JOURNAL OF EXPERIMENTAL ZOOLOGY (MOL DEV EVOL) 306B:89–106 (2006)

From the ''Modern Synthesis'' to Cybernetics: Ivan Ivanovich Schmalhausen (1884–1963) and his Research Program for a Synthesis of Evolutionary and Developmental Biology

GEORGY S. LEVIT[1], UWE HOSSFELD[1], AND LENNART OLSSON[2]*
[1]*Institut für Geschichte der Medizin, Naturwissenschaft und Technik, Ernst-Haeckel-Haus, Friedrich-Schiller-Universität, D-07745 Jena, Germany*
[2]*Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität, D-07743 Jena, Germany*

ABSTRACT Ivan I. Schmalhausen was one of the central figures in the Russian development of the ''Modern Synthesis'' in evolutionary biology. He is widely cited internationally even today. Schmalhausen developed the main principles of his theory facing the danger of death in the totalitarian Soviet Union. His great services to evolutionary and theoretical biology are indisputable. However, the received view of Schmalhausen's contributions to evolutionary biology makes an unbiased reading of his texts difficult. Here we show that taking all of his works into consideration (including those only available in Russian) paints a much more dynamic and exciting picture of what he tried to achieve. Schmalhausen pioneered the integration of a developmental perspective into evolutionary thinking. A main tool for achieving this was his approach to living objects as complex multi-level self-regulating systems. Schmalhausen put enormous effort into bringing this idea into fruition during the final stages of his career by combining evolutionary theory with cybernetics. His results and ideas remain thought-provoking, and his texts are of more than just historical interest. *J. Exp. Zool. (Mol. Dev. Evol.) 306B:89–106, 2006.* © 2005 Wiley-Liss, Inc.

FAMILY, CHILDHOOD AND EARLY CAREER

Ivan I. Schmalhausen's ancestors lived in Germany (Bremen) until his grandfather Johann Schmalhausen moved to Russia. Johann graduated from Berlin University and after a short period of teaching mathematics in Reval (then part of the Russian Empire, now Tallinn in Estonia), he moved in 1839 to St. Petersburg as inspector of the Main Pedagogical Institute (Schmalgausen, '88, p 7). When the Pedagogical Institute was closed in 1860, Johann Schmalhausen (now renamed Fedor Fedorovich Schmalhausen) took a position as assistant to the Director of the Library of the Academy of Sciences' Foreign Department. The Director was Karl Ernst von Baer (1792–1876).

Fedor Federovich had two sons and a daughter. The youngest son, Ivan (Johannes) Fedorovich Schmalhausen (1849–1894), became known as one of the founding fathers of Russian paleobotany (Piliptchuk, 2001). He held a Chair in Botany in Kiev (nowadays the capital of the Ukraine)[1] and was awarded a corresponding membership (1893) of the Russian Academy of Sciences. He is also known for his early favorable comments on Mendel's experiments (e.g., Schmalhausen, 1879).

In 1877, I.F. Schmalhausen married Luise Wirt (in Russia—Luisa Ludwigovna Schmalhausen) from Hagenburg (close to Bremen in Germany). They had two sons and a daughter. The youngest son, born on April 23, 1884, in Kiev, was

---

*Correspondence to: L. Olsson, Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität, Erbertstr. 1, D-07743 Jena, Germany.
E-mail: Lennart.Olsson@uni-jena.de

[1] In 1878, he obtained a professorship in Botany, however, initially as an ''extra-ordinary'' professor and only later (1886) did he become ''Ordinarius'' (full professor).

Received 30 June 2005; Accepted 31 October 2005

DOI: 10.1002/jez.b.21087.

Ivan Ivanovich Schmalhausen (Fig. 1).[2] The family resided in an apartment on the territory of a botanical Garden and Schmalhausen spent his first years in the midst of the experimental field, surrounded by passionate naturalists (Schmalgausen, '88, p 22).

In the year Schmalhausen began studies at the Gymnasium (1894), his father suddenly died of a perforated ulcer and Luisa Ludwigovna had to take care of him alone. It is known that in the Gymnasium young Schmalhausen focused on the exact sciences to the neglect of the humanities (Schmalgausen, '88, p 23). In 1901 he graduated and enrolled at Kiev University, but was expelled a year later having taken part in the student disturbances. In 1902 he resumed his university studies at Kiev. Initially, Schmalhausen was interested in chemistry and planned to take technical chemistry under Nikolaj A. Bunge (1842–1915). He missed the deadline, however, because of illness. Around this time Schmalhausen became acquainted with the founder of the Russian school of evolutionary morphology, Alexej N. Sewertzoff (1866–1936), who in the same year (1902) took up a Chair in Zoology in Kiev. This coincidence was to have an overwhelming influence on Schmalhausen's career.

In 1904 Schmalhausen, under the guidance of Sewertzoff, completed his first scientific work on the embryonic development of lungs in a grass snake *Tropidonotus natrix*. Already in this very early work, Schmalhausen discussed several issues of importance in his later research, such as the problem of the causal relationships between ontogeny and phylogeny, and form and function (Schmalgausen, '88, p 31).

Because of financial problems Schmalhausen started his pedagogical career early, teaching at the Higher Women's Courses from 1905.[3] At the same time he published his first papers (e.g., Schmalhausen, '07, '08). As a consequence of his pedagogical and research activities and because of the First Russian Revolution (1905–1907), Schmalhausen graduated only in 1909 with a first-class diploma.

At that time, Schmalhausen lived alone (his mother and sister had moved to Italy) and Sewertzoff was taking care not only of his scientific career, but also of his private life. 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 by Sewertzoff and his family (Schmalgausen, '88, p 35).

Fig. 1. Portrait of I.I. Schmalhausen. Courtesy of Nauka Press, Moscow.

One year later (1910), Schmalhausen married Lydia Kozlova, a teacher of French from a small provincial Russian town. The important XIIth Congress of Russian Naturalists and Physicians (1910), where Sewertzoff first presented his concept of *phylembryogenesis* (Levit et al., 2004), took place when Ivan was courting Lydia and Schmalhausen did not participate in the meeting. So Sewertzoff presented Schmalhausen's paper on limb development in *Salamandrella keyserlingii* to the Congress.

