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ORIGINAL PAPER

The roots of Evo-Devo in Russia: Is there a characteristic "Russian Tradition"?

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Abstract This paper raises the general question of whether there are any national peculiarities that characterize the scientific and philosophical roots of Russian-language evolutionary developmental biology. The researchers and theories are surveyed which, with hindsight, have been crucial for the Russian tradition when it comes to general methodological principles and constituting concepts. Based on published works and archival documents the main concepts of the "founding fathers" of the Russian tradition with their "Western analogues" are compared. The focus is on A. O. Kowalevsky (1840–1901), I. I. Metschnikov (1945–1916), A. N. Sewertzoff (1866–1936), I. I. Schmalhausen (1884–1963) and the parallelisms between them and E. Haeckel (1834–1919), V. Franz (1883–1950), and C. H. Waddington (1905–1977). In addition, the problem of specific influences constituting the Russian-language context of the Modern Synthesis is addressed. The major thesis of this paper is that the very character of the Russian developmental biology and its intellectual environment predisposed a strong bias towards environmentalist interpretations and thus anticipated what we now call "ecological developmental biology".

Introduction

Are there something like national traditions in science? And, if yes, is it possible to describe a kind of specific Russian tradition in evolutionary developmental biology? Looking through the most recent textbooks introducing this intensively developing research field, one can easily come to a conclusion that the very question on science as national adventure seems absurd. Science is *per definitionem* an international enterprise. For example, in the representative university textbook written by the well-known Russian biologist Archil Dondua (St. Petersburg University), we find a list of forerunners of contemporary evo-devo and include names of scientists of various nationalities such as Caspar Friedrich Wolff, Karl von Baer, Alexandr Kowalevsky, Ilja Metschnikoff, Ernst Haeckel, Ivan Pavlov, Oskar Hertwig, Wilhelm Roux and others (Dondua 2005). At the same time the cultural, political and geographic peculiarities existing in various countries can lead to the biases in the national scientific schools. Russia, and later the Soviet Union, at any time of its history in modern times possessed a number of specific features altogether. One of the specific features was determined by the unique territory of Russia, which made possible for biologists to investigate into the strikingly diverse ecosystems analyzing adaptive processes in the unlike environments (Kolchinsky 2006, p. 177). This was complemented by the trend to the broad theoretical generalizations, the feature shaped in Russia under the influence of German romantic thinkers. All this was accompanied by the periods of partial scientific and political isolation, which followed the 1917 revolutions. In addition paternalistically organized Russian scientific schools more or less loyally developed the methodology and ideas of their fathers-founders. As a consequence, the distinguishable biases within the Russian scientific

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This paper is an extended version of my talk delivered to the *First and founding meeting of the European Society for Evolutionary Developmental Biology (EDD)*, 16–19 August (Prague, Czech Republic). I thank Scott Gilbert for inviting me to this meeting

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traditions appeared, which however does not mean that these traditions can be opposed to the other national schools.

This paper raises the general question of whether there are any national peculiarities that characterize the scientific and philosophical roots of Russian-language evolutionary developmental biology. I develop my arguments along the lines of Gilbert and Bolker, who claimed that "although most of developmental biology lost interest in the environmental regulation of development, this environmentalist tradition lived on in Russia, eventually becoming a major part of the Soviet agenda for developmental biology" (Gilbert and Bolker 2003).

The specificity of Russian evo-devo is related to the general character of the Russian Synthesis in evolutionary biology. The concepts analyzed here are only those concepts, which can be classified as being at the "roots" of evo-devo in Russia, without approaching the complex matter of modern evolutionary developmental biology, which is partly a result of the export and re-export of various Western trends. My objective is to focus on some episodes and not to try and reconstruct the entire prehistory of evo-devo in Russia. It is not my intention here to reproduce the complete biographies of the scientists discussed. I use biographical data only to elucidate the questions of scientific priority and influences.

From von Baer to Kowalevsky and Metschnikoff: a tradition crystallizes

One of the first German-language evolutionists, *Karl Ernst von Baer (1792–1876),* is at the same time regarded as the founder of the Russian school of developmental biology. Von Baer made, however, no clear statements about evolutionary mechanisms. With regard to evolution von Baer combined rather incompatible approaches in his worldview, namely, the naturphilosophical (*Naturphilosophie*) speculations and causal-naturalistic analysis (Raikov 1961, pp. 413–438). As *Naturphilosoph*, von Baer was under some influence of the Schellingian views interpreting Nature as an entity continually "evolving" towards perfection, driven by its own will and climbing from one stage to another. The last and highest stage of this process is man. Proceeding from this romantic philosophical principle von Baer accepted evolution as a historical fact in his early works (e.g., von Baer 1828), but was at the same time sceptical about the ultimate causal explanation of evolution in terms of natural science (Raikov 1961, p. 424).[1] The metaphysical elements, which can be interpreted as natural-philosophical can be found even in the last works of von Baer (von Baer, 1864, 1876). Along these lines von Baer developed the concept of goal-directed creation ("zielstrebige Weltschöpfung"). He distinguished between *Zielstrebigkeit* (goal-directedness) and *Zweckmässigkeit* (which can be translated as expediency or appropriateness).[2] The notion of *Zielstrebigkeit* reflects a kind of lawfulness and determinacy of natural phenomena as seen by the naturalist. *Zweckmässigkeit* by contrast is a supernatural force: the world's will directing its entire development. *Zweckmässigkeit* is incognizable and belongs on the field of faith, and is responsible for the general design of the universe.

As an empirical evolutionist, however, von Baer was quite cautious in making theoretical generalisations. As his biographer B. E. Raikov (1880–1966) pointed out (Raikov 1961, pp. 435–436), in the 1830s von Baer accepted transmutation (evolution) only within species/genera, whereas in the 1850s he already accepted transmutation up to classes, in accordance with empirical findings. After the publication of Darwin's "The Origin of Species" (1859) and works by the brothers Alexander Kowalevsky (1840–1901) and Vladimir Kowalevsky (1843–1883), von Baer accepted that various classes, such as fishes, amphibians, and reptiles, were phylogenetically related. Yet he made no comprehensible statements concerning a hypothetical mechanism of transmutation. Already in the early works von Baer was quite critical about the Lamarckian mechanism of use and disuse. The works of Etienne Geoffroy St. Hilaire (1772–1844) were at that time, with all probability, unknown to him. Von Baer considered the Darwinian hypothesis of natural selection to be speculative (von Baer 1876b) and favored saltationist models, although he emphasized that there are too little empirical evidences for decisive statements on "forms" of evolution. The only idea of von Baer with a remote resemblance to Lamarck's "pouvoir vivre" is the concept of *Zielstrebigkeit*. However, *Zielstrebigkeit* is not a "force" in the Lamarckian sense. In his well-known example illustrating *Zielstrebigkeit* (von Baer 1876a, p. 178) von Baer talks about the clock, which was designed for a certain purpose but functions causally and obey the laws of mechanics. Thus, no special force is needed for this mechanism to work. In von Baer's eyes evolution exists, it is a purposefully designed, although not immediately directed and causally functioning process.

In evolutionary developmental biology von Baer is also well known for the so-called "von Baer's law", which claims that features of the adult forms appear in a certain sequence during embryonic development, and that this

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[1] I do not attract modern Anglo-Saxon literature on Baer to analysis, because here I am first of all interested in the Russian self-reflection of Baer's views.

[2] The German words 'Zweck' and 'Ziel' can both be translated into English as 'goal'.

sequence corresponds to the hierarchy of systematic categories (e.g., family-genus-species), to which the individual belongs. Von Baer's law should not be confused with Haeckel's view "of the pressing back of adult ancestral stages into the young stages of the descendants" (de Beer 1932). Sewertzoff, who later incorporated "von Baer's law" in his concept of anaboly (see below) stressed the difference between this law and Haeckel's recapitulation: "v. Baer's law shows us the order in which the characters which are present today in adult animals were established; the law of recapitulation shows us, on the contrary, the order in which the ancestral characters, which once were present in the adults of the ancestors of the discussed forms, but have been replaced by other characters in the recent adult animal, develop" (Sewertzoff 1931, p. 278–279).[3] It is important to stress, in this respect, that von Baer's notorious typology was in his eyes supported by this law and vice versa, because the type determines the direction of embryonic development. Von Baer's typology came into being more as a result of embryological generalisations than as a consequence of platonic "essentialism".

In addition, it is worth to remark that von Baer carried out his embryological research mostly during his Königsberg period (1817–1834). After having moved to St. Petersburg, von Baer devoted himself to anthropology, geography and zoology, but left embryology completely, even neglecting the embryological literature. He came back to theoretical embryology only in 1841, when he started to teach at the Medical-Surgical Academy, but his attempts to continue experimental embryological studies failed (Raikov 1950, p. 522).

Thus, although von Baer [along with other scientists such as Ch. Pander (1794–1865), G. E. Stchurovskij (1803–1884)] had a significant influence on Russian developmental biology, his work did not give rise to a research program unifying experimental praxis with theoretical approaches around the mid-nineteenth century. It seems that "evolutionary embryology as a science did not exist at the time when Kowalevsky and Metschnikoff embarked on a scientific career" (Bljacher 1959, p. 10). However, von Baer's idea of evolution as a causal and empirically describable process implicit within his "teleological evolutionism" (Kolchinsky 2006, p. 104) survived in the works of the later generations of developmental biologists and, first of all, in the studies of *Alexander Onufrievitch Kowalevsky (1840–1901)*.

