible. For example, when the English farmers decided to get cows with thick hams, they soon abandoned this attempt since they perished too frequently during delivery. Evidently such cases provoked an idea on the limitations to variability; Darwin wrote this on such cases: "Will a gooseberry ever weigh more than that produced by 'London' in 1852? Will the beet-root in France yield a greater percentage of sugar? Will future varieties of wheat and other grain produce heavier crops than our present varieties? These questions cannot be positively answered; but it is certain that we ought to be cautious in answering them by a negative" (Darwin 1883, p. 228). Thus, he expressed doubt about the existence of limitations, which could essentially influence upon the successes of selection, and correspondingly upon evolution. To cancel this problem he absolutely pointed out the impossibility to prove any stance regarding this subject: "the ordinary belief that the amount of possible variation is a strictly limited quantity, is likewise a simple assumption [1]" (Darwin 1872, p. 82). Approximately the same analysis was conducted by Darwin concerning "unknown laws of growth," which could cause the presence of non-adaptive characters in organisms. He believed that selection could do everything by small steps over a long period, comparing natural selection with an architect who is forced to

build a majestic building with crude stones and yet fulfils this task successfully.

Darwin's viewpoint on constraints seems to follow logically from his theory. Probably, he realized, to pay attention to the restrictions to variability would be conclude that these very constraints direct evolution. That would be unacceptable, as he intend to exclude anything he couldn't known. For instance, he could show clearly the existence of "fluctuations"—smallest distinctions among closely related organisms or their parts—and such distinctions could be always revealed and explained by small environmental distinctions. For example, even the seeds in one boll are different because their position respect to the nutritive canals differs, i.e., the seeds get different amounts of nutrition and become different. The source of such fluctuations seems to be explainable, while there wasn't and clearness in the explanation to the sources of the limits to variation. Therefore, Darwin tried to avoid this topic and he did it quite successfully. (The limits of variation were not mentioned even in the special study devoted directly to the analysis of Darwin's concept on variation, Winther 2000.)

Darwin had not only collected abundant facts on variability and discussed them carefully, but also placed the discussion on the properties of variation in such a manner that it will not surprise the reader. He noted repeatedly that selection itself does not cause changes and that it is based on the material provided by "nature". He evidently did not wish to see the analysis of this "nature" at the foreground of his theory and manage to postpone it for the future.

As it is known, Darwin prepared his famous book *On the Origin of Species* (1859) rather hastily as a brief version of his theory, because he had received a letter and manuscript by A. Wallace, who had elaborated a similar concept. Darwin did not include his analysis on the limits of variation in this "brief version"; previously, he planned to write a "Big species book" which would contain a wider spectrum of topics. After the publication of the "brief version" Darwin finished this work, but presented the additional parts in the form of separate treatises on domestication. He placed the chapter on the properties of variation only at their end. Darwin himself had noticed that it would be necessary to begin from this topic, but such layout appeared more convenient. In the chapter on the natural selection he wrote the following: "Hence our discussion on the causes and laws of variability ought in strict order to have preceded the present subject, as well as inheritance, crossing, etc.; but practically the present arrangement has been found the most convenient" (Darwin 1883, p. 176). "The present arrangement" in this case means the citation of abundant facts concerning selection and heredity in the beginning, and somewhere in the end some ideas about the nature of variability. It turned out that

Darwin constructed first the majestic building of a new theory, and later began to strength its foundations and to study the appropriateness of the ground. Numerous critics seized the opportunity to point on such structure.

THE CRITICISM AND THE FORMATION OF AN ALTERNATIVE VIEWPOINT ON VARIATION (BEFORE THE "EVOLUTIONARY SYNTHESIS")

Even some advocates of Darwin expressed disagreement with his viewpoint on the constraints on variability. Hence, Thomas Huxley (1825-1895) and August Weismann (1834-1914) claimed, that it was absolutely impossible to assume the existence of variability that can fluctuate randomly in every possible direction (Weismann 1868; Huxley 1894). However, both where marginal commentaries while dealing with more clear topics. Huxley placate himself by reducing the question to an absurd example: "A whale does not tend to vary in the direction of producing feathers, not a bird in the direction of developing whalebone" (Huxley 1894, p. 181). The opponents of Darwin paid attention to the cases when the tendency to vary seemed to be available but the variation did not take place. Those include the cases of the tendency to variation of feathers; it seems that all birds have such tendency, but not all birds demonstrate it.