In 1911, Sewertzoff moved to Moscow to take up a Chair in Comparative Anatomy and a year later offered Schmalhausen a position as assistant. Schmalhausen began teaching comparative

---

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

[3] Higher Women's Courses were private educational institutions giving college-level training to female students. In the Russian Empire, women were allowed to attend university only as so-called "free listeners", excluding them from obtaining university degrees.

anatomy together with another young assistant, Boris S. Matveev (1889–1973). Matveev later trained Nikolai V. Timoféev-Ressovsky (1900–1981), whose work, like Schmalhausen's, was concerned with themes important for the so-called "Modern Synthesis" in evolutionary biology. In Moscow Schmalhausen also worked on his Master's thesis on the evolution of the unpaired fins in fishes and immediately after being awarded an M.Sc. degree (1914), left for Anton Dohrn's (1840–1909) Stazione Zoologica di Napoli, where he extended the experimental basis of his morphological studies. Schmalhausen later wrote an introduction to the Russian edition of Dohrn's *Der Ursprung der Wirbelthiere* (1875), in which he praised Dohrn's principle of correlation between form and function as important for modern biology (Schmalhausen, '37a).

Schmalhausen's research in Italy was interrupted by WWI and he was forced to return to Russia earlier than planned. Back in Moscow he intensified the work on his Ph.D. thesis and in 1916 received his degree in zoology for a study on amphibian limbs from an evolutionary perspective. Some of his results were published in English (Schmalhausen, '17).

Having completed his Ph.D. thesis, Schmalhausen applied for a position as "extraordinary professor" in zoology in Jurjev (now Tartu in Estonia), a position which at the beginning of the century had been held by his teacher Sewertzoff. Schmalhausen was appointed in 1918. However, during the application time Russia underwent the February and October Revolutions and German troops occupied Estonia including Jurjev/Tartu. Thus Schmalhausen moved to Voronezh together with the rest of the evacuated faculty from Jurjev University.

The established scientist

In Voronezh, Schmalhausen held a Chair in Zoology and Comparative Anatomy (1918–1921). His assistant was E.V. Rylkova (Matveeva), who had graduated from Moscow University and was the first female scientist in Russia allowed to work towards a professorship. Because of everyday difficulties and a high load of administrative, organizational and pedagogical work, Schmalhausen had little time for research. He did, however write his first textbook in comparative anatomy during this period (Schmalhausen, '23). In 1921 he was offered a Chair in Zoology in the Higher Institute of the People's Education in Kiev, which was built on the basis of Kiev University. One year later Schmalhausen was elected into the All-Ukrainian Academy of Science, which was organized in 1918 by Vladimir I. Vernadsky (1863–1945), the founder of biogeochemistry (Sytnik et al., '88). In 1924 Schmalhausen became head of the Microbiology Institute, later renamed the Institute of Biology and Zoology and now known as the Schmalhausen Institute of Zoology. Schmalhausen formally remained head of the Institute until the beginning of the Second World War and the evacuation of the Ukrainian Academy to Ufa. In 1927, as part of the so-called "Week of Russian Science", Schmalhausen and other leading Russian scientists visited Berlin. There he met the leading comparative anatomists Franz Keibel (1861–1929) and Rudolf Fick (1866–1939).

In the meantime the Higher Institute of the People's Education was transformed—after several reorganizations—into Kiev State University (today—the National Taras Shevchenko University of Kyiv) and returned to the university pattern of research, education, and scientific degrees. Although Schmalhausen was actively involved in the process of reorganization, he intensified his studies on *phenogenetics*, which ultimately would lead him to develop the concept of *morphogenetic correlations* and to a holistic approach to ontogenesis. Draft versions of his first theoretical books (Schmalhausen, '38, '39) were written already during the Kiev period (Schmalgausen, '88, p 105). Thus the basic ideas of Schmalhausen's evolutionary theory, including the concept of stabilizing selection, were initially developed and, partly, published already during the Kiev period (Schmalgausen, '88, p 70).

In 1936 evolutionary biologists at Moscow University organized the Department of Darwinism (now the Department of Evolutionary Theory) and invited Schmalhausen to be the department Chair. A year earlier he was awarded full membership of the Academy of Sciences of the USSR. In parallel, Schmalhausen already had become (in 1936) head of the Moscow Institute of Evolutionary Morphology founded by his teacher A.N. Sewertzoff in 1934 (nowadays known as the A.N. Sewertzoff Institute of Ecology and Evolution). At the same time he remained the director of the Zoology institute in Kiev. Because of this, Schmalhausen moved to Moscow only in 1937 and did not take over the Darwinism department until 1939.

When the Soviet Union was attacked by Germany, the Academy of Sciences in Moscow was evacuated to the beautiful resort Borovoje, surrounded by lakes and forests in northern Kazakhstan. Many outstanding scientists thus came to live and work together. The influence of some fellow scientists can be seen clearly in Schmalhausen's work, e.g., the biogeochemist V.I. Vernadsky, the founder of the nomogenesis theory and the theory of geographic zones, Leo (Lew) S. Berg (1876–1950) (Levit and Hoßfeld, 2005), and V.N. Sukachev (1880–1967), who coined the concept of *biogeocenosis* as an elementary unit of the *biosphere*.

It was here in Borovoje that Schmalhausen wrote his two most influential books, *The Problems of Darwinism* ('46a) and *Factors of Evolution* ('46b). The first versions of these books were written in artificial isolation and without access to literature and data. The first draft of *Factors* was completed already early in 1943 (Schmalgausen, '88, p 113). In the first part of 1945, Schmalhausen contacted the expatriate Theodosius Dobzhansky (1900–1975), whom he knew since the Kiev period, and asked for help with an English edition of *Factors*, which was finally published in 1949.[4] In the fall of 1943 Schmalhausen returned to Moscow and started to give lectures on Darwinism again. Half a year later, as the Academy of Science celebrated its 60th anniversary, Schmalhausen fell ill with influenza, and doctors soon found a glaucoma, which led to blindness on one eye. This impeded Schmalhausen's (especially empirical) research significantly. Even so, after WW II Schmalhausen seemed to be at the zenith of his career. In 1945 he was awarded the Order of the Red Banner and a year later the prize of the Presidium of the Academy of Science. But the awards could not save Schmalhausen from Trofim D. Lysenko (1898–1976). This agronomist without much formal education, who developed a strongly ideologically affected form of neo-Lamarckism, enjoyed the support of Joseph Stalin. Lysenko initiated changes to Soviet biology, which led to the physical elimination of numerous outstanding biologists.[5] The most striking example is Nikolai A. Vavilov (1887–1943), who disappeared in a prison camp. It was extremely dangerous to criticize Lysenko in this situation. However, first in the *Literaturnaja Gazeta*[6] (1947) and then in his paper at the conference on Darwinism (February 3–8, 1948) Schmalhausen, along with the plant physiologist D.A. Sabinin (1889–1951) and the ecologist A.N. Formozov (1893–1973), openly attacked Lysenko and described Lysenkoism as a kind of naïve 19th century mechano-Lamarckism. In August 1948, Lysenko organized a notorious session of VASKhNIL (The All-Union Academy of Agricultural Sciences), which plunged Soviet biology into aggressive obscurantism. Schmalhausen was one of the major targets of this session. Already in the beginning of his opening speech, Lysenko accused Schmalhausen of propagating ''formal autonomism'' and for concentrating on the wrong aspects of the Darwinian heritage, thus blocking the expansion of the ''creative kernel of Darwinism''. The bulk of Lysenko's speech was devoted to criticizing Schmalhausen.[7]