Kowalevsky spent his childhood in the Dinaburg district of the Russian Empire (at that time a Russian province and now part of Latvia) (Nekrasov and Artemov 1951). In 1856 he moved to St. Petersburg (then the Russian capital) and after some detours enrolled (1859) at the University to study natural sciences. However, already one year later Kowalevsky left St. Petersburg for Heidelberg and later to Tübingen (1861), where he was trained in zoology and comparative anatomy by Franz von Leydig (1821–1908). In Heidelberg, Kowalevsky began to work on *Amphioxus*, which later became one of his favorite research objects. In Tübingen, he improved his skills in microscopy (Piliptchuk 2003, p. 23). Kowalevsky graduated in 1863 and a year later he started, in Naples, his detailed embryological studies on *Amphioxus.* Around that time Kowalevsky was already under strong influence of Darwin's "Origin of Species", which he read in the early 1860s in German translation (Bljacher 1959, p. 14). The exact timetable of these first years of Kowalevsky's scientific creativity is of great importance, because of the question of a possible influence of Fritz Müller's (1822–1897) "Für Darwin" on Kowalevsky.[4] With all probability Kowalevsky moved to Naples already having developed a detailed research program and became acquainted with Müller's work in Naples, where he shared an apartment with Müller's Russian translator Nikolai Nozhin (1841–1866) (Nekrasov and Artemov 1951). Thus one can argue that Kowalevsky was directly influenced by Darwin's evolutionary views as they were formulated in the "Origin of Species" (1959) and converted them into an embryological research program with evolutionary purposes. In Naples, Kowalevsky not only begins his pioneering works on *Amphioxus* and invertebrates, but also meets *Ilja Iljich Metschnikoff*[5] *(1845–1916)*, who together with Kowalevsky played a crucial role in the growth of developmental biology in the Russian speaking world.

Back in St. Petersburg (1965), Kowalevsky defended a magister thesis on the "History of development of Amphioxus lanceolatus or Branchiostoma lumbricum" (Kowalevsky 1865). This little book can be seen as a turning point in the development of evolutionary embryology in Russia (Piliptchuk 2003, p. 58). Already in these early years Kowalevsky succeeded in softly revolutionizing both the empirical study and the theoretical objectives of developmental biology. His contemporary, the English zoologist Sir

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[3] German original: "Das Gesetz von v. Baer zeigt uns, in welcher Reihenfolge sich die auch jetzt beim erwachsenen Tier bestehenden Merkmale seiner Vorfahren anlegten; das Gesetz der Rekapitulation zeigt uns dagegen, in welcher Reihenfolge die ancestralen Merkmale, die einst bei den erwachsenen Ahnen der in Rede stehenden rezenten Form vorhanden waren, aber beim rezenten erwachsenen Tier durch andere Merkmale ersetzt worden sind, sich ausbilden" (Sewertzoff 1931, p. 279).

[4] More details on Fritz Müller's in place in evolutionary morphology, e.g., in Breidbach (2006).

[5] There are various transliterations of his name in the scientific literature, which include *Elie Metchnikoff*, *Il'ia Mechnikov*, *Ilja Metschnikow* and *Elias Metschnikoff*. He used the latter version himself in foreign-language publications.

Edwin Ray Lankester (1847–1929) emphasized that, although Albert Kölliker (1817–1905) and Robert Remak (1815–1865) already studied the development of some tissues from embryonic cells, it was Kowalevsky, who “in small transparent embryos (such as those of Ascidia, Amphioxus, Sagitta and Argiope) traced the history of adult organs cell by cell to the original egg-cell. It is this procedure which must immortalize Kowalevsky” (Lankester 1902). From the standpoint of evolutionary theory his merit was in proving that the ontogenesis of Amphioxus combined the characters of vertebrates and invertebrates such as a one-layer ciliated blastula, brachial clefts etc. Kowalevsky thus began to tear down the boundaries constructed by von Baer’s more rough, “typological” classification (Mirzoyan 1963, p. 133). Von Baer, who attended Kowalevsky’s magister thesis defense (1865) encouraged the young scientist to continue his studies and highly appreciated his results (Piliptchuk 2003, p. 62). Two years later (1967), Kowalevsky together with Metschnikoff was awarded his first von Baer-Prize, and von Baer was among the referees for the prize (Ovsjannikov 1870). Metschnikoff obtained his prize for proving the existence in insects of germ layers homologous to those in vertebrates. This demonstrates that Metschnikoff, who was at that time only 22 years old, was already an established scientist. Metschnikoff’s entire early career was very impetuous. Originating, as well as Kowalevsky, from a provincial region of the Empire, a village close to Kharkov (now in the Ukraine), he graduated from the Kharkov University at the age of 19 and subsequently improved his knowledge abroad.

Ever since they first met in Naples, Kowalevsky and Metschnikoff remained in close scientific and personal contact, although Metschnikoff was often (especially at first) critical about Kowalevsky’s descriptions. If they were not working together at the Novorossijsk University, where Metschnikoff (1870–1882) and Kowalevsky (1874–1890) spent many productive years, they were in an intensive letter exchange (Poljanskij 1955; Gaisinovich 1974). Taken together they described ontogeneses of almost all groups of invertebrates and lower chordates, and discovered homologies in their early embryonic stages (Mirzoyan 1963, 1974). They discovered the close connection between the coelomic cavities of higher Metazoa and the gastrovascular system of Coelenterata. They elaborated a universal theory of germ layers, declaring homology of the germ layers in all Metazoa, and contributed to investigations into the problem of recapitulation. The concept of homology of germ layers as a universal principle proving that homology goes beyond any separate “type” of animals was formulated by Kowalevsky already in 1871 (Kowalevsky 1871), and this was part of the empirical basis for the Darwinian monophyletic view of evolution. Darwin himself highly appreciated Kowalevsky’s work. Via the letters of his brother, the founder of Russian evolutionary paleontology, Vladimir Kowalevsky (1842–1883) had an intensive letter exchange with Darwin; the latter became aware of A. Kowalevsky’s work. Darwin appealed to Kowalevsky’s (Kovalevsky) discoveries in the second edition of *The Descent of Man* (Darwin 1874).

Also the “German Darwin” Ernst Haeckel (1834–1919) appreciated Kowalevsky’s work very much. In his *Anthropogenie* Haeckel wrote: “The most significant germ histories in the recent time were those of Kowalevsky” (Haeckel 1874, p. 49). It is astonishing in this respect that both Kowalevsky and Metschnikoff were either indifferent or even hostile to Haeckel and his theories. In contrast to Darwin there was no letter exchange between Kowalevsky and Haeckel. The Archive of the Ernst-Haeckel-Haus in Jena holds not a single letter to Haeckel, either both from Kowalevsky or from Metschnikoff, although there are more than 100 letters from other Russian correspondents in the Archive (Hossfeld and Breidbach 2005). This is even more curious considering that Kowalevsky’s younger brother Vladimir made his doctoral work under Haeckel’s supervision (Uschmann 1956), and that the Gastraea theory was to a significant extent based on Kowalevsky’s data. In the 185 letters from Kowalevsky to Metschnikoff we find only 7 short mentions of Haeckel (Gaisinovich 1974). There are several possible reasons for this cold relationship between the two friends and Haeckel. Historians of science have pointed out many times that Kowalevsky and Haeckel had very different scientific “temperaments”. Kowalevsky was much more cautious in interpreting empirical data: “As to ‘Gastraea’ theory, one can quite definitely claim that Kowalevsky could not formulate the theory as it was done by Haeckel, because he knew the comparative-biological data much better than Haeckel, who insufficiently worked on his own” (Nekrasov and Artemov 1951). Metschnikoff (1876, quoted from: Gourko et al. 2000, p. 90) was even more straightforward: “As often happens, when a great scientist is hesitant to draw a crucial conclusion because of insufficient proof, this claim is made by a less careful dilettante. In our case this role is played by Haeckel with his gastraea theory. Everything really valuable and scientifically proven in this theory belongs to others, mostly to Kovalevsky”. Due to his work with *Coelenterata* (*Cnidaria* & *Ctenophora*) Kowalevsky was very aware that gastrulation by ingression is as possible as by invagination, and that Haeckel’s theory is hardly applicable to the developmental processes in hydroid polyps. In other words, Kowalevsky was much less inclined than Haeckel to hasty schematizing, but rather saw his work as a long-term empirical research program ultimately aimed at proving the Darwinian monophyletic view of evolution. It is also important that Kowalevsky admitted alternative ways of gastrulation without absolutizing one way as it was done by Haeckel.

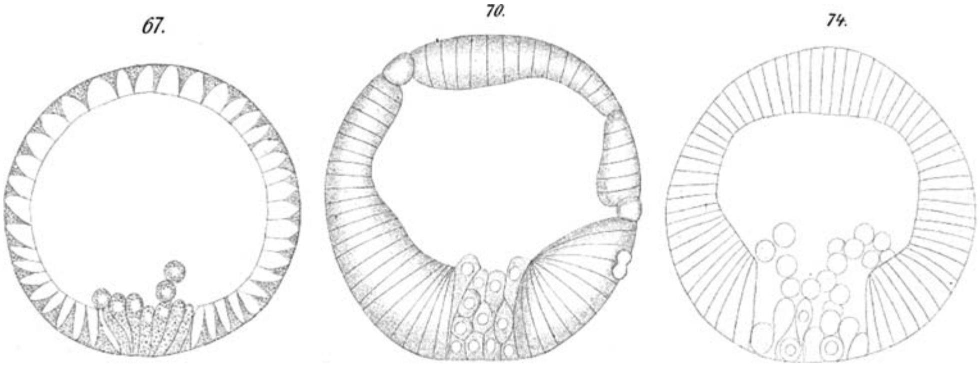

Fig. 1 Some examples of Metschnikoff's picturing of the migrating cells and mesoderm formation (from Metschnikoff 1885). *Pict. 67* Blastula of Sphaerechnius granularis at the beginning of the first seven mesoderm cells migration [Auswanderung der ersten sieben Mesodermzellen]; *Pict. 70* an older blastula of Strongylocentrotus lividus. *Pict. 74* a stage of very intensive mesoderm formation [Ein Stadium mit einer sehr intensiven Mesodermbildung]