The treatises by the Russian writer Nikolay Danilevsky (1822-1885) contain one of the most expressive examples in the discussions on this subject. One of the failures founded by him in Darwin's books concern the analysis of domestic birds—hens, geese and pigeons. Darwin wrote that hens are highly variable, because man selected them for numerous purposes, for instance, to get meat, or to get eggs, or to get decorative birds, or to satisfy the amateurs of gamecocks. The pigeons are also very variable, as they became decorative birds. But geese are not variable, and according to Darwin, it happens because man breeds them with only one purpose, to eat them.

Danilevsky was indignant with such interpretation: "This means, that if geese would fall in the hands of the whimsical amateurs, we could get the geese with peacock tails, the geese with colored feathers, the crested geese, the dwarf geese If the geese would fall in the hands of the amateurs of bird fights, the geese would acquire spurs or some other weapons?" Danilevsky claimed definitely that "Darwin confuses the cause and consequence: the goose has remained constant not because he did not fall in the list of decorative birds, which are appreciated for the beauty and strangeness of form and plumage, but on the contrary, it did not become decorative bird like pigeons and hens, because it was and it is a non-variable species due to its nature!" Danilevsky added to this speculation the notice that in some parts of Russia, the amateurs of geese-fights existed just as the amateurs of cock-fights. Despite the necessity to fight, the geese

have acquired neither spurs nor any other weapon. Moreover, Danilevsky pointed out the fact that some birds—pheasants and peacocks—also remained unchanged, though they became decorative birds, and therefore a great variety of them should be expected (Danilevsky 1885, p. 203).

Darwin realized the problem of explaining such facts in terms of his theory. He noted that geese have "a non-variable nature," but nevertheless tried to account for similar cases in terms of natural selection. Thus, he paid attention to the fact that the variability of the cats is smaller that the variability of dogs, and the variability of donkeys is smaller then the variability of horses. He explained such facts by the disadvantages of selection: cats have the habit to wander at nights and behave as they like, so it is difficult to control their crossings; donkeys are used mainly in poor farms, which just struggle to survive and have no the chance to plan a rational breed.

Criticizing Darwinism, Danilevsky was unable to propose an alternative idea. It is partly explained by the fact that he died suddenly; he published only the first volume and a small part of the second volume of his *Critical Research of Darwinism*. Anyhow, other authors developed similar ideas elaborating special non-Darwinian evolutionary concepts.

One of the main trends in non-Darwinian evolutionary concepts was formed in the 1860s on the basis this idea: living organisms have a predisposition to vary in certain directions, and this very predisposition determines the trends of evolution, first of all, irrespectively from adaptation and selection; as the crystals grow taking a certain form, so phylogenetic trends evolve following their internal laws. In the nineteenth century, the advocates of this concept based were mainly on the indirect evidences on the restricted number of variation directions—the existence of non-adaptive characters, the phylogenetic regularities known from fossil record, parallelisms (Koellicker 1864; Naegeli 1865, 1884; Hyatt 1966; Cope 1868; for a review see Popov 2005, 2008). Furthermore, since the 1890s, this trend was partly related with the studies concerning constraints or definite directions in variability.

In 1893, the German zoologist Wilhelm Haacke (1855-1912) introduced the term "orthogenesis", which was used later for everything concerning definite directions in evolution and especially for non-Darwinian concepts claiming for internal forces in evolution. The primary meaning of "orthogenesis" corresponds to the meaning of the modern term "constraints on variation". Wilhelm Haacke introduced this term presenting his theory on heredity, which was very close to the theory of "*germ plasm*" by Weismann (Haacke 1893). As is known, Weismann postulated the existence of particles inside the cells, which determine heredity. Haacke assumed that these particles were polyhedrons, and to compose a harmonic entity such particles should joint each other in precise combinations, and such com-

binations became apparent in the capacity of organisms to vary only in definite directions. Haacke called this capacity "*orthogenesis*," counterpoising it to "*amphigenesis*," the ability to vary in every possible direction.