This ''scientific'' criticism of Schmalhausen and other anti-Lysenkoists was followed by administrative persecution. D.A. Sabinin did not endure the mental torture and committed suicide. Schmalhausen lost all his positions and assistants. Still a full member of the Academy, he was downgraded to a senior researcher at the Zoological Institute in Leningrad and this only due to the support from the Institute's director E.N. Pavlovsky (1884–1965).

Although at the VASKhNIL session in 1948, Schmalhausen's teacher A.N. Sewertzoff, as Adams correctly pointed out (Adams, '80, p 221), was still praised as an ''outstanding Darwinian'',[8] the official position towards the scientific heritage of A.N. Sewertzoff was also revised, and in 1952–53 his views were declared ''scholastic'' and ''antievolutionist''. As a consequence,

---

[4] Dobzhansky's foreword to the English translation of Schmalhausen's *Factors of Evolution* (1949/1986) is a very important document of the early reception of the Modern Synthesis. Dobzhansky writes that an ''upsurge of activity in evolutionary biology unprecedented since the time immediately following the publication of Darwin's ''Origin of Species'', ''caused'' by convergence and unification of the contributions to evolutionary thought coming from various biologic disciplines. [...] Genetics, systematics, comparative morphology and embryology, paleontology, and ecology have all been profoundly influenced by and have made important contributions to evolutionary thought. [...] A trend toward unification and synthesis [of the different disciplines] has set in'' (p xv). Dobzhansky lists several ''synthetic treatments'': Dobzhansky ('37), Mayr ('42), Simpson ('44), Huxley ('42) and Rensch ('47) and comes to the conclusion: ''The view of evolution which emerges from all these several treatments is very largely the same. We have arrived at a biologic synthesis. The book of I.I. Schmalhausen advances the synthetic treatment of evolution'' (p xv). See also Reif et al. (2000).

[5] Fore more details on Lysenkoism see Regelmann ('80), Arosevskij ('94), Höxtermann (2000), Hagemann (2002), Hoßfeld and Olsson (2002), Roll-Hansen (2005).

[6] *Literaturnaja Gazeta* (Literary Newspaper) was an important forum for intellectual discussion in the Soviet Union not only for literature, as the name might suggest.

[7] Shorthand record of the 1948 VASKhNIL Session (July 31–August 07): Moscow: OGIZ-SELKHOZGIZ, 1948. The same in German: Die Lage in der biologischen Wissenschaft. Tagung der Lenin Akademie der Landwirtschaftlichen Wissenschaften der UdSSR. Verlag für Fremdsprachige Literatur, 1949, p 13.

[8] Die Lage in der biologischen Wissenschaft. Die Rede Eichfelds, p 82.

Schmalhausen's theory was also stigmatized as ''metaphysical'' and anti-scientific (Schmalgausen, '88, p 160). Schmalhausen retreated to his Datscha and studied terrestrial vertebrates as an independent scholar. Fortunately Joseph Stalin died on March 5, 1953, and the situation slowly changed for the better. In 1955, Schmalhausen became head of the embryology laboratory in the Zoological Institute (Leningrad) and began to write a monograph on the origin of terrestrial vertebrates, which was later published also in English (Schmalhausen, '68). For this monograph and a series of papers he was awarded the Ilya Mechnikov Gold Medal (1963). Earlier (1959), Schmalhausen had been honoured with the Darwin medal (Fig. 2) by the Leopoldina Academy in Halle (Saale), Germany (Kaasch et al., 2006).

The last years of Schmalhausen's life were astonishingly productive. He worked intensely on a reformulation of his evolutionary theory in terms of cybernetics, in parallel incorporating the latest biological data into his theoretical system. His death on October 7, 1963 interrupted him in the midst of new book plans. Posthumously Schmalhausen and his research group were awarded the A. O. Kowalevsky Prize[9] (1965).

DIE DEUTSCHE AKADEMIE
DER NATURFORSCHER
LEOPOLDINA
VERLEIHT
AUS ANLASS DES VOR HUNDERT JAHREN
ERFOLGTEN ERSCHEINENS DES
DARWINSCHEN WERKES
‹ON THE ORIGIN OF SPECIES›
HERRN PROFESSOR DR.
I.I. SCHMALHAUSEN
AKAD. D. WISS. D. UDSSR,
MOSKVA, B. KALUZHSKAYA 14
DIE
DARWIN-PLAKETTE
FÜR BEDEUTENDE LEISTUNGEN
AUF DEM GEBIETE
DER EVOLUTIONSFORSCHUNG
UND GENETIK.

HALLE/SAALE, DEN 10. MAI 1959

PRÄSIDENT

Fig. 2. Darwin Medal signed by Kurt Mothes, the President of the Leopoldina Academy

SCIENTIFIC CONCEPTS

''The organism as a whole''

Schmalhausen's holistic approach to the organism (as opposed to understanding it as the sum of its genetically determined characters) was the first and decisive theoretical step in creating what was later to become known as the theory of dynamic and stabilizing selection. His theory was based on extensive empirical studies. Schmalhausen was 53 years old when he published his first theoretical paper on evolution (Schmalhausen, '37b) and a year later his first book on the subject appeared named (in literal translation) *The Organism as a Whole in its Individual and Historical Development* (Schmalhausen, '38).