Metschnikoff, by contrast, proposed an alternative to the Gastraea theory, which he called the *parenchymella* and later the *phagocytella theory*. He elaborated the fundamentals of the theory while working in Novorossijsk (1870–1882) and developed it further in Odessa and Paris, where he (since 1888) was given perfect research conditions in the Pasteur Institute. By analogy with parenchymula (the flagellate larva of calcareous sponges), Metschnikoff postulated a hypothetical primary organism *phagocytella* consisting of two cell layers: an exterior layer—the ectoderm or kinoblast, and an interior layer—the parenchyma or phagocytoblast. All tissues in a multicellular organism develop from these two kinds of cells. As Metschnikoff himself puts it: "My hypothesis is that phagocytella possesses two primary tissues, kinoblast and phagocytoblast, which, however, were not as distinctly separated from each other as the embryonic layers of the majority of Metazoa; it seems that the replenishment of phagocytoblasts from inwardly migrating kinoblast cells took place for quite a while" (1886; quoted from Gourko et al. 2000, p. 199). Metschnikoff proceeded from the observations of flagellated cells migrating into the central embryonic cavity from the blastula and forming the endoderm. Later, these cells lose their flagellum and become amoeboid (Chernyak and Tauber 1988). Since *phagocytella* was a more primitive organism than *gastraea*, further differentiation into the endoderm and mesoderm was possible by different ways (Fig. 1).[6]

By contrast to Haeckel's scheme, which presupposed a rigid ontogeny mechanically reflecting a phylogenetic history, Metschnikoff's hypothesis allowed adaptive changes at every stage of embryogenesis (Mirzoyan 1974, p. 87). This idea was to play a crucial role in the Russian and some other continental schools of evolutionary developmental biology.[7]

The second important feature of Metschnikoff's theorizing was his emphasis on the symbiotic properties of the organism, which he developed in the later period of his career. Embryological studies ultimately brought him to observations of amoeboid mesodermal cells, which in higher organisms retained their digestive capacity. He proposed that these cells, in higher organisms, could be refunctioned for defense of the organism against intruders (Todes 1989, p. 93). Thus, the *phagocytic theory* came into being, the discovery for which he ultimately was awarded with the Nobel Prize (1908).

Both theories (*phagocytic theory* and *phagocytella theory*) are based on the idea of intracellular digestion. Metschnikoff's theory of immunity in the most general form predicts, however, not only that some amoeboid cells of the organism are crucial for immunity, but also that the organism is a symbiotic system, which includes somatic cells and microflora necessary for the normal functioning of the organism (Frolow 1984, p. 205ff). Metschnikoff's well-known habit of drinking lactic acid daily was based on his theoretical conviction that the harmful microbial flora can be supplanted by friendly symbionts. In other words, Metschnikoff proceeded from the idea of the organism as a kind of complex biocoenosis or ecosystem. This also included the idea of the "struggle for existence" between the cells in the organism. Metschnikoff illustrated this idea with the metamorphosis of the tadpole into an adult frog. For example, the disappearance of the tail occurs because of phagocytic activity (1892; quoted from: Gourko et al. 2000, p. 211). From this viewpoint, infection was a struggle between this symbiotic system and intruders threatening the survival of the organism.

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[6] The description of Metschnikoff's view on mesoderm formation, e.g., in Brauckmann and Gilbert (2004).

[7] A critical account of Metschnikoff's evolutionism can be found in Winsor (1972).

In summary, Kowalevsky and Metschnikoff continued the tradition laid by Baer's empirical studies into the embryological processes and developed two crucial ideas, which then determined the direction of Russian evolutionary developmental biology. The first is their idea of evolutionary plasticity of all stages of embryonic development, with a special emphasis on the role of early stages. As I will show below, this concept was developed in the works of A. N. Sewertzoff. The second crucial point, however, was the view of the organism as an agent of symbiotic/antagonistic biocoenotic interrelations, which became especially significant at the time of the Russian Evolutionary Synthesis.

The Russian tradition matures: Alexei Sewertzoff and his German "analogue" Victor Franz

Sewertzoff had his major influence in Russian- and German-speaking countries, and his theory was arguably the most fundamental and radical revision of Haeckel's biogenetic law in the first third of the twentieth century. Although Sewertzoff constantly stressed that his primary concern was morphological regularities, he evidently committed himself to a selectionist explanation of evolution in his later works. Sewertzoff's theory was paralleled by some comparable, although not identical concepts developed in other national traditions. In Germany, the zoologist Victor Franz (1883–1950) must be mentioned first.

The core of the theoretical system of *Alexei Nikolajevich Sewertzoff (1866–1936)* is the concept of phylembryogenesis (Levit et al. 2004). In its final form, this concept was the result of more than 25 years of research into the phylogeny–ontogeny problem, and the last version of the theory can be found in the Russian editions of *Morphological Regularities…* (Sewertzoff 1939, 1949). The ideas and terminology of this theory are still presented in Russian textbooks, but otherwise relatively unknown, although Gould discusses them briefly in his classic *Ontogeny and Phylogeny* (Gould 1977).

Sewertzoff's purpose was a radical revision of Haeckel's view on the relationships between ontogeny and phylogeny in order to rescue the idea of recapitulation. Just like Metschnikoff, Sewertzoff thought very highly of Fritz Müller's (1821–1897) approach to the problem of recapitulation: "It was F. Müller who proposed that evolutionary changes of the adult forms arise not only from the sum of variations of these forms (this is what Darwin, Haeckel and Weismann discussed), but proceed by means of *gradual alterations of embryonic and larval development*" (Sewertzoff 1949, p. 374). Haeckel and his immediate followers argued that "phylogeny is the mechanical cause of ontogeny" (Haeckel 1874, p. 5) but neglected the idea of an evolutionary impact of ontogeny on phylogeny.

Among German language biologists, Sewertzoff viewed the idealistic morphologist Adolf Naef (1883–1949) as someone who approached the problem in a way comparable to his own. Naef formulated the so-called "*law of terminal modifications*": "The stages of morphogenesis are the more conservative in the recapitulation of the original development, the closer they are to its beginning, and the more progressive, the closer they are to its end" (Naef 1917, p. 57).[8] In Sewertzoff's view, Naef's concept as well as his own was quite close to the original ideas of Fritz Müller. The same basic assumption that "phylogeny is due to modified ontogeny" was shared by Victor Franz (as discussed below), Walter Garstang (1868–1949), Adam Sedgwick (1854–1913) and Gavin de Beer (1899–1972) (Sewertzoff 1949, pp. 389–397).

The theory of phylembryogenesis was along the same lines and represented, in a certain sense, a return to Müller's concept of recapitulation, as opposed to Haeckel's biogenetic law (Severtzov 1990). The phylembryogenesis theory assumes that deviations in the course of ontogenesis can cause changes in adult structures. Sewertzoff saw this idea in contrast to the concept of *coenogenesis*, where embryonic adaptations do not affect the adult stages. As Sewertzoff's student Schmalhausen later commented: "Phylembryogeneses are embryonic changes related to the phylogenetic development of the adult organism. Since every individual deviation is rooted in the process of ontogenetic development, the natural selection of such deviations inevitably results in the reorganisation of ontogenesis. The only question is at which stages and why these changes occur" (Schmalhausen 1969, p. 357). To answer this general question Sewertzoff distinguished three basic modes of phylembryogenesis.

Anaboly

Changes to ontogeny by extension. This should explain "von Baer's law". Sewertzoff insisted on the principal difference between 'von Baer's law' and Haeckel's recapitulation. He maintains that *morphogenesis* is a period lasting from the beginning of ontogeny to the stage at which an individual acquires its most characteristic features. Therefore, anaboly can be defined as an extension of morphogenesis. The exact connection between "von Baer's law" and anaboly consists in that anaboly taking place when the last stages of morphogenesis of a certain organ, which are similar to the adult organ in the ancestor, are completed

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[8] German original: "Die Stadien einer Morphogenese sind so konservativer in der Rekapitulation der ursprünglichen Entwicklung, je näher sie dem beginn, um so progressiver, je näher sie dem Ende derselben stehen".

by addition of new stages to their ontogenesis (Sewertzoff 1931, p. 275). Hence, Sewertzoff argued, anaboly is the simplest, the slowest and phylogenetically the most basal mode of phylembryogenesis (Sewertzoff 1934).

Deviation

Deviation is a departure from the usual course of ontogeny, which occurs in the middle stages. Sewertzoff adapted the term "middle stage deviation" from V. Franz (1927), although he knew that the same phenomenon was described earlier by Naef (1917), and added new contents to this term. In contrast to anaboly, "middle stage deviation" does not extend morphogenesis. As evidence of this mode Sewertzoff appeals, for example, to the evolution of scales in vertebrates. Comparing reptiles and fishes, he concludes that the development of the reptile scale recapitulates only the early embryonic stages of fish scale development, whereas later stages show no sign of recapitulation (Sewertzoff 1949, p. 429).

Archallaxis

Although deviation explains the phenomenon of partial recapitulation, archallaxis explains cases with no recapitulation at all. Briefly defined, archallaxis is an evolutionarily significant modification occurring in the earliest stages of ontogeny (Sewertzoff 1927). A more extensive definition was given by Schmalhausen (1969, p. 358): "Archallaxes are primordial alterations, which manifest themselves in temporal shifts of the beginning of [the development of] an organ (*heterochrony*[9]) as well as in changes to its initial mass or position (*heterotopy*), or in changes of the initial differentiation processes". Archallaxis is characterized by the absence of recapitulation of ancestral features. Some features, like the number of metameres, vertebrae, and teeth can develop, Sewertzoff concluded, only through archallaxis.