Unlike "orthogenesis", the "*gemmen*" concept didn't get any support. The American zoologist Charles Otis Whitman (1842-1910) presented the most remarkable evidence on it. In 1892, he started a series of studies on the variation of pigeons, which continued over eighteen years. Unlike the founders of genetics, Whitman tried to extend the scope of his studies as much as possible; besides the experiments on crossing and selection, his research included phylogenetic, embryological and taxonomic studies. Whitman came to the conclusion that he proved the reality of orthogenesis by characterizing various regularities within the possible changes in pigeons, observed in their variability, the differences among species and their orthogenesis. For example, in their breeding, it was possible to get an easy step-by-step reduction of pigmentation in the plumage during several generations, to get white pigeons. Such a reduction always takes place in a definite direction: from forepart of the body through the spotty variant and the variant with two stripes on wings. The pigment was not lost evenly and gradually in the whole surface of the pigeon, and it did not disappear in any other direction (Whitman 1919).

In the years that followed some new evidences on orthogenesis appeared. The studies by Nikolay Vavilov (1887-1943) on "homological series of variability" seem to be the most remarkable in this field (Vavilov 1922, 1968). He collected an extensive material relative to cultivated plants, and revealed a lot of parallel variations among numerous species. For example, among cereals the ears could be branchy on not branchy, they could be bearded or not bearded; the color of their seeds could be white, yellow, red, grey, black or deep-brown. Vavilov showed that it is possible to detect all these kinds of variability in each cereal species. Moreover, a similar phenomenon exists at plants which are not in direct relationship. For instance, identical variants of the root form could be detected at beet (fam. Chenopodiacea), carrot (fam. Umbelliferae) and at turnip (fam. Cruciferae). Some variants occur through all the plant world—gigantism, dwarfism, fasciation, albinism. In some cases, Vavilov could predict the discovery of new plant forms. For example, among pumpkins and melons lobate forms were known, yet unknown in watermelons, so Vavilov expected the discovery of lobate watermelons, and were surely found in the southeastern Russia. Such predictions reminded the Russian scientists how Dmitry Mendeleev predicted the discovery of new chemical elements after his formulation of the periodic law. This is why, at least in Russia, Vavilov was often called the "Mendeleev of biology" (see Popov 2002, 2008a, b, for details).

Some facts of parallel variability were certainly known before Vavilov's studies, but were not cited as an indication of the general laws determining variation. Yet Darwin mentioned such facts, but did not emphasize them; he considered such examples as an indication on the common origin of species: various species could be similar not only in diagnostic features, but also in their variations. Vavilov also explained the existence of homological series by common origin, but he stressed on defined directions in variability and correspondingly in evolution. Moreover, he paid attention to the fact that different mutations could create identical phenotypes, i.e., the number of possible phenotypes is smaller than number of possible mutations. From this fact it is feasible to conclude that even data from a huge amount of mutations does not contradict the model of evolution on rails.

Vavilov found a mutual understanding with the Russian authors of the concepts of directed evolution—L. S. Berg (1876-1950) and D. N. Sobolev (1872-1949)—and collaborated with them. However, none of them got the possibility to extend such studies due to the political conditions of those days. Darwinism occupied in the Soviet biology the same place as Communism in ideology; all studies should be conducted under the sign of development and defense of Darwinism. Nonetheless, in some letters Vavilov expressed some heretical thoughts: "What coniferous have in common with cereals, or pumpkin and water-melon with wheat? But their cycles of variability are similar in many respects. There is also a huge abundance of such parallelisms both at mushrooms, and at animals. It is very easy to find them in any detailed monograph on some large group and even on genera. Reading *Mutationstheorie,* scrutinizing closely the mutations we can see that all of them pass in form of orthogenetic rows" (Pis'ma Vavilova 1977, p. 104).

Some investigators of heredity also found evidences of "orthogenetic mutations". The German geneticist (of Russian origin) Viktor Jollos (1887-1941), considered his data as the expression of "directed mutation": the wild type of *Drosophyla* produced a mutation of eye color—*dark eosin*, the mutants *dark eosin* produced mutants *light eosin*, then in such a manner *yellow*, *ivory* and *white* mutations appeared. Other sequence of mutations was not observed, and wild type could not produce immediately those mutations, which followed *dark eosin*. Jollos called this phenomenon "directed mutation," having in view that they reflect the evolutionary tendencies to vary in certain direction irrespectively of adaptation. He compared such changes with the facts on evolutionary trends known from fossil record, like the series of transformations within the horse ancestors (Jollos 1931).