This volume develops, on the one hand, the correlation theory of Schmalhausen's teacher A.N. Sewertzoff, but on the other hand, follows entirely Schmalhausen's empirical results. His basic objective was a critique of the neo-Darwinian understanding of the organism as a ''mosaic of characters'' and against the simplified concept of evolution as ''differentiation'' as opposed to ''integration''. The idea of ''integration'' or ''centralization'' had already been clearly expressed by Johann W. von Goethe (1749–1832) and was an important part of German morphology as developed by, for example, Victor Franz (1883–1950) and the idealistic morphologists Adolf Naef (1883–1949), and Edgar Dacqué (1878–1945) (Meister, 2005). Schmalhausen stated his objective more precisely: ''In the present work, we[10] 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, '38, p 4). In later works, he defined integration as a mutual

---

[9] The Kowalevsky Prize of the Academy of Sciences (established in 1940 for embryology, re-established in 1994 for developmental biology and embryology) and awarded to Soviet (later Russian) scientists should not be confused with the *International* Kowalevsky Medal for comparative zoology and embryology. The international prize was founded in 1910, but never awarded until it was re-established in 2001 (Dondua and Aleksandrov, 2002).

[10] 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.

adaptedness of all parts and functions of the organism, providing general stability of the system (Schmalhausen, '69, 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".

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, '38, p 14–15). Correlations can be classified into genomic, morphogenetic, and functional or ergontic form-building correlations (e.g., that the notochord determines the development of the nervous system).

Various forms of correlations play different roles and dominate different stages of ontogeny, in Schmalhausen's view. Thus *genomic correlations* are usually detectable at late stages of autonomous morphogenesis, which show no direct morphogenetic and functional dependency: For example, Drosophila mutants with rudimentary wings also have shortened hind legs, and mutations with shortened legs also have a modified wing venation. *Morphogenetic correlations* are correlations which reflect "interdependencies in the epigenetic factors of individual development" and can be described at the very beginning of their determination (Schmalhausen, '69, p 327). *Ergontic correlations* manifest themselves in the subadult or adult forms, when morphogenesis is already largely completed. The dependency between the development of nerves and their peripheral target organs is an example of ergontic correlations. An example from Schmalhausen is that if sensory organs are removed experimentally, the corresponding nerves or nervous centers do not develop properly. Similar ergontic correlations exist between the development of a certain muscle and the corresponding nerves, blood vessels and skeletal parts (Schmalhausen, '69, p 330).

Correlations are contrasted, in Schmalhausen's vocabulary, with *coordinations*. This serves to highlight the idea of concerted phylogenetic transformations of the correlations themselves. Introducing the concept of coordinations, Schmalhausen comments: "Since the organism is an interconnected whole, it must keep its property of wholeness also in the course of evolution. This would mean the coordinated [evolutionary] transformation of its organs and parts" (Schmalhausen, '69, p 340). Thus, coordinations in phylogeny reflect the holistic nature of the organism in the same way that correlations do in ontogeny.

Schmalhausen distinguished between topographic, dynamic and ecological coordinations. *Topographic coordinations* are the concerted spatial changes of organs which do not correlate functionally, such as the brain and the skull. *Dynamic coordinations*, by contrast, appear in the evolution of ergontic correlations (evolution of various sensory organs, or the upper and lower jaws). The so-called *ecological (biological) coordinations* (coordinations between ectosomatic organs) refer to the coordinated phylogenetic development of characters which manifest no immediate correlations of any kind. Whereas in the first two cases we can have a process of coadaptation of characters, in the last case there is only an indirect adaptation to an environment. Schmalhausen uses the relationship between the form and structure of teeth, on the one hand, and the form of maxillary muscles, on the other hand, as examples. He also refers the body lengthening accompanied by limb reduction seen repeatedly in the evolution of reptiles to the same category of coordinations (Schmalhausen, '69, p 343).

Schmalhausen's concept of correlations and coordinations partially anticipated the current idea of evolutionary and developmental modules (Gilbert and Bolker, 2001; Gass and Bolker, 2003; Schlosser and Wagner, 2004). Correlations and developmental modules can be applied synonymously as far as they are based on pleiotropic effects. Also, the methods of identification, for example, determining "how profoundly their absence disrupts development as a whole" (Gass and Bolker, 2003) seem to be analogous to a certain extent. At the same time, it must be clearly stated that the concept of developmental modules is much more inclusive than Schmalhausen's correlations. As Gass and Bolker (2003) point out "a developmental module is less an object than it is a resource", which can include a gene, a set of gene products or a signaling pathway, etc. Correlations are a predominantly morphological concept originally developed by Sewertzoff. However, correlations are resources as well in that they serve as a basis for the formation of coordinations.

The same can be said about evolutionary modules: to the extent that they are structural—morphological, they are analogous to coordinations. One can rephrase Gass and Bolker's (2003) definition (''*an evolutionary module is the phenotype resulting from both the composition and the connectivity of the particular suite of developmental modules involved in its construction*'') of the relationships between evolutionary and developmental modules in Schmalhausen's terms: *Coordinations are the phenotypic structures resulting from both the composition and the connectivity of the particular suite of correlations involved in their construction in the course of phylogeny.*

So what does the machinery of evolution look like in the light of Schmalhausen's classification? The initial evolutionarily significant changes occur in the organs which do not correlate in ontogenesis (biological coordinations). Later evolution will involve morphogenetically and ergontically correlating characters and ultimately also transforms topographic coordinations (Mirzoyan, '83).

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 ('79) 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, '38, p 29).

An important consequence of Schmalhausen's concept of ''the organism as a whole'' is the claim that the phenotypic system of correlations is more conservative than the hereditary structures. In other words it tries to explain different rates of molecular and morphological evolution. The adaptations of various parts of the organism can proceed by way of direct mutual adaptations of different parts of the differentiating organism to each other (integration). Although correlations are not necessarily heritable, correlative changes ''appear to be quite heritable in those cases when one of the members of a correlative chain undergoes a heritable transformation (as the first manifestation of a certain mutation)'' (Schmalhausen, '69, p 336). Mutations constitute the basic machinery of creating or destroying correlations, since ''each mutation means alteration in the system of genomic and morphogenetic correlations'' (Schmalhausen, '69, p 332). The destruction of unnecessary correlations plays an important role in stabilizing selection (see below). The summation of such mutations in the absence of natural selection can result in structural disintegration. Schmalhausen uses domesticated species which have lost their ability to exist in the wild by loss of important characters as an example. Only the presence of natural selection gives a direction to the correlative transformations, whereby new and advantageous forms of organization can appear. As discussed below, these forms react differently to environmental factors, i.e., manifest various adaptive modifications.