All three modes of phylembryogenesis exist in *positive* and *negative* forms. The negative form of anaboly is the deletion of the last stage of ontogeny (as opposed to its extension). Negative deviation and negative archallaxis means the regress of primordia in the middle or early stages of embryonic development, respectively (Sewertzoff 1949, p. 402).

The evolution of a certain feature can combine various modes of phylembryogenesis. For example, a feature can, for a certain period, evolve by means of anaboly, but later convert to archallaxis (Sewertzoff labels such cases as "secondary archallaxis"). Obviously various features of the organism can evolve by different modes.

In summary, the theory of phylembryogenesis separated the problem of recapitulation from Haeckel's "biogenetic law". Sewertzoff could show that the recapitulation of features of the adult ancestors cannot even in principle take place by "middle stage deviation" and archallaxis. Therefore recapitulation cannot be a reliable method for constructing phylogenies. At the same time phylembryogenesis—a comprehensive concept postulating variability at all stages of ontogeny—made it possible to integrate the ontogeny–phylogeny problem into the framework of the Darwinian explanatory paradigm. Further work in Russia along these lines, attempting a synthesis of phylembryogenesis theory and evolutionary morphology with population genetics, was performed mostly by I. I. Schmalhausen and his school.

It is, however, important to emphasize that morphological evolution, in Sewertzoff's theoretical system, follows environmental changes, that both progress and regress have important evolutionary roles, and that all organs and features of organisms can be classified into endo- or ecto-somatic organs that evolve in a correlated fashion. Sewertzoff assumed that evolution is an adaptive process, such that most organs evolve as adaptations to certain environments (Sewertzoff 1914, p. 67; 1949, p. 175). Yet different organs vary in their relationship towards the environment and can be classified into *ecto*- and *endosomatic* (Sewertzoff 1914, p. 127; 1931, p. 334). Organs which are functionally in direct contact with the environment (e.g., skin, teeth, eyes) are ectosomatic, whereas organs which are only indirectly related to it (e.g., heart, kidneys) are endosomatic. These are adaptive as well, but their adaptiveness is of a secondary nature: they do not react directly to changes in the environment. Changes in endosomatic organs and in the organism as a whole are reactions to alterations of ectosomatic organs, although this does not necessarily mean a temporal delay (Sewertzoff 1931, p. 334). In this view (known as Sewertzoff's theory of correlation), slow, continuous and directed environmental changes acting primarily on ectosomatic organs, which, in their turn, cause alterations on the endosomatic level, are of evolutionary significance. Because the organismal changes track environmental changes, Sewertzoff labels evolution as an "ectogenetic process" in order to contrast his views with the various forms of directed evolution (orthogenesis) discussed at the time (Sewertzoff 1949, pp. 184, 186, 187). Although he emphasized that his immediate concern was the morphological regularities of evolution, he explicitly acknowledged that the Darwinian 'hypothesis' is the mechanism most compatible with his approach (Sewertzoff 1949, pp. 184–185).

Does this "ectogenetic" evolution have a general direction? Sewertzoff noted that some biologists reject the

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[9] The terms *heterochrony* and *heterotopy* were coined by Haeckel.

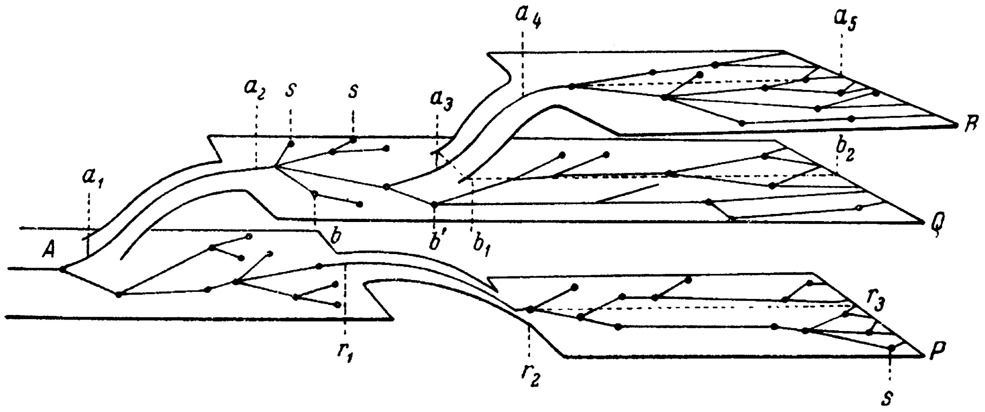

Fig. 2 Sewertzoff's general scheme of the evolutionary process; the lines a_1–a_2 and a_3–a_4 designate aromorphosis, a_2–a_3, b_1–b_2, a_4–a_5, r_2–r_3 = idioadaptations, *s* specialization; the line r_1–r_2 describes regressive evolution. From Sewertzoff (1949, p. 251)

idea of biological progress completely (and argue that an amoeba is as adapted to its environment as is a tiger), whereas some think that evolution is permanently progressive. To solve this controversy, Sewertzoff suggested two different kinds of evolutionary processes: (1) biological evolution and (2) morpho-physiological evolution. In a paper from 1929, written in a rather unidiomatic English, Sewertzoff defined *biological* (= ecological) *progress*, as follows: "The biological progress is, therefore, characterized: (1) by increase of the number of individuals; (2) by progressive migrations, i.e. by the hold of new geographical areas[10]; (3) by the breaking up into new subordinate systematic groups" (Sewertzoff 1929, p. 85). The decrease in all these indices would, on the contrary, indicate a *biological or ecological regress*. In sum, biological progress (or regress) is equivalent to victory (or defeat) in the struggle for existence (Sewertzoff 1949, p. 189–192).

Sewertzoff's primary concern was, however, *morpho-physiological progress*, which does not necessarily coincide with biological progress, because, Sewertzoff reasoned, many biological forms show no or minimal morphological change over very long geological periods. (He offers certain *protozoans* and *brachiopods* as examples.) Sewertzoff's deliberations on progress and regress resulted in his well-known scheme of evolutionary modi, which reflected the Darwinian way of interpreting evolutionary changes and found their explanation in the theory of phylembryogenesis, which showed how modified ontogeny changed the course of phylogeny (Fig. 2).

Yet, as already mentioned above, Sewertzoff was not the only scientist trying to reform evolutionary morphology proceeding from the assumption that "phylogeny is due to modified ontogeny". Perhaps, the most striking similarity was between Sewertzoff's approach and the concept of the German zoologist Victor Franz (1883–1950). According to Hossfeld (2001) and Hossfeld and Olsson (2003a, b) Franz was one of the crucial figures for the development of the evolutionary tradition in German morphology and developmental biology.

It is revealing that in a very early paper Franz already appealed to the problem of hierarchies in phylogenetic history (Franz 1907), which later became the central idea of his whole research. In this paper he protested against the evident simplifications in comparative morphology and raised the issue of reliable criteria for morphological perfection. In addition, he expressed doubts about the applicability of the "causal-mechanical" approach to complex biological systems and pleaded for "mechanical-purposeful" explanations.

In his later works, Franz explicitly made his true ambitions in elaborating and propagating the idea of a ladder towards perfection, which he attempted to convert into a universal biological category. In his mature programmatic book "Die Vervollkommnung in der lebenden Natur" (The Perfectioning in Living Nature) (Franz 1920) he surveys the history of the idea of progress towards perfection starting with the Bible and Aristotle and then proceeding through the middle ages to the modern scientific era. As well as the idealist morphologists he gives much attention to the ideas of Kant and Goethe. From Kant Franz extracted the "objective", "ecological" criteria of perfection. According to Franz, Darwin had an equivocal role in the story, because he was quoted by both champions and opponents of the theory of perfection. In the early twentieth century the discussion initiated by Goethe and later by Haeckel faded somewhat and was resumed only by Franz himself.

Franz's own concept of perfection entirely follows *his* interpretation of Haeckel, Goethe and Kant, although under consideration of the Darwinian concept of the struggle for existence, which he saw as absolutely compatible with his idea of progress.[11] He distinguishes a *morphological* (Goethe, Haeckel) concept of perfection centered on

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[10] With the "hold of new geographical areas" is meant the enlargement of the territory inhabited by a species.

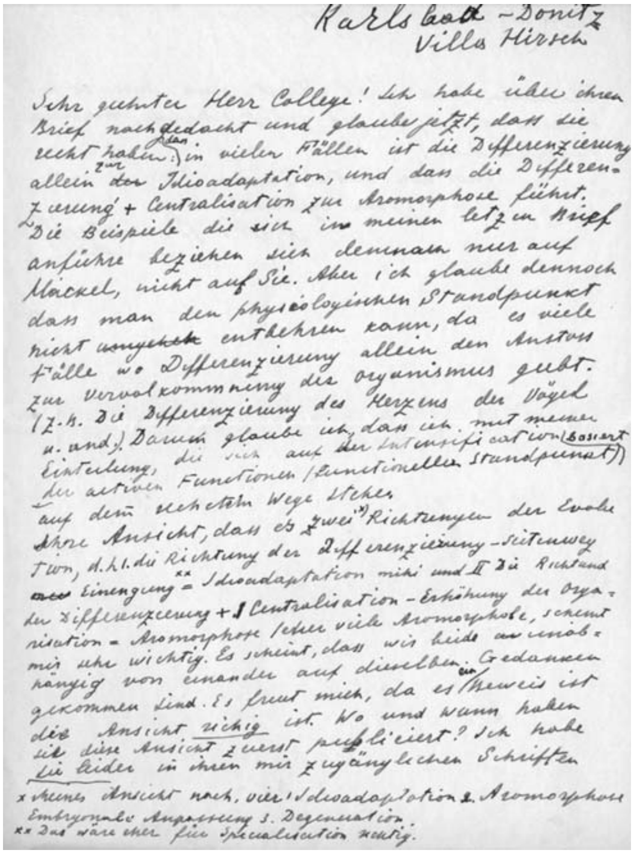
[11] Compare: "Darwin never seriously doubted that progress has been the general rule in the history of life" (Ospovat 1995, p. 212).

differentiation and centralization and an *ecological* approach (Kant) to perfection compatible with the Darwinian struggle for existence (Franz 1920, p. 108). The idea that the process of perfectioning goes by means of centralisation, and differentiation was central to his fundamental book "Geschichte der Organismen" (History of Organisms), in which Franz applied these criteria to the thorough morphological analysis of phylogenetic history (Franz 1924). In a book published 15 years after "The Perfectioning…" Franz introduced the concept of "supremacy" [Überlegenheit] and reformulated his idea of a ladder towards perfection: "Since 1920, I have argued that in the history of organisms the *supremacy* or *potency of victory* [Siegeskraft] in the struggle for existence always increases with the increase of *differentiation* and *centralisation*; this becomes observable due to increasing temporal and spatial ecological expansion (multiplication of species, propagation etc.) of various family trees" (Franz 1935, p. 2).