Such an "orthogenetical genetics" has not become popular. Its failure was aggravated by the fact that the careers of the authors mentioned were tragically broken. Vavilov was repressed and died in prison; Whitman

died suddenly, when his studies on pigeons were not finished; Jollos was forced to emigrate from Nazi Germany, could not find the possibilities to continue his researches and died shortly after emigrating. The new science on heredity developed in other directions, which led to the formation of modern Darwinism. Instead of regularities, limitations, trends, etc., variety and randomness attracted the attention.

Besides the genetic studies, at least one research contributed greatly to the understanding of the constraints on variation, that is *On growth and form* (1917, 1942) conducted by D'Arcy Thompson (1860-1948; Thompson 2004). This scientist focused on the correlation of the organic phenomena to mathematical patterns and physical laws. Thereby, he described in detail all possible limitations to the organic forms, determined by their physical conditions. He traced such constraints from some evident cases (like the limitation on the size of the flying animals) up to the finest details of the action of surface-tension or crystallisation in cells and tissues. Thompson did not address his work directly to criticize Darwinism; however, he expressed some disagreements with Darwin and Darwinians concerning some significant points. Thus, Thompson argued against their "doctrine of the independence of single characters," developing the idea of a strong correlation of all parts of the organism with each other. Moreover, he also criticized the adaptationistic program. For example, polemicizing with Ernst Haeckel (1834-1919), he rejected the adaptationistic explanations of the form of the sponge-spicule and Radiolaria. Thompson considered such structures as crystals, which have a definite form due to their chemical and physical characteristics. Concerning Radiolaria, he added that several kinds of them are equally drifted by waves, and that is why any explanation of the evolution of their form in terms of the Darwinian struggle for existence is meaningless.

THE PROBLEM OF THE CONSTRAINTS IN MODERN DARWINISM

Since Darwin's time to the formation of modern Darwinism, a lot of new data and concepts on the constraints to variation were developed, but it hardly influenced the "architects of evolutionary synthesis". Darwinism did not change in this respect; the authors of the treatises which formed the soul of modern Darwinism abound on data concerning other phenomena and hide the problem of constraints. They tried to convince everybody that selection can create anything, and so it was meaningless to think about the material provided by nature to be selected. Almost all authors of modern Darwinism tended to discredit every indication about evolutionary constraints. For example, G. L. Stebbins (1906-2000) claimed that the famous discoveries by W. Johannsen on the limits of selection and variability were meaningless [2] because Johansen worked in a garden in

Denmark instead of a tropical forest, and so he could not realize the abundance of natural variability (Stebbins 1980). G. G. Simpson (1902-1984) claimed "that much of the rectilinearity of evolution is rather a product of the tendency in the minds of scientists to move in straight lines than of a tendency for nature to do so" (Simpson 1944, p. 164). Nevertheless, at the same time Simpson admitted that the concept of random variability proceeding in every possible direction is absurd. J. Huxley (1887-1975) eliminated the inconvenient material by posing that the evolution contains so a huge set of aspects, processes, phenomena, mechanisms and principles, all of which are investigated insufficiently, that absolutizing any one of them (except natural selection) is impossible. He noted that something like orthogenesis is possible an exception, but it is insignificant in comparison with the Darwinian factors (Huxley 1942). Bernhard Rensch (1900-1990) in such cases applied the parsimony: method if we already have a good explanation, there is no necessity to look for others (Rensch 1954).

Analyzing deeply the question on such constraints or its regularities they felt less confidently. One curious example of such analysis is the discussion on the horns of mammals. Speculating on the properties of variation, Rensch cited as an example the variety of horns at antelopes; their horns could be straight, bent and spiral; the spiral horns could have various numbers of coils. From his viewpoint, there is so great variety that there cannot any doubt that every possible form of horns could arise. Even so, some researchers of nature had a richer imagination. Rupert Riedl, for example, drew a series of figures of hypothetical horned animals which do not exist in a nature: antelopes with three horns or antelopes with horns growing downwards. Thus he substantiated the idea that such variety of horns (as well as all other organic structures) is limited (Riedl 1975).