The theory of stabilizing selection

The theory of stabilizing selection is the theory of ''autonomization'' and ''normalization'' of populations and is at the center of Schmalhausen's theoretical heritage. Schmalhausen credits the American naturalist John T. Gulick (1832–1923), who coined the concepts ''balanced'' and ''unbalanced'' selection, as his forerunner (Gulick, '05). He follows Gulick in that he distinguishes two kinds of selection, i.e., *dynamic*[11] and *stabilizing* selection. Dynamic selection is caused by changes in ''ecological conditions and biocenotic relationships'' (Schmalhausen, '69, p 237), when existing developmental mechanisms are confronted with new circumstances. The summation and integration of heritable variation and the change of the ''mean norm'' results in a shift of the variation curve, i.e., in creating a new ''mean norm'' or two or more new norms. This is, Schmalhausen argued, a very Darwinian form of natural selection, adaptation to novel environments. Instead of ''environment'' Schmalhausen used the more precise term ''biogeocenosis''. He wrote: ''Thus, the foundation of the dynamic form of natural selection is the changing position of a population in the biogeocoenosis, which confers advantages to certain variants, while others appear to be in an unfavorable position'' (Schmalhausen, '69, p 237). The concept of biogeocenosis was

---

[11] Although we here use the received translation of Schmalhausen's term ''dvizhuschchij''/''preobrazujustchij'' as ''dynamic'', we find this widespread term unlucky, because both forms of selection are in fact equally dynamic. A better translation would be ''shifting'', ''moving'' or ''directed'' selection. The German translation of the term as ''verschiebende Form der Auslese'' (Timoféev-Ressovsky et al., '75, p 148) is more instructive.

coined by Schmalhausen's friend V.N. Sukachev (Sukatschew) and refers to the elementary structural unit of the biosphere, which includes both biotic and abiotic environments functioning as an interconnected system.[12] Schmalhausen was aware of the analogous term ''ecosystem'' coined (1935) by Arthur Tansley (1871–1955), but preferred ''biogeocenosis'' as a more precise term which attaches biocoenoses to certain geographical landscapes.[13] Also N.W. Timoféev-Ressovsky, the geneticist whose work was important for creating a ''Modern Synthesis'' in evolutionary biology in both Russia and Germany, preferred biogeocenosis to ecosystem. He stressed that although the notion of biogeocenosis coincides with the notion of ecosystem as a description of the functional characteristics of biosystems, the important difference is that a biogeocenosis is a precise, clearly definable spatial unit (biohorological unit) (e.g., Timoféev-Ressovsky, '61)

In contrast to the dynamic form of selection, stabilizing selection operates in stable biogeocenoses, i.e., in a situation of dynamic equilibrium between populations and biogeocenosis undergoing certain (e.g., cyclic) changes. Under these circumstances, when an environmental factor fluctuates around a mean value, the so-called ''norm'' has adaptive advantages leading to stabilization of phenotypes and populations. The effect of stabilizing selection ''increases in the presence of the rapid and at the same time irregular fluctuations of environmental factors (continental or montane climate, passive transfer or migration of organisms, etc.)'' (Schmalhausen, '90, p 144). With ''stabilization'' Schmalhausen meant the acquisition of more independence from external factors, and from factors which influence the process of individual development. Stabilizing selection can be a ''dynamic'' and essentially creative force continually establishing new patterns of ontogenetic development. In an unpublished manuscript (cited by O. Schmalgausen) Schmalhausen clearly stated that stabilizing selection means ''radical transformation (perestrojka) of individual development'' (Schmalgausen, '88, p 138). Mutations are the driving force for this: ''During the process of selecting normal individuals, the elimination of harmful variations takes place as well, and, at the same time, a continuous summation of all these mutations takes place, which can be integrated into the normal phenotype'' (Schmalhausen, '69, p 238).

The stabilization machinery works according to the biblical principle: ''For unto every one that hath shall be given, and he shall have abundance: but from him that hath not shall be taken away even that which he hath''.[14] In small populations of organisms of low complexity, where mutations are clearly expressed phenotypically, stabilizing selection contributes to the genetic homogeneity of the population and ultimately to the loss of evolutionary plasticity (the so-called *immobilization* of species). However, if regulatory mechanisms are already well developed, stabilizing selection will promote further development of the population's plasticity and autonomy by improving the regulatory mechanisms of development. At the same time, the impact of stabilizing selection on the phenotype leads to its ''normalization''.

This stabilizing selection, as described by Schmalhausen, operates dichotomously, on the one hand stabilizing the genetic structure of the population, and, on the other hand, optimizing development in such a way that the so-called ''norm of reaction'' becomes restricted, which makes the organism more autonomous in relation to its environment. A norm of reaction is a specific reaction of the organism to certain environmental conditions (*modifications*), and is determined by the organism's prehistory (Schmalhausen, '46b, p 19) or in other words by the range of phenotypic expression of a given genotype (Wake, '96). For example, leaves of *Anemone pulsatilla* which have developed in the shade are much more cleft compared to light-exposed leaves of the same plant. A simple example of a modification is the transformation of muscles as a result of regular training. Such modifications are non-heritable and not necessarily adaptive. Non-adaptive reactions, which Schmalhausen calls ''*morphoses*'', 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 protects adaptive reactions ''against possible disturbances by fortuitous external influences'' (Schmalhausen, '49, p 81). Yet these two forms of selection (dynamic and stabilizing) are abstractions. In biological reality both types of selection operate simultaneously. Environmental conditions change continually and dynamic selection occurs continuously. However,

---

[12] Sukachev was awarded (in 1950) the V.V. Dokuchaev Gold Medal (after Vassily Dokuchaev, 1846–1903, founder of genetic soil science) for his work on biogeocenoses.

[13] The term biogeocenosis is in the modern Russian literature often used as a ''geographical'' version of the more inclusive concept ''ecosystem'' (e.g., Zherikhin, 2003, p 410–525).

[14] Matthew 25:29, King James Bible.

environmental changes are often slow enough to allow stabilizing selection to take effect.