On the ontogenetic level Franz presented a concept analogous to the phylembryogenesis theory of Sewertzoff. In 1927 Franz coined a notion of "biometabolic modi" (Hossfeld and Olsson 2003b). Since Franz insisted on the scientific priority of his concept in relation to Sewertzoff, it is important to stress, that the first documented attempt to formulate the basics of the phylembryogenesis theory was made by Sewertzoff in 1910 in his talk to the XII congress of Russian naturalists and physicians (Sewertzoff 1910), the term *phylembryogenesis* was coined 2 years later (Sewertzoff 1912). Just like Sewertzoff's "phylembryogenesis", Franz' "modi" described the ways the ontogenetic changes can influence phylogeny (Franz 1927; the English version quoted from Hossfeld and Olsson 2003b):

1. Transgression, extension or prolongation of the ontogeny beyond the former adult stage [. . .];
2. Shortening or abbreviation of the ontogeny in comparison to the former adult stage [. . .];
3. Divergence or deviation of the ontogeny in comparison to the corresponding former adult stage. The deviation occurs in two forms, as far as we can see: (a) larger with each stage [. . .], (b) only at a certain stage [. . .]
4. A change in ontogeny that culminates at a certain stage.

It is evident that Franz's classification is analogous to Sewertzoff's, but what is the actual difference between these concepts? The letters of Sewertzoff to Franz can shed some light on this problem (Fig. 3).[12]


Karlsbad – Donitz
Villa Hirsch

Sehr geehrter Herr College! Ich habe über Ihren
Brief nachgedacht und glaube jetzt, dass Sie
recht haben: dass in vielen Fällen ist die Differenzierung
allein zur ~~der~~ Idioadaptation, und dass die Differen-
zierung + Centralisation zur Aromorphose führt.
Die Beispiele die sich in meinen letzen Brief
anführe beziehen sich demnach nur auf
Haeckel, nicht auf Sie. Aber ich glaube dennoch
dass man den physiologischen Standpunkt
nicht ~~[illegible]~~ entbehren kann, da es viele
Fälle wo Differenzierung allein den Anstoss
zur Vervollkommnung des Organismus giebt.
(z. B. die Differenzierung des Herzens der Vögel
u. and.) Darum glaube ich, dass ich mit meiner
Einteilung, die sich auf der Intensification (basiert
der activen Functionen (functionellen Standpunkt))
auf dem rechten Wege stehe.
Ihre Ansicht, dass es zwei*) Richtungen der Evolu-
tion, d. h. I. die Richtung der Differenzierung – Seitenweg
~~[illegible]~~ Einengung** = Idioadaptation und II die Richtung
der Differenzierung + Centralisation – Erhöhung der Orga-
nisation = Aromorphose (aber viele Aromorphose), scheint
mir sehr wichtig. Es scheint, dass wir beide unab-
hängig von einander auf dieselben Gedanken
gekommen sind. Es freut mich, da es ein Beweis ist
die Ansicht richtig ist. Wo und wann haben
Sie diese Ansicht zuerst publiciert? Ich habe
sie leider in Ihren mir zugänglichen Schriften

x meiner Ansicht nach, vier: 1. Idioadaptation 2. Aromorphose
Embryonale Anpassung 3. Degeneration.
xx Das wäre eher für Specialisation richtig.

Fig. 3 The letter of A. N. Sewertzoff to V. Franz

Two letters from Sewertzoff to Franz were presumably written towards the end of 1920s, when Sewertzoff began writing his major work (Sewertzoff 1931). The letters demonstrate that when beginning his "Morphological Regularities" Sewertzoff knew little about Franz's mature concept and became acquainted with it due to the letter exchange with Franz. Therefore Sewertzoff is extremely cautious in his judgments, although at the same time he is resolute enough to make himself understood. Concerning Franz's theory of progress Sewertzoff states: "To my view, the major difference between our views is that your classification proceeds from the morphological standpoint, whereas I come from the morphological–physiological standpoint."[13]

Differentiation alone, Sewertzoff concludes, can be a misleading feature. For example, adhesive tails of chameleons are better differentiated than those of lizards, but nevertheless one cannot say that the chameleon is at a higher evolutionary stage than the lizard. I did not succeed,

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[12] Two letters from Sewertzoff to Franz were found by Uwe Hossfeld in the Archives of the Ernst-Haeckel-Haus. They are presumably written in the late 1920s, before Sewertzoff (1931) published his major work.

[13] Sewertzoff's original text in German: "Meines Erachtens besteht der Unterschied zwischen unseren Ansichten hauptsächlich darin, dass Sie bei der Klassification der Entwicklungsrichtungen vom rein Morphologischen Standpunkte ausgehen; ich dagegen gehe vom morpho-physiologischen Standpunkte aus."

Sewertzoff concludes, in creating a concept of evolutionary directions in accordance with Haeckel's principles (differentiation and centralization). In the second letter Sewertzoff astonishingly approves Franz's concept of two evolutionary directions (*differentiation alone* that leads to specialization, i.e. ideoadaptation in Sewertzoff's terms and *differentiation + centralisation* which leads to a significant increase in the level of organisation) at the same time emphasizing that he himself distinguished four evolutionary directions (*aromorphosis ideoadaptations*, *coenogenesis, morphophysiological regress*). In fact, Franz's concept setting morphological criteria in the foreground and so far eclipsing functional aspects were less sensitive to such cases as morphological degradation accompanied by biological (ecological) progress. Sewertzoff's theory of evolutionary directions was much more sophisticated than that of Franz. The same can be said about the phylembryogenesis theory as compared to the concept of "biometabolic modi", because both parts of their theoretical systems (the concept of progress and the concept of ontogenetic novelties) are interconnected. Franz viewed both Sewertzoff and Adolf Naef as scientists working along lines similar to his own approach, although Franz and Sewertzoff both rejected Naef's typology (Franz 1927, pp. 37–38).[14] As early as 1917 Naef reformulated Haeckel's "biogenetic law" into the "law of terminal modification" and thus took a decisive step towards explaining phylogeny by ontogeny: "Stages of morphogenesis are as conservative in the recapitulation of initial development, the closer they are to its beginning, while the more progressive, the closer it [morphogenesis—*auth.*] is to the end" (Naef 1917, p. 57). Yet it was Franz, who, in parallel with Sewertzoff, proposed the hypothesis of exact ontogenetic mechanisms underlying phylogenetic changes.

At the same time, Sewertzoff was not entirely correct in characterizing Franz's approach as purely morphological. The "biometabolic modi" concept had even more inclusive criteria than phylembryogenesis, because they contained not only physiological (*metabolic*), but also ecological criteria (Franz 1927, p. 43). Yet, in fact Franz employed physiological data as auxiliary criteria, whereas Sewertzoff considered morphological characters taken together with their physiological aspects and, ultimately, phylogenetic consequences. And this is the crucial point: Sewertzoff's scheme of ontogenetic changes reflects and predicts (retrodicts) the scale of evolutionary novelties they induce. Franz's system is purely heuristic (cf. Hossfeld and Olsson 2003a, b). Therefore Sewertzoff does not see principal differences in cases where Franz does. For example, Franz's abbreviation and prolongation both fall under Sewertzoff's anaboly (negative or positive). Franz's deviations are classified in relation to "von Baer's ontogenetically increasing divergency" (Franz 1927, p. 16). This means deviations, which increase in the course of ontogeny. The snail *Paludina neumayri*, to use Franz's example, evolved into *Paludina pyramidalis* and further into *hungarica* and in the Pliocene developed an angular-knotty form (*tulotoma*). It is clearly identifiable that in the course of *tulotoma* evolution only the peripheral coils change their form, whereas central parts remain smooth. This analysis of differences between the adult stages is distinct from Sewertzoff's middle-stage deviations or archallaxis (primordial alterations), which differ because they have various effects on the further evolution. The most radical and quick evolutionary changes (aromorphoses) are due to series of changes at the very early stages of ontogenetic development.

In summary, Sewertzoff created a concept, where the evolutionarily significant changes can appear at every stage of ontogeny, although with different impact on phylogenesis. This concept was tightly connected with his theory of morphophysiological progress (regress) and his correlation theory. Despite the fact, that Sewertzoff elaborated his theory in much more detail than Franz, Sewertzoff presented an integral theoretical system which connected the environmental evolution with the morphophysiological progress. In that sense he continued the line of Kowalevsky and Metschnikoff. By contrast, his closest German analogue Franz did not succeed in creating such a comprehensive theoretical system.

The Russian tradition culminates: Ivan I. Schmalhausen and his British "analogue" Conrad H. Waddington

Ivan Ivanovich Schmalhausen[15] (1884–1963) was a direct student of Sewertzoff, and his theoretical system can be seen as a direct development of Sewertzoff's theoretical insights. Yet, Schmalhausen's mature theoretical writings appeared at the time of the Modern Synthesis, and his theoretical system was much more inclusive than that of Sewertzoff and involved genetic, ecological, cybernetic and many other aspects.