Rensch carefully increased the number of similar examples and some of them seem to be even less successful. He paid attention to an interesting mammal from the Sulavesi island—the babirussa. This animal looks like a wild pig, its tusks having a very strange form, they grow upwards, and the tips of them are bent inwards. It is difficult to imagine how the animal could use them; they seem to be appropriate only for fixing its head at the tree branches, but the babirussa hardly had such necessity. Rensch cited this case as an evidence of unlimited variation; he believed that nature provide every possible material for selection, useful and not useful. In the case of the babirussa, a meaningless kind was accidentally saved by selection because it was not harmful (Rensch 1954).

Th. Dobzhansky (1900-1975) and E. Mayr (1904-2005) also discussed this problem and their analysis is especially remarkable. There are whole chapters concerning this topic in the first of their famous books (Dobzhansky 1937; Mayr 1942), but in further treatises such chapters get reduced

and at last disappear. It just happened that such discussion came to a dead end. Such a situation could be traced in the case of the analysis of the variation of one bird species—*Pachycephala pectoralis*: 12 races of this species were described in the islands of Pacific Ocean. To characterize them, Dobzhansky (based on Mayr's data) composed a table demonstrating the combinations of 5 characters. Each character could have 2 variations (Dobzhansky 1937, p. 54) and 8 combinations were found in nature. Mayr cited this data (1942) to demonstrate the abundance of variability, noting that such combinations provide an unlimited array of races. However, it is easy to calculate that the number of possible combinations is 32. Eight is not "almost 32", and the absence of 24 variations did not attract attention since the belief in unlimited variation was already firmly established. Nobody asked the question whether these variations were eliminated by natural selection or whether they never existed due of the limits to variability (see Kovalenko and Popov 1997 for details).

This example is absent in the subsequent writings by Dobzhansky and Mayr (except for the second edition of the book *Genetics and the Origin of Species*, 1941), and the discussion on the degree of variability disappeared. Even stating the question on the degree of variability or on the limits of variation became extremely inconvenient. To stop any speculations on this subject, the following viewpoint was formulated: "it is less important for the understanding of evolution to know how genetic variation is manufactured than to know how natural selection deals with it" (Mayr 1963, p. 25). Darwin was of the same opinion: "variability sinks to a quite subordinate position in importance in comparison with selection" (Darwin 1883, p. 236). Satisfied by such ideas, the authors of modern Darwinism preferred to ignore the question on constraints.

A NEW PROTEST

The critics who thought too much on the properties of variation, appeared after the Pyrrhic victory of modern Darwinism as they did after the appearance of Darwin's theory. In some cases, they followed the existing orthogenetic tradition in evolutionary biology. This tradition kept mainly in the countries outside the English-speaking ones; in France, for example, alternative theories were on the foreground of biology for a long time after the formation of the modern Darwinism. The most active French evolutionists of that time—Pierre-Paul Grassé (1895-1985) and Albert Vandel (1894-1980)—supported the idea of spontaneous directed evolution (Vandel 1964, 1968; Grassé 1943, 1963, 1977). In the Russian underground biology, the non-Darwinian tradition also existed, and sometimes at the moments of political liberalization it appeared on the surface. In 1970s the burst of popularity of Berg's "nomogenesis" (the most famous Russian

version of directed evolution concept) was noted, the works by Berg on evolution were reprinted, and a lot of papers on this subject were published (Berg 1977). The new burst of its popularity took place after the breakdown of the socialist system, and some new directed evolution concepts appeared (Akhnazarov 2002; Kovalenko 2003). In Spain, some paleontologists rather actively developed ideas of directed evolution (Aguirre 1957; Crusafont Pairó 1960). In Germany, some studies also were conducted in terms of the orthogenetic tradition (see Reif 1983); besides the development of the existing tradition, the idea of the evolution on rails was often stated as a new concept. Also, Swedish cytogeneticist A. Lima de Faria, Japanese scientists and some German morphologists claimed on directed evolution without any references to their predecessors (Lima de Faria 1988, 1995; Gutmann 1994, 1996, 1997; Kawamura 2002).

The activists of modern Darwinism waved away these concepts easily declaring them anachronisms. It seems that the other fact made a greater influence on modern Darwinism: some of its advocates felt failures in the "true faith" of biology. Without any heretical influences, it is possible to note that something is wrong with the Darwinian viewpoint on variation. Despite the efforts of geneticists and selectionists, there are no blue-eyed flies, no blue roses, no lupines without alkaloids, no mammal having six extremities, no Infusorians weighting ten kilos, etc. If to pay attention to similar cases, the heretical thoughts concerning the unlimited power of natural selection arise inevitably. Therefore, some advocates of Darwinism allowed for some heretic penetration.