In *Factors of Evolution* Schmalhausen gave a detailed illustration of how the dynamic-stabilizing machinery works. He considered *Acacia pycnantha*, which develops leaf-like structures (phylloclads and phyllodes) as an adaptation to dry conditions. The replacement of leaves by leaf-like structures proceeds autonomously during ontogeny without environmental influences. Schmalhausen asserts that this can be explained only as a result of periodic droughts followed by compensating modifications. Under such xerophytic conditions, this adaptive modification became a stable (heritable) character due to stabilizing selection which eliminated individuals who responded prematurely to occasional wet periods by developing normal leaves. Then the dynamic form of selection completed the process by making the newly appeared organs into leaf-like structures with a low rate of evaporation, i.e., adapted to a dry environment (Schmalhausen, '46b, p 144, '49, p 86).[15] This example shows that stabilizing selection is a complex form of adaptation to fluctuating environments which can create new heritable adaptive mechanisms. Stabilizing selection generates the key adaptations which can liberate organisms from the rule of chance.

Modes of evolution

Schmalhausen's theory of modes of evolution originates from the ideas of Sewertzoff, but Schmalhausen has modified Sewertzoff's notions and made them more specific in accordance with his theoretical purposes, which were much more ambitious than those of his teacher. Sewertzoff never tried to create a general (synthesized) evolutionary theory, his work was focused on the morphological regularities of evolution (Levit et al., 2004)

Like Sewertzoff, Schmalhausen rejected the concept of directed evolution (orthogenesis) as it was coined by Wilhelm Haake (1855–1912), popularized by Theodor Eimer (1843–1898) and developed in Russia by Schmalhausen's friend Lew (Leo) Berg. The retrospective view, Schmalhausen argued, can give the impression that evolution is directed, because ancestors of any existing form can be represented as a specific phylogenetic line. However, he argued, the fossil record shows that evolution is often divergent, with different lines developing in different directions or in parallel (Schmalhausen, '69, p 402).

At the same time, evolution is not a chaotic adventure and ''evolution of a certain organism cannot go in any arbitrary direction'', because ''the historically shaped structure of an organism constrains the possible directions of the evolutionary process'' (Schmalhausen, '39, p 123). Thus the fossil record points to radiations from common ancestors rather than simple orthogenetic evolutionary patterns. So Schmalhausen rejected orthogenesis and accepted 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 (Plate, '13, p 508; see also Levit and Hoßfeld, 2006). Schmalhausen also permitted ''Deperet's rule of progressive specialization'' (after the French paleontologist Ch. Deperet, 1854–1929), which claims that only a few evolutionary directions are advantageous for highly specialized species. They therefore tend to become more and more specialized (Schmalhausen, '39, p 127).

But all these phenomena, he argued, can be explained in purely selectionist (Darwinian) terms and by a general theory of evolutionary modes. As Sewertzoff and others had done before him (Hoßfeld and Olsson, 2003; Levit et al., 2004), Schmalhausen distinguished between biological and morpho-physiological progress. Biological progress is the increase of adaptedness (as evidenced by more successful reproduction) and can be realized in the following modes:

Aromorphosis. Both term and concept follow Sewertzoff's initial idea faithfully: ''Aromorphoses are evolutionary processes releasing organisms from too narrow environmental restrictions. [...] All major aromorphoses are expressed in the transformation of the entire organization'' (Schmalhausen, '69, p 410). Aromorphoses are usually connected with clearly definable morphophysiological changes resulting in immediate adaptive advantages. Thus the aromorphoses, which ultimately led to the appearance of mammals, were based on such seemingly insignificant characters as hair. Further steps towards ''mammalness'' are connected with the reduction of heat emission and increasing metabolic intensity.

Allomorphosis is another term for Sewertzoff's ideoadaptations (Levit et al., 2004). Schmalhausen was unhappy with ideoadaptations, for the reason that it literally means a ''heritable organismic

---

[15] In our view, the English translation (1949) is less clear here than the Russian original.

change'' that can be applied to all evolutionary modes. ''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, '39, p 135). It is a ''routine'' evolutionary mode.

Telomorphosis[16] is close to Sewertzoff's notion of specialization and indicates the transition into highly unusual environments (Schmalhausen, '69, p 413). Telomorphosis is characterized by progressive differentiation of certain characters and reduction of others. Schmalhausen gives the example that basal extant vertebrates such as lampreys are well adapted to their semi-parasitic lifestyle, but narrowly specialized. Schmalhausen sees telomorphosis as characterized by a deceleration of the rate of evolutionary change due to stabilizing selection. It has later been noted that the early stages of *specialization* can proceed quite rapidly and then slow down as when multifunctional organs become increasingly specialized (Severtzov, '90, p 193).

Hypermorphosis results from sudden environmental change leading to destabilization of organism–environment relationships, and ultimately to overdevelopment of certain characters (or general body hypertrophy) accompanied by the disturbance of *coordinations*. Schmalhausen uses as an example the huge tusks of the pig *Babyrousa babyrussa* (Schmalhausen, '69, p 415–416), another example often used in this debate was the Irish Elk with its ''oversized'' antlers. Hypermorphosis was one of the preferred arguments of those favoring orthogenesis, because of its apparently non-adaptive character. Schmalhausen, however, thought hypermorphosis could be explained in Darwinian terms. According to Schmalhausen's concept of correlations–coordinations (see above), an organism is not necessarily a perfectly adapted construction. He thought that hypermorphosis indicates biological regression due to lack of adaptive plasticity, which may ultimately lead to extinction (Schmalhausen, '83, p 216).

Catamorphosis is a notion modifying Sewertzoff's concept of ''general degeneration'': C. is 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, '83, p 216). Like hypermorphosis, catamorphosis can result in extinction. In other words, catamorphosis is a degenerative despecialization driven mainly by the reduction of *ectosomatic* organs followed by destruction of the corresponding correlations. Schmalhausen thought that catamorphic changes can proceed very rapidly, because degenerative mutations are widespread and can quickly ''satiate'' a population in the absence of barriers. He viewed the origin of, e.g., bryozoans, tunicates and aphids as examples of catamorphosis.

Hypomorphosis is a special case of catamorphosis, which takes place if the environment changes in such a way that certain later developmental stages are never attained. As a result, an organism is forced to mature lacking these last stages. A characteristic example given by Schmalhausen is the Mexican axolotl *Ambystoma mexicanum*, which does not normally metamorphose into a land living form.