Schmalhausen's theory, as well as Sewertzoff's, consists of three major parts.[16] The first part is his theory of the *organism as a whole* published in 1938 in the book of the same name (Schmalhausen 1938). This volume develops,

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[14] It can be argued, however, that Naef was under the influence of Sewertzoff.

[15] There are several transliterations of his name: Schmalgauzen, Schmal'gausen, Šmalgauzen and so on. Here, I use the back-transliteration of his German name that he himself used for non-Cyrillic publications.

[16] Below I follow Levit et al. (2006).

on the one hand, the correlation theory of Sewertzoff, but on the other hand, follows entirely Schmalhausen's own empirical results. His basic objective was a critique of the neo-Darwinian understanding of the organism as a "mosaic of characters" and especially the simplified concept of evolution as a "differentiation–centralization" process as expressed by Haeckel and Franz. Schmalhausen stated his objective more precisely: "In the present work we[17] concentrate on something different—here that relative integrity, which is characteristic for the developing organism, i.e. the integrative factors of ontogeny and phylogeny and their role in the very process of individual and historical development will be discussed. These problems have been completely neglected" (Schmalhausen 1938, p. 4). In later works he defined integration as a mutual adaptedness of all parts and functions of the organism, providing general stability of the system (Schmalhausen 1969, p. 337). True to Sewertzoff's school, Schmalhausen combined both morphological and physiological approaches to the problem of differentiation and integrity and talked about "morphophysiological progress" (Levit et al. 2006). There is sufficient evidence, Schmalhausen argued, supporting the idea of correlations at all stages of ontogeny. These correlations determine the course of ontogeny. It is evident already at the blastomere stage, because when isolated a separate blastomere develops differently from when in an intact embryo. However, one can observe correlations also in late developmental stages. Schmalhausen mentions endocrine control in vertebrate development as an example. The organism develops as a whole at all developmental stages due to the complex system of regulative correlations (Schmalhausen 1938, p. 14–15).

In the phylogenetic perspective, Schmalhausen maintained, it is impossible to explain the entire embryogenesis by adaptations. This is a very important claim, which appeared repeatedly in his theory. Also particular morphoses are in his view not necessarily adaptive (see below). Thus Schmalhausen would not subscribe to what Gould and Lewontin (1979) later labeled the "adaptationist program", which explains all organismic features exclusively as adaptations. Yet, as a general rule embryonic evolution obeys the same laws as the evolution of adult organisms: "Since the evolution of adult animals proceeds by means of selection of heritable individual variations (mutations), we have no reasons to think that the evolution of the embryo proceeds in a different way" (Schmalhausen 1938, p. 29).

Schmalhausen's theory of evolutionary modi originates from the ideas of Sewertzoff as well, but Schmalhausen has modified Sewertzoff's notions and made them more specific and appropriate for his theoretical purposes, which were much more ambitious than those of his teacher. Like Sewertzoff, Schmalhausen rejected the concept of directed evolution (orthogenesis) as it was coined by Wilhelm Haacke (1855–1912), popularized by Theodor Eimer (1843–1898) and developed in Russia by Schmalhausen's friend Lew (Leo) Berg (1876–1950) (Levit and Olsson 2006). However, he argued, the fossil record shows that evolution is often divergent, with different lines developing in different directions or in parallel (Schmalhausen 1969, p. 402). He appealed in this respect to the idea of "orthoselection" coined by the German zoologist Ludwig Plate (1862–1937). Plate claimed that, although individual variations are random, only a few phyletic directions are progressive (in any sense of the word) and therefore persist under selective pressure (Levit and Hossfeld 2006).

Schmalhausen adopted Sewertzoff's crucial term aromorphosis, which he defined as evolutionary process "releasing organisms from too narrow environmental restrictions. [...] All major aromorphoses are expressed in the transformation of the entire organisation" (Schmalhausen 1969, p. 410). Here, Sewertzoff's less explicit concentration on the relationships between organism and environment was formulated with all possible clarity. Sewertzoff's ideoadaptation which Schmalhausen made into allomorphosis and again tied its definition to the environment: "Under A. we understand a modification of the organism connected with some alteration of the environment, which however preserves the established relationships of constrained adaptation" (Schmalhausen 1939, p. 135). Sewertzoff's "specialization" was transformed into "telomorphosis" and became an indicator of the transition into highly unusual environments (Schmalhausen 1969, p. 413). A new term "hypermorphosis" was coined to describe the results of sudden environmental change leading to destabilization of organism–environment relationships, and ultimately to overdevelopment of certain characters (or general body hypertrophy) accompanied by disturbance of coordination. Sewertzoff's concept of "general degeneration" was replaced by "catamorphosis" and defined as "a manifestation of changing relationships between organism and environment accompanied by structural simplification and restoration of an organism's plasticity (due to increased fecundity and loss of specialized characters) (Schmalhausen 1983, p. 216). Catamorphosis is a degenerative despecialisation driven mainly by the reduction of ectosomatic (Sewertzoff) organs followed by destruction of the corresponding correlations. At last, "hypermorphosis" describes a special case of catamorphosis, which takes place if the environment changes in

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[17] The Russian scientific tradition prescribes using "we" instead of "I" and "us" instead of "me" also in the works by a single author to stress the rootedness of a scientist in his scientific school.

such a way that certain later developmental stages are never attained, such as in the Mexican axolotl (*Ambystoma mexicanum*).

Thus, all evolutionary modi were described by Schmalhausen in their relation to the environment. It is thus not surprising that during his entire scientific career Schmalhausen strived to develop an exact definition of what "environment" means. In his last works he found an answer in a new approach, which he called "cybernetics" and his central concept of stabilizing selection was introduced in new terms. I, herein, skip Schmalhausen's early formulation of this concept as it was introduced in his classic *Factors of Evolution* (Schmalhausen 1946, 1949) because this is his most well-known book, and instead concentrate on the much less-known later version of this theory. Schmalhausen assumed that evolution can be described as an "automatic", regulative process. At the core of this process we find the population as a "primary evolving entity". The biogeocenosis operates as a regulating mechanism in this process. Schmalhausen was arguably under the influence of the environmentalist tradition represented by Vladimir Ivanovich Vernadsky (1867–1945) and Vladimir Nikolajevich Sukachov (1880–1967) (e.g., Sukatschow 1969). Vernadsky was one of the most influential (or perhaps the most influential) natural scientists in Russia at this time (Fig. 4). He was the founder of biogeochemistry (the term was coined by Vernadsky) and developed the first scientific theory of the biosphere (Vernadsky 1926, 1930). Examining living matter from the biogeochemical viewpoint, Vernadsky arrived at the conclusion that the chemical compounds of the different species do not reflect the chemical composition of their environment, but, on the contrary, living matter has determined the geochemical history of almost all elements of the Earth's crust in the process of making the environment favorable to itself. Thus, living matter shapes the biosphere into a self-regulating system. The structure of the biosphere is described as a dynamic equilibrium: "Not a single point of this system is fixed during the course of geological time. All points oscillate around a certain midpoint" (Vernadsky 1997, pp. 225–227).

Fig. 4 Environmentalism meets evolutionary morphology: V.I. Vernadsky and A.N. Sewertzoff in an academic health center Uzkoje in 1934 (the farthest two figures on the *right*, Sewertzoff is *sitting*). Vernadsky commented in this respect: "These meetings with him [Sewertzoff, auth.] in Uzkoje, when he was already in poor health, were the last ones; only in these years I have realized his importance" From Vernadsky (1942, 2006, p. 103)

Sukachov, one of the most influential figures in Russian twentieth century phytocenology[18], employed the idea of self-regulatedness of the system "living matter-environment" to the analysis of a less inclusive, but more tractable natural system: the biogeocenosis. This concept was coined by Sukachov in developing the idea of "natural zones" presented by Vernadsky's teacher Vassily Dokuchaev (1846–1903). Biogeocenosis describes the entire biocenosis and its inert environment as a relatively stable and self-regulating system. As another crucial figure of the Evolutionary Synthesis, the Russian-German geneticist Nikolai Timoféev-Ressovsky (1900–1981) commented on it: "The biogeocenoses are dynamic systems, which at the same time can be in a state of dynamic equilibrium over quite a long biological time period (in the course of many generations of living beings residing in this biogeocenosis)" (Timoféev-Ressovsky et al. 1975, p. 309).

In this tradition, the biosphere is defined as the sum total of biogeocenoses. In contrast to the term "ecosystem", predominantly used in the Western world, biogeocenosis comprises *all* biotic factors and all biotic dependencies in a relatively isolated system occupying clearly detectable zones (e.g., a pine forest or a swamp). Schmalhausen saw biogeocenosis as the central stabilizing factor in evolution: "Thus, in this case one can reveal the intimate interconnection between the regulator (biogeocenosis) and the object to be regulated (population)" (Schmalhausen 1968, p. 40).

In Schmalhausen's theory, the phenotype mediates the flow of information between population and biogeocenosis (Fig. 5).

The struggle for survival, resources and reproductive success shape the information flow. Furthermore, every phenotype can be seen as a sum of "signals" and "symbols" (coloration, smell, shape etc.) used for communication within a species and between a species and its environment. This contributes to the information field of a biogeocenosis. In summary: "Individuals of any species influence the biogeocenosis with all their activities and so far 'inform' it about the state of the population"

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[18] Phytocenology is in Russia an established part of geobotany and biogeocenology. It corresponds roughly to plant community ecology, but with an emphasis on the geographic and geological aspects.