For example, in the beginning of the book on the order in nature by S. A. Kauffman, he greatly reminds orthogenesis and other non-Darwinian concepts. He stated the question: why nobody includes self-organization in the evolutionary theory? There is nothing mystical in this process. Kauffman stated the main arguments which place the basis to attend to this process: the tautological character of the doctrine of fitness and survival; panselectionism, weaknesses of functionalist explanations, abundance of variation, epistemological adequacy of population genetics, missing phenotypes, phenotypic stasis, macroevolutionary challenges. The authors of the concepts of directed evolution stated almost all of these arguments. Kauffman set himself the objective to integrate such arguments with the theory of natural selection based on mathematical models. The achievement of this objective is obviously very difficult, even unrealizable, and after such a huge work, the author concludes that he has made only the first steps in this direction.

One of the sources of heresies in evolutionary biology is the problem of novelties in evolution. For example, D. Sobolev when discussing evolution almost failed to mention Darwinism, pretending that this theory was called evolutionary only due to some misunderstanding, since it does not

explain the appearance of new forms, just their conservation after their appearance (Sobolev 1913, 1924). Berg expressed a similar viewpoint: selection is not a creating force, but a destroying one (Berg 1926). The same stance was expressed in some modern studies: "A theory of evolution that focuses so firmly on destructive rather than creative forces cannot be other than seriously incomplete" (Arthur 2000, p. 50). L. Yampolsky and A. Stolzfus (2001) claimed that the existing population-genetic models are based on the prior assumption on the availability of variability, and thus they underestimate mutation pressure. However, mutation means the appearance of a novelty, and so biases strongly the course of evolution. These authors supported the "internalist" approach, i.e., the significance of internal factors of evolution, which led to homoplasy, parallelism and directionality. This means the reformulation of the idea of orthogenesis in some other "language".

Sometimes the facts supporting such a criticism or corrections to Darwinism coincide with the facts cited by the advocates of the idea of directed evolution. Gould and Lewontin criticizing the "Panglossian paradigm" cited a particular variety of shells (from the studies by A. Seilacher), which could hardly be explainable in terms of Darwinian factors. The representatives of different invertebrate types—mollusks and brachiopods—could have very similar shells. Not only the form of shell, but the patterns of the ornamental lines and their coloration appeared in parallel. It is difficult to explain such cases in terms of adaptation, especially taking into account the fact that the coloration often remains hidden in the living animal, since the clams possessing them either live buried in sediments or remain covered with a periostracum so thick that the colors cannot be seen (Gould and Lewontin 1979). The shells were always one of the favorite examples of the advocates of directed evolution concepts. Yury Filipchenko (which was known outside Russia mainly as the author of the terms "macro-" and "microevolution") also cited the similarities among the shells of the representatives of different types. The shells of foraminiferans are so similar to the shells of extinct cephalopods that they were initially considered mollusks. The name "Foraminifera" was invented by analogy of "Siphonifera", the old name of cephalopods. It means that "the laws of growth and step-by-step enrollment of primary straight shell are probably equal, irrespectively of the fact if this shell belongs either to unicellular rhizopod or to the highly developed representative of mollusks" (Filipchenko 1924, p. 253).

CONSTRAINTS ON VARIATION AND "MODERNISTIC" DARWINISM

It is considered that modern Darwinism changed significantly since the time of its formation. One of the most important changes became apparent

in its penetration of aspects concerning developmental biology. This means that traditional scheme "selection-mutation" contains a gap—the distance between the mutation and the phenotype exposed to selection, where developmental biology filled this gap successfully revealing the special forces influencing the path from gene to phenotype. One of such processes is the constraint to the number of possible directions of variation. Even when taking into account this reason, many authors do not see any necessity for an addition to the standard Darwinian models. They find quite traditional the explanations posed by evo-devo researches. What is the reason for introducing new mechanisms if the accepted ones explain well everything?