The concept of different modes of evolution combined with natural selection introduces an element of predictability into evolutionary theory as developed by Schmalhausen. He wrote, for example, that the ''aromorphosis of a flourishing form will quite lawfully result in allomorphosis'' (Schmalhausen, '69, p 429), and allomorphosis will, in its turn, ''quite lawfully'' transit into telomorphosis.

Evolutionary theory and cybernetics

In the last period of his scientific career, Schmalhausen was occupied by the idea of explaining evolution in terms of cybernetics. But in the USSR cybernetics was initially not much more in favor than genetics. In the early 1950s, several important ideological journals published papers stigmatizing cybernetics as a ''sterile flower of bourgeois science'' and an ''ideological weapon of the imperialistic reactionaries'' (Pospelov and Fet, '98). The Soviet *Kratkij Filosofskij Slovar* (Short Philosophical Dictionary) (1954) defined cybernetics simply as a ''pseudoscience''. Nevertheless, already in 1955 an introductory paper on cybernetics written by its enthusiasts S.L. Sobolev, A.I. Kitov and A.A. Lyapunov was published in the influential philosophical journal *Voprosy Philosofii* (Problems of Philosophy) (Sobolev et al., '55). The last author of this crucial paper, the mathematician Alexej Andreevich Lyapunov (1911–1973) played an essential role not only in advancing mathematics and cybernetics, but also in the resistance to Lysenkoism.

---

[16] Corresponds to *telemorphosis* in the early works (e.g., Schmalhausen, '39, p 141).

Lyapunov organized a seminar on cybernetics at Moscow University, and edited the book series *Kibernetitcheskij Sbornik* (Collected Papers on Cybernetics) and *Problemy Kibernetiki* (Problems of Cybernetics). The deputy minister of defense, Academician and Admiral Axel Ivanovich Berg (1893–1979), who realized the significance of cybernetics early on, played an important role in promoting it. Cybernetics also attracted evolutionary biologists, and many papers on genetics and evolutionary theory were published in Lyapunov's *Problems of Cybernetics* (started in 1958). Authors included N.V. Timoféev-Ressovsky, R.L. Berg, and I.I. Schmalhausen. In the 1960s Lyapunov worked on applying mathematical theory to biology, and in 1968 he edited a volume of Schmalhausen's work on cybernetics and related issues. This was done in collaboration with Schmalhausen's former student the geneticist Raissa Lvovna Berg (daughter of Leo S. Berg).

In their introduction to the book, the editors emphasized that the ''cybernetic'' works of Schmalhausen were written under the strong influence of Vladimir Vernadsky's theory of the biosphere as a self-regulating system (Vernadsky, '26, '65; Levit, 2001). Schmalhausen discussed Vernadsky's ideas with him in Borovoje (Jaroschevsky, '95, p 278). The editors comment: ''Vernadsky succeeded in exploring the reciprocity of the evolutionary process and the idea of stabilization in living nature at the level of the biosphere. However, within the framework of biology itself these important concepts—constancy and historicism—were disregarded until the work of Schmalhausen'' (Berg and Lyapunov, '68; see also Berg, '96).

Schmalhausen proceeded from the assumption 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''. Biogeocenosis operates as a regulating mechanism in this process. V.N. Sukachov (e.g., Sukatschow, '69), the most influential figure in Russian 20th century phytoceonology[17] (Ghilarov, 2006) introduced this term to develop the concept of ''natural zones'' coined by Vernadsky's teacher Vassily Dokuchaev (1846–1903). Biogeocenosis describes the entire *biocenosis* and its inert environment as a stable and self-regulating system. As Timoféev-Ressovsky puts 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., '75, p 309). The biosphere is defined as the sum total of biogeocenosis. In contrast to the term ''ecosystem'', predominantly used in the Western world, biogeocenosis comprises *all* abiotic factors and all biotic dependencies in a relatively isolated system occupating 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, '68, p 40).

The phenotype mediates the flow of information between population and biogeocenosis. 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'' (Schmalhausen, '68, 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 competition between individuals and results in differentiation and restructuring of a population, while *macroevolution* is a ''principally different'' level of evolution based on ''inter-group competition'' (or on competition between different lineages and phyla[18]) and results in a restructuring of species and higher taxa (Schmalhausen, '74, 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, '68, p 176).

---

[17] Phytocenology is in Russia an established part of geobotany and biogeocenology (Mirkin, '85; Kull, '88). It corresponds roughly to plant community ecology, but with an emphasis on the geographic and geological aspects.

[18] Similar to G.G. Simpson's ''Megaevolution'' (Simpson, '44).

A possible quantitative approach to determining the rate of evolution in biogeocenosis was expressed by Schmalhausen in the formula:

$$\Delta p = p_1 q s = (H_1 I - H I_1 / I_1 - H I_1)(1 - H/I),$$

where I is general information, whereas H is average information; I_1 and H_1 symbolize the quantity of information introduced by a positive phenotypic variant into the following generation; p is the frequency of the selected variants and p_1 the frequency of the selected variants in the next generation; q is $1-p$, i.e., the frequency of the non-selected variants; s is a coefficient of selection determined by the relative frequency of the variants **A** and **B** in the biogeocenosis: when $s = 1$ (maximum, i.e., one variant has completely replaced the other), then $\Delta p = q$ (Schmalhausen, '68, p 151–152).

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, '68, p 135).

The latter statement seems paradoxical because ''stabilization'' or ''normalization'' is often interpreted in terms of simple phenotypic unification, and unification means decrease of phenotypic information (most phenotypes appear to be very similar). Yet Schmalhausen's stabilizing selection is the major creative force in evolution establishing a new norm, which is more stable due to the newly fabricated mechanisms for secure transmission of hereditary information and defense against possible disturbances (including mutations).

Stabilizing selection encourages an optimal heterozygosity of a population and creates regulative mechanisms of a newly established heterozygote norm: ''An optimal level of stability and evolutionary mobility will be achieved due to the stabilizing form of natural selection based on the elimination of less stable individuals and intergroup competition within a population and a species. It is the intergroup competition and group selection that leads to the optimal ratio between basic factors of evolution: mutability, tempo and modes of reproduction as well as various forms of polymorphism and different ways of its maintenance on the genetic level'' (Schmalhausen, '68, p 170). Schmalhausen emphasized that the phenotypic homogeneity achieved (although not always) due to the stabilizing selection is only an ''apparent homogeneity''. Behind this appearance one can detect a complex combination of ontogenetic stability with the stability of the complex genetic structure of a population. In both cases, stability is based on the existence of regulative (homeostatic) mechanisms. ''That is why'', Schmalhausen concludes, ''the stability of an individual is combined with its adaptive reactivity and the stability of population structure—with its excellent evolutionary mobility'' (Schmalhausen, '68, p 197). Thus, adaptive evolution is based on both forms of natural selection and represents a complex body of self-regulating systems ranging from the ''organism as a whole'' to the biogeocenosis (Fig. 3).