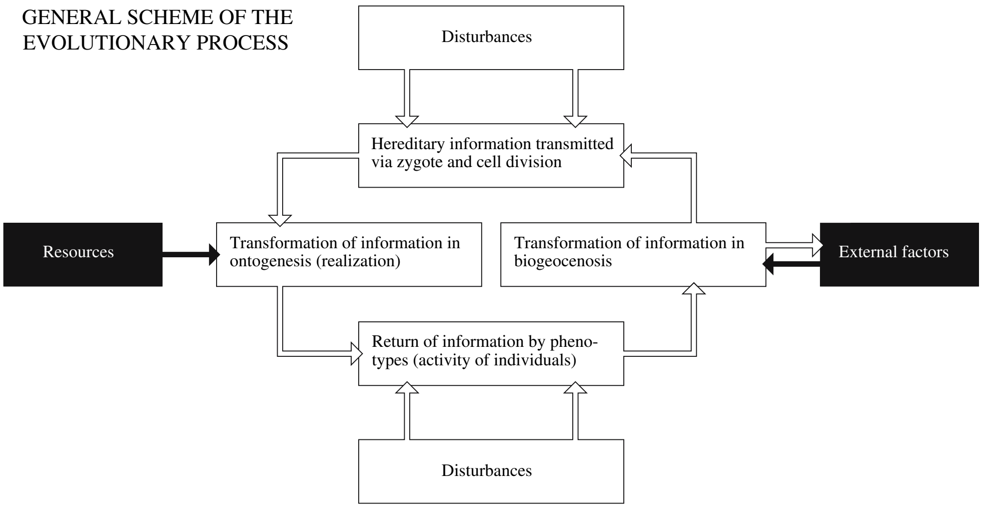

Fig. 5 General scheme of the evolutionary process. Redrawn in slightly modified form from Schmalhausen (1968, p. 42)

(Schmalhausen 1968, p. 48). The biogeocenosis controls phenotypes at *all* stages in their life cycles by the dynamics of resources available to competing individuals within a population. Schmalhausen saw individual selection as accompanied by the process of group selection. He made a clear distinction between micro- and macroevolutionary processes. *Microevolution* is based on a competition between individuals and results in differentiation and restructuring of a population, whereas *macroevolution* is a “principally different” level of evolution based on “inter-group competition” (or on competition between different lineages and phyla[19]) and results in a restructuring of species and higher taxa (Schmalhausen 1974, p. 7). Macroevolutionary processes tend to increase the rate of evolutionary change. The interaction of micro- and macroevolutionary mechanisms gives rise to various modes of evolution (see above). Schmalhausen sees natural selection as being the result of a complex system of self-regulation of biogeocenoses (Schmalhausen 1968, p. 176).

In accord with this approach, Schmalhausen also reformulated his major concepts of dynamic and stabilizing selection as subdivisions of natural selection. Dynamic selection leads to accumulation of certain mutations. This “saturates” the population with selected heritable homozygote and heterozygote mutations. As a consequence the structure of the hereditary code (recorded in DNA) becomes more complex, but the quantity of the hereditary information (in individuals and populations) decreases. In other words, the appearance of a new mutation (a series of mutations) means increase of hereditary information at the genotypic level, but dynamic selection creating a new “mean norm” decreases the general amount of heritable information detectable at the phenotypic level.

“Stabilizing selection”, Schmalhausen continues, “leads to absolutely different results both in transforming the hereditary code and in structuring particular phenotypes and entire populations. First of all, strict strong elimination of heritable deviations from the norm makes them rare. This leads to normalization of the population, and the quantity of both hereditary and phenotypic information increases due to the rarity of deviations” (Schmalhausen 1968, p. 135).

Schmalhausen’s adaptive evolution is thus based on both stabilizing and dynamic selection and represents a complex body of self-regulating systems ranging from the “organism as a whole” to the biogeocenosis.

It has been pointed out many times that Schmalhausen’s theory looks strikingly similar to *Conrad Hal Waddington’s (1905–1975)* concept of “canalization” and that Schmalhausen’s “autonomization” is the same as Waddington’s “genetic assimilation” often associated also with the so-called “Baldwin effect” (after James M. Baldwin, 1861–1934) (Matsuda 1987; Gilbert 1994, 2003; Hall 1998, 2001). As Gilbert puts it: “Genetic assimilation is the process by which a phenotypic response to the environment becomes, through the process of selection, taken over by the genotype so that it becomes independent of the original environmental inducer. This idea had several predecessors, including those hypotheses of J. M. Baldwin, and is essentially the same as Schmalhausen’s hypothesis of genetic stabilization” (Gilbert 2003). The analogous idea was expressed by Hall: “In Russia, Ivan Schmalhausen independently arrived at mechanisms extraordinarily similar to Waddington’s genetic assimilation and canalization. He called his processes autonomization and stabilizing selection and invoked norm of reaction” […] “Schmalhausen’s autonomization was Waddington’s genetic assimilation and vice versa” (Hall 1998, p. 311). Moreover, as well as Schmalhausen, Waddington also thought of development in terms of a “cybernetic process” (Waddington 1953, 1975, pp. 209–230; Gilbert 2003). One of the most radical statements was made by Amundson

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[19] Similar to G. G. Simpson’s “Megaevolution” (Simpson 1944).

(2005, p. 193): “Many of Waddington’s concepts involving the role of development in the evolutionary process were anticipated or duplicated by I. I. Schmalhausen. [...] *The theoretical differences between them are slight* [my ital.].”

Is this really the case? Did Schmalhausen, who came from a different and rich scientific tradition, produce a theory which is equivalent to that of Waddington? The first possible answer is simply to look into the letter from Schmalhausen to Waddington, which, fortunately, has been kept in the Archives of the Russian Academy of Sciences.[20] The letter is written in English at the beginning of the 1950s (Schmalgausen 1988, p. 131), with all probability in 1953 or 1954. Waddington never answered this letter. It is important to note that this was a hard time for Schmalhausen. In 1952–1953 the official position towards the scientific heritage of A. N. Sewertzoff was revised under the pressure of Lysenkoists, and his views were declared “scholastic” and “antievolutionist”. As a consequence, Schmalhausen’s theory was also stigmatized as “metaphysical” and anti-scientific (Schmalgausen 1988, p. 160). In this situation Schmalhausen looked for any kind of support for his views, and it is not surprising that he thanks Waddington for his unintentional support of Schmalhausen’s ideas: “I was delighted by the appearance of your articles in *Nature* (1952) and *Symposia* (1953). I consider the convergence of our ideas very significant, and it strengthens [my] conviction that the idea of stabilizing selection has a future. In any case, I don’t feel anymore so solitary in [my] understanding in the mechanism of evolution, as it seemed to me quite recently. I should like to thank you sincerely for this moral support.”[21] Waddington, in his turn, was obsessed by the struggle for priority and in his well-known letter to Dobzhansky complained that the latter quotes Schmalhausen instead of quoting his papers (Waddington 1975, p. 96). Schmalhausen begins with the statement that the idea of stabilizing selection “found its expression already in my book *The organism as a whole*, which appeared in 1938, and was briefly stated in the book *Paths and laws of the evolutionary process*, published in 1939, where the term ‘stabilizing selection’ was used for the first time.” Schmalhausen also excuses himself for writing the *Factors of Evolution* in the isolation of evacuation: “I am very sorry, that I was writing my book in war-time and could not get acquainted with your articles of 1942.”[22]

Then Schmalhausen goes directly to the terminological problems and argues that stabilizing selection can also be, in a broad sense, called normalizing selection, since it favors the “norm”. At the same time, stabilizing selection can operate differently and that reflects different organisms and their connections to their environments. On the one hand, stabilizing selection leads to stabilization of the genetic structure of a population; on the other hand, it leads to stabilization of individual development: “Thus the stabilizing operation is manifested (1) in a stabilization of the processes of development of the individual (dependent forms of development are substituted by regulatory and autonomous ones), and (2) in an immobilization of populations and species (a “normalization” of individuals composing them). Your term ‘normalization’ I consider as quite appropriate, although it may be also understand in a broader sense, and in this case the same doubts will arise, as those, expressed in connection with the term ‘stabilization’.”.

Schmalhausen also discusses the Baldwin principle. The Baldwin effect was seen by Waddington as an alternative to Schmalhausen’s stabilizing selection. Most of Waddington’s and Schmalhausen’s contemporaries understood the concept “to be that organisms may be able, by non-genetic mechanisms, to adapt themselves to a strange environment, in which they can persist until such time as random mutation throws up a new allele which will produce the required developmental modification” (Waddington 1975, p. 89). Waddington himself viewed the Baldwin effect as a “theoretical possibility”; however, “at most no more than the limiting case toward which genetic assimilation tends when the operation of selection of the genetically controlled capacity to respond is minimally effective” (Waddington 1975, pp. 90, 92).[23]

Schmalhausen was against equating stabilizing selection with the Baldwin effect. In the letter he expressed this idea quite clearly: “Finally, the Baldwin principle, according to my opinion, is only an accessory result of the stabilization of individual development (when dependent forms of development, due to the integration of regulating morphogenetic systems, are substituted by autonomous development, this process being of course accompanied by a reconstruction of the genetic basis of development). If I compared mutations with their phenocopies (and even proposed the term “geocopy”), it was only to show that in some cases even the elementary hereditary factors can produce an effect, similar to that of an environmental factor.”

Schmalhausen’s student, the well-known Russian geneticist M. M. Kamshilov (1910–1979) also reported that

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[20] ARAN, f. 1504, op. 3, l. 27–29.

[21] Here and later I quote Schmalhausen’s letter as it was written, without any intervention into style and spelling.

[22] Schmalhausen wrote the major parts of the book in Kazakhstan in the scientific health resort Borovoje, where he was, on the one hand, isolated from the international scientific community, but, on the other hand, came into close contact with Vernadsky, Leo Berg, Sukachev and other outstanding representatives of Russian environmentalism.