The Darwinian approach was often accused of tautology: the surviving organisms are the fittest ones, considered the fittest because they have survived. A similar tautology was revealed in the speculations on constraints: "whatever has not changed must have been constrained, and whatever has changed must not have been constrained" (Eberhard 2001, p. 206). For example, specific moveable abdominal lobes exist in the males of sepsid flies, and these structures are extremely rare at the other flies. Maybe the insects have some obstacles to produce such structures, and only a small part of them could overcome them, thus, constraints determined evolution (Wagner and Müller 2002). The other viewpoint states that there is no special pressure of sexual selection in the other species, while at sepsids it does. To support this last viewpoint, the data on multiple (twice repeated) origin of such structure at sepsids is cited; this means that male sepsid are slowly "wandering across the phenetic landscape" under the action of selection (Eberhard 2002, p. 7).

Adaptationistic "Panglossian paradigm" still satisfies many modern authors dealing with constraints. If a change is detected, this means that it was useful and it appeared in the process of mutations and selection—such is the logic often represented. For example, in trilobites, the ability to enroll increased in the course of evolution—meaning a better protection against predators (Hughes, et al. 1999). Moreover, modern studies often tend to find a selectionistic explanation at any price, to the point that in numerous studies disparate efforts were undertaken to substantiate an explanation in terms of natural selection for the finest details of the vein structure of the wings of flies (see Gilhirst, et al. 2000).

Nevertheless, some acceptance to criticism and attempts to consider reforms are observed. The constraints are at least examined now as a possible explanation to evolutionary phenomena, while previously they were absolutely ignored. For example, the appearance of the *Bauplanen* as a problem disturbed evolutionists for a long time. The main body plans appeared hundreds millions years ago and then they just changed, not producing new ones. Maybe constraints were involved here? Some aut-

hors believe there are no reasons for such an idea. In the process of saturation and structurization of the ecological space, the conditions became not suitable for the occurrence of new body plans, so that is why they have not appeared. Anyhow, with such interpretation the authors considered the possibility of an explanation in terms of evolutionary constraints (Ciampaglio 2002, 2004). In some cases, it was admitted that the lack of the material for variability was a significant factor influencing evolutionary events; for example, the number of cotyledons at plants varies very poorly, and so it was explained both by selection and lack of variability (Conner, Agrawal 2005). Other authors claim for the necessity to take into account both selection and the "specifics of design" within evolutionary explanations. Take the selection towards miniaturization of salamanders, which resulted in some significant changes in their form: the small size of buds of extremities led to the decreasing of the number of fingers, the necessity to close the packing of cells led to the changes in form of the head and the nervous system, etc. Therefore, to explain the evolution of salamanders it is necessary to take into account both design limitations and functionalist interpretations (Wake 1991). Finally, in the discussions on this two possibilities—selection and constraint—sometimes it was accepted that constraints were more significant in some cases. For instance, the differences in pigmentation in different segments of Drosophila have a strong interaction with developmental genes, and these interactions are less likely to be a consequence of natural selection, so are better interpreted as evolutionary constraints (Gilbert 2000).

Such discussions usually concern isolated evolutionary cases. Attempts to draw more general conclusions usually fall into the formulation of "compromises": panselectionism certainly is not the best position, but it does not mean that it will necessary turn into panconstraintists (Arthur 2001); constraints and selection are not opposite forces but complementary ones (Fusco 2001); phenotype is a compromise between constraints and selection (Gilbert 2000); the constraints could even contribute to adaptation because unconstrained variation slows down evolution (Wagner 1988).

The best way to "solve" a question on constraints on variation is to place them in the long list of every other possible constraint: "Ontoecogenophyloconstrints" (Antonovics, Tienderen 1991); structural, functional, genetic, developmental, cellular, metabolic, maternal constraints (Hall 1992), etc. Such list can be very long, as any change in one direction means the constraint in some other direction. By developing this idea it is possible to conclude that the whole biology is a series of constraints. It is evident that in such context, any one kind could be considered as more important than the other. The idea of the possibility of evolution on rails became concealed, like in the previous Darwinian writings.

In general, modern research on constraints remains in the bosom of Darwinian "Holy Writ" of biology. Anyhow, the perspective of their fallout from the Darwinian paradigm is quite probable. The first concepts on directed evolution were also stated as additions or slight precisions to Darwin's theory, to later become oppositions. Carl Naegeli in the 1860s claimed that he just added "the theory of perfection" to Darwin's "theory of utility" aiming to explain non-adaptive structures (Naegeli 1865). Albert Koellicker, also in the 1860s, noted that his theory of heterogeneous development was close to Darwin's theory, whereas it removes from biology the teleological doctrine of utility (Koellicker 1864). In what follows, these authors and his numerous advocates counterpoised their views to the Darwinian ones (Koellicker 1972; Naegeli 1884) as they explored idea of directed evolution more profoundly.