The self-regulating character of these processes is expressed not only in the evolution of the ''organisms as wholes'', but also in the ''evolution of evolution'', that is in the evolution of the mechanisms (or factors) of evolution (Schmalhausen, '74, '68, p 73). Thus the appearance of diploidy contributed significantly to the growth of evolutionary plasticity or evolvability.

Schmalhausen and Waddington

It has been pointed out many times that Schmalhausen's stabilizing selection 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, '87; Gilbert, '94, 2003; Hall, '98, 2001). As Gilbert

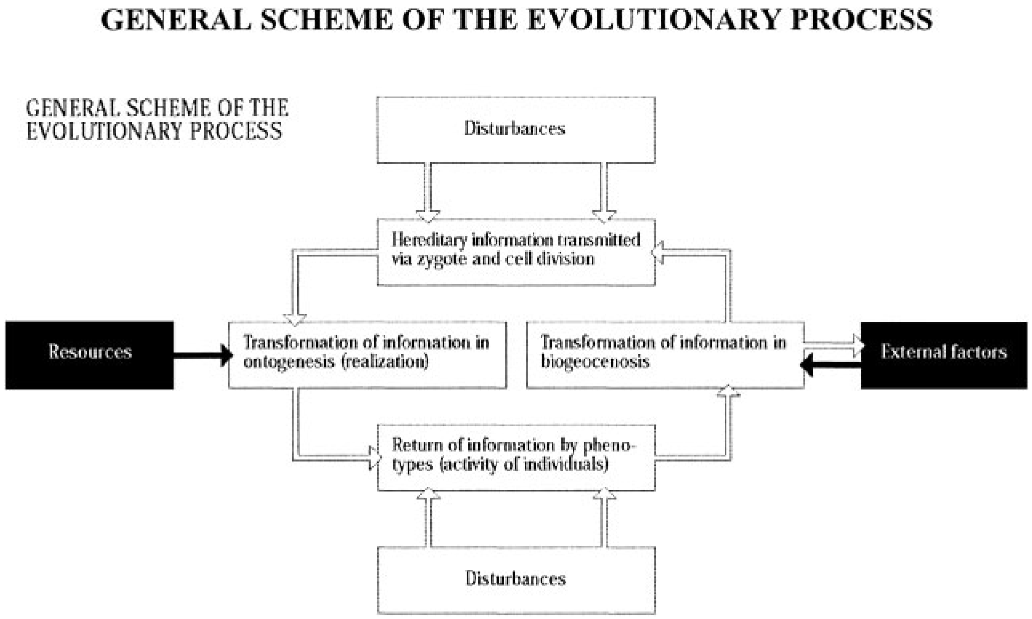

Fig. 3. General scheme of the evolutionary process. Redrawn from Schmalhausen, ’68, p 42.

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, ’98, p 311). Moreover, as well as Schmalhausen, Waddington also thought of development in terms of a “cybernetic process” (Waddington, ’53, ’75, p 209–230; Gilbert, 2003). With so much parallelism the question arises whether there was any difference in principle between their theories. How do the “Baldwin effect” and “genetic assimilation” relate to “stabilizing selection”?

The simplest case is the “Baldwin effect”, because Schmalhausen commented on it himself in his late works. The Baldwin effect was seen by Waddington as an alternative to his genetic assimilation. 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, ’75, 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, ’75, p 90, 92).[19]

Schmalhausen was against equating stabilizing selection with the Baldwin effect. Thus the well-known Russian geneticist M.M. Kamshilov (1910–1979), who worked in close cooperation with Schmalhausen for many years, reported that 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, ’74).

In the posthumously published comments to the second (1969) edition of the *Problems of Darwinism*, Schmalhausen made an 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

---

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

form of selection stabilizing selection, which G. Simpson later called centripetal selection.[20] 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* (our italics). 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 are also experimental data in favor of this theory (Kamshilov, Waddington)'' (Schmalhausen, '83, p 351).

In another part of this paper Schmalhausen also clearly supported Waddigton's notion of canalization: ''Every adaptive modification is an expression of a norm of reaction, which went the long way of historical development under changing conditions. It is connected with the establishment of ''canals'' through which a certain modification develops (Waddington talks about the ''canalization'' of development). An external factor operates only to switch the development into one of the existing canals'' (Schmalhausen, '83, p 350).

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, '68, p 409).

In conclusion, Schmalhausen was in his later works clearly against equating the Baldwin effect with stabilizing selection and interpreted Waddington's experiments as evidence in favor of his own theory. Yet, despite many similarities, differences between Schmalhausen's and Waddington's theories are also evident. In summary, the differences between the two theories include:

Waddington neglected Schmalhausen's distinction between adaptive modifications and morphoses (Waddington, '75, p 96–98). This distinction played an important role in Schmalhausen's criticism of total adaptationism.

Schmalhausen credited biogeocenosis as the ''arena of the primary evolutionary events'' (Schmalhausen, '83, p 294). His stabilizing selection (as well as dynamic selection) works in this multi-level biosystem. Thus, Schmalhausen's theory was not ''muddled up'' (Waddington's expression) in not distinguishing various kinds of stabilizing selection (Waddington, '75, p 98), but approached the subject from a different point of view. As Severtzov (grandson of Schmalhausen's teacher Alexej S. Severtov), who works along Schmalhausen's original lines, sums up: ''Stabilizing selection preserving already existing adaptations operates in nature due to the counterbalance 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.

Schmalhausen and contemporary approaches in evolutionary biology

Because Schmalhausen's book ''Factors of Evolution'' was translated into English in 1949, his work up until then is relatively well known also outside the Russian-speaking world. His later research, in which he tried to use cybernetics to analyze evolutionary questions, was never translated into English and has remained almost completely unknown outside Russia. Interestingly, in the last 15–20 years, a new understanding of complex systems (not limited to biology) has prospered