[23] For a detailed analysis of differences between the Baldwin effect and the genetic assimilation see Hall (2001).

Schmalhausen had told him in early 1946 that he only used the Baldwin effect as a "pedagogical device" to make the concept more illustrative (Kamshilov 1974). In the posthumously published comments to the second (1969) edition of *Problems of Darwinism* Schmalhausen made another assertive statement: "The critics have suggested that what I understand under stabilizing selection is in fact a variety of phenomena. This is wrong. I call that form of selection stabilizing selection, which G. Simpson later called centripetal selection.[24] The results of this kind of selection are diverse, but not the stabilizing selection itself (this I have pointed out earlier). *The suggestions about the similarity [of stabilizing selection] and the Baldwin effect are wrong* (italics added). The Baldwin effect is a by-product of stabilizing selection under certain conditions. The theory of stabilizing selection is not a Lamarckian one. It is completely compatible with our modern conception of Darwinism. However, it also contributes something new—the idea of a stable hereditary apparatus as a basis for the mechanism of individual development for its progressive autonomization. In addition to much indirect evidence there is also experimental data in favor of this theory (Kamshilov, Waddington)" (Schmalhausen 1983, p. 351).

In the second Russian edition of *Factors of Evolution* Schmalhausen stated clearly that a phenotypic modification has no effect on the genotype and that what actually happens is "a change of the factors of development of the adaptive feature, which had earlier already been included in the inherited norm of reaction" (Schmalhausen 1968, p. 409). At the same time Schmalhausen supports Waddington's concept of epigenetic systems: "A substitution of external factors of development by the internal ones is thus a general result of the operation of stabilizing selection in fluctuating surroundings. It controls the development of numerous correlational systems of a regulatory type ("epigenetic" systems). This means, in particular, the dominance of the norm, an establishment of autoregulatory and autonomous mechanisms of development, more and more independent on the fortuitous changes of the external factors."

Yet, despite many similarities overshadowed by terminological differences, the true distinctions between Schmalhausen's and Waddington's theories are also evident. One important point is that Waddington neglected Schmalhausen's distinction between adaptive modifications and morphoses (Waddington 1975, pp. 96–98). This distinction played an important role in Schmalhausen's criticism of adaptationism. Morphoses are, in Schmalhausen's terms, non-adaptive reactions, which take place either if an organism finds itself in a new environment or as a result of a mutation. Under predictable environmental conditions stabilizing selection, however, protects adaptive reactions "against possible disturbances by fortuitous external influences" (Schmalhausen 1949, p. 81).

The most important difference between two theories consists in Schmalhausen's emphasis on biogeocenosis as the "arena of the primary evolutionary events" (Schmalhausen 1983, p. 294). His stabilizing selection (as well as dynamic selection) works in this multilevel biosystem. At first glance Waddington means the same, when he claims that "environmental stresses produce developmental modifications" (Waddington 1975, p. 56); however, the difference here lies in the interpretation of what "environment" means. For Schmalhausen, "environment" meant the biogeocenosis (a clearly detectable natural zone) as a self-regulating system incorporated in the global self-regulating system, the biosphere.[25] Waddington's "environment" is much less clearly defined.

Thus, Schmalhausen's theory was not "muddled up" (Waddington's expression) in not distinguishing various kinds of stabilizing selection (Waddington, 1975, p. 98), but approached the subject from a different point of view. As Severtzov (grandson of Schmalhausen's teacher Sewertzoff), who works along Schmalhausen's original lines, sums up: "Stabilizing selection preserving already existing adaptations operates in nature due to the counter-balance of various vectors of dynamic selection" operating in a biogeocenological context (Severtzov 2004). In other words stabilizing selection is *per definition* due to the balance between different kinds of selection. Different approaches to the subject were partially connected with Waddington, perhaps having an experimental and Schmalhausen an observational bias. Schmalhausen's concept of stabilizing and dynamic selections can be fully understood only in the context of his theoretical system as a whole, which also includes the theory of evolutionary modes (directions) and the morphologically–physiologically based concept of an organism as a whole, as well as a separation of integrations and correlations.

Epilogue and conclusions

I end the story with Schmalhausen, because in my view he represents the apogee of the Russian (pre)evo-devo tradition. In the 1960s–1970s the iron curtain became a bit less

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[24] Schmalhausen's idea here was surely not to equate his theory to Simpson's, but to stress the Darwinian character of his concept. Timoffeev-Ressovsky et al. (1975, p. 148) used the terms "centripetal" and "stabilizing" selection synonymously.

[25] Schmalhausen, as a cautious and well-trained scientist, never exaggerated the field of his competence and very rarely employed the term "biosphere".

rigid, and Russian scientists became more involved in international scientific developments. The "Western" theoretical approaches "diluted" the nationally colored traditions. Molecular biology appeared on the stage. The Lysenko-centered histories of Soviet science make it hard to believe, but the first Institute of Molecular Biology in Russia was founded by Vladimir Engelgardt (1894–1984) as early as 1957, although first under the protective name (to protect itself against the notorious Lysenko) of the Institute of Radiation and Physical-Chemical Biology, but already in 1965 it was renamed into the "Institute of Molecular Biology". Two years later the *Journal of Molecular Biology* came into being. Molecular biology as an "essentially reductionist research program" (Bowler and Morus 2005, p. 209) significantly influenced the morphologically embossed biological landscape. In this sense the developments in the 1970s and later cannot be interpreted as Russian "roots" of evolutionary development biology anymore. At the same time, Sewertzoff and Schmalhausen left a strong scientific school, which still exists. The present Chair of the Department of Biological Evolution, A. S. Severtzov, the grandson of A. N. Sewertzoff and an immediate pupil of Schmalhausen, works along Schmalhausen's original lines. However, an analysis of the latest developments in Russian evolutionary developmental biology deserves a special investigation.

What was then the specificity of the Russian school in evolutionary developmental biology as described for the authors presented above? There were three presumable peculiarities. First, in contrast to Haeckel's influential theory, which proceeded from the idea of a rigid ontogenesis mechanically reflecting a phylogenetic history, the Russian school founded by Kowalevsky and Metschnikoff from the very beginning allowed adaptive changes at every stage of embryogenesis. In other words, the concept of the evolutionary plasticity of ontogenesis at all stages appeared simultaneously with the school itself. Second, there was a bias (gaining strength over time) in the Russian-speaking tradition in developmental biology to connect developmental processes with environmental regulation. This began already in the work of Metschnikoff and culminated with Schmalhausen. Third, the organism as well as its environment were approached as integral systems. Holism was used for the analysis of adaptive processes also in other major scientific traditions; however, in Russia it was coupled with two other important peculiarities and incorporated into the Darwinian Synthesis, whereas, for example in the German lands, holism was allied with anti-Darwinian theoretical movements (Hossfeld 2002).

As my comparative essay suggests, each major figure in Russian biology had an analogous figure in the "Western" world of the same time. Similar theoretical processes took place in the German, English, and Russian speaking lands. Nevertheless, the peculiarities mentioned above can be delineated. How can the peculiarities of the Russian development of evo-devo be explained?

n the situation of paternalistically oriented scientific schools[26] and a self-awareness of scientists as an "order of science" putting "transcendental moral values" to their scientific mission (Kolchinsky 2006, p. 160), scientific concepts developed like a snow ball irrespective of changing scientific generations. So the integral way of analysis, the environmental bias and the idea of evolutionary plasticity of the entire ontogenesis, including its very early stages, in a certain sense preprogrammed the way Russian developmental biology proceeded. The generations of "pupils" worked within the frameworks of the research programs founded by the "teachers". The second reason is the extraordinarily strong environmentalist school, which appeared in Russia approximately at the same time (late nineteenth–first half of the twentieth century) as evolutionary biology. This environmentalism had an exceptionally strong influence on the traditional biological fields. Under "environmentalism" I understand here the tradition, which appeared in the late nineteenth century due to the founder of genetic soil science Vassily Dokuchaev, and culminated in the works of Vernadsky "as a key environmental thinker" in Russia (Oldfield and Schaw 2006), and was represented also by such towering figures of Russian natural science as Sukachov and Lew (Leo) Berg, who coined the concept of geographical zones. "Environmentalists" tried to develop an exact theory of environmental perturbations and their influences on the organismic processes. Perhaps it is better to say that living beings were approached as parts of more inclusive natural systems up to the biosphere. At the time of the Modern Synthesis and post-Synthesis (in Ernst Mayr's terminology), evolutionary biologists made this tradition instrumental for the exact definition of organismic environments as self-regulating systems. As Timoféev-Ressovsky emphasized: "The biosphere in its entirety consists of more or less complex biotic and abiotic components, i.e. biogeocenoses. In other words, the biogeocenoses are the precise environments in which the evolutionary process of any group of living organisms takes place" (Timoféev-Ressovsky et al. 1975, pp. 249).

The "separateness" of living organisms was often put in a global perspective. As one of the major figures in Russian comparative morphology of that time, Vladimir Beklemishev (1890–1962), claimed that all life on Earth can be

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[26] The relationship between teacher and pupil was sometimes literally paternalistic. For example, as Schmalhausen was in poor health Sewertzoff himself looked after him and Schmalhausen spent the summer of 1909 in Sewertzoff's Datscha (summer house), assisted personally by Sewertzoff and his family.

described as a "global morphoprocess" (Beklemishev 1964, 1969, 1994). This means that the totality of living matter on our planet is seen as a unitary process continuous both in space and time. It has not been interrupted since the first life began. This global process embraces the whole Earth and can be understood only on a planetary scale. All parts of this global morphoprocess can be considered as a 'particular morphoprocess'. There are also other examples of the extraordinarily strong influence of global and environmentally centered approaches on evolutionary biology, developmental biology, and evolutionary morphology in Russia and Soviet Union. This theoretical context made Russian versions of these scientific fields unique.

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