Such perspective for modern studies on constraints seems to be feasible as the elaboration of methods for investigating this phenomenon reveals some failures in the traditional evolutionary models. Practically everyone engaged in the studies on constraints noted the absence of adequate methods. Does the absence of some variation means the lack of selection or the lack of the material for variability? To answer such questions some authors propose to pay attention to convergences (Sommer 1999). However, pay attention to convergences and the spirit of orthogenesis heresies arises inevitably. This phenomenon, as well as homoplasy or parallelism is a serious inconvenience to interpretations in terms of natural selection. One of the most famous modern Russian Darwinists, L. Tatarinov, admitted that: "the reasons of the abundance of parallelisms remain unclear. Random hereditary variation should cause a rather uniqueness of features, even in the case of the adaptation of related species to a similar environment" (Tatarinov 1976, p. 190). From a Darwinian viewpoint, evolution should take place mainly in the form of divergence. The exiting methods of phylogenetic reconstruction, elaborated in conformity with Darwinism, tend to conceal convergences because they are based on revealing differences. That is why abundant data on convergences remain hidden (see Moore and Willmer 1997, for a detailed analysis of hiding convergences in modern comparative studies).

According to evo-devo, to study constraints is necessary in order to pose a selection pressure and to look whether the expectable kinds of variation appear (Maynard Smith, et al. 1985). The other side of such target setting means that it is necessary to characterize all possible kinds of potential variability, and to create a system of co-ordinates to estimate the observed variability. Such research is conducted rarely. At least some of them are sharply opposed to the theory of natural selection. Thus, Å. Kovalenko claimed that she "collected an empirical material, which did not correspond to the Darwin's viewpoint on the properties of variability" (Kova-

lenko 2003, pp. 193-194). She emphasizes that she has come to such a conclusion under the pressure of the facts obtained during empirical researches, without any theoretical influence. The source of formulation of such alternative was the fact that the number of available variations is significantly less than the number which could be calculated theoretically. This was shown on the example of the sacrum of various species of Anura—only 45 variations from 288 possible were revealed in process of mass breeding and sampling in nature. Moreover, not only the number, but also the qualitative structure of variants was constant for the species. The set of variations was identical in samples from different populations, in the offspring of different organisms, in the series of young and adult individuals. Even the frequency of definite variations turned out to be rather constant for a particular species. Maybe it would be possible to get all range of probable variations even from one pair. If that is the case, the need to use natural selection for explaining the variation in nature would seem excessive, though it could take place as a "special case": "in any conditions and at any form of elimination, the species would be represented to those variations, which have higher probability in the spectrum of its variability" (ibid., p. 207).

CONCLUSION

The problem of the constraints on variation was not solved neither within the framework of the proper Darwin's theory, nor within the framework of modern Darwinism. Both Darwin and the authors of the modern version of natural selection theory were sharply opposed to include concepts based on constraints, and tried to conceal or discredit any data on this subject. To ignore the problem, they refer to an abundance of facts from other fields of biology. This move has turn the constraint phenomenon to be considered a "special case", insignificant to the general theory.

In the works of the modern followers of Darwin, the contradiction of selection and constraints seem to be less sharp. Constraints are examined and in some special cases considered as the effective factor of evolution. This means an allowance into Darwinism through the back entrance. However, such "compromises" were limited to isolated instances within empirical studies. Otherwise, if recognized, the limitation to variation will always and everywhere affect evolution, and this means that evolution is a movement on rails, instead of wandering through the vast space of adaptation. If that is the case, selection should be considered a destructive force. Moreover, such a standpoint is not Darwinism anymore, it is orthogenesis, and it cannot be included into the Darwinian paradigm. Any compromise between both positions is hardly possible now, because the tendency to favor at any price selectionistic explanations for evolutionary phenomena dominates biology.

NOTES

1 This passage was added in 6th edition of the *Origin of Species*, absent earlier.
2 Wilhelm Johannsen (1857-1927) conducted a research on selection in pure lines of beans over 6-7 generation. It turned out that the limits in variation of any character were reached soon, and any selection pressure could overcome them.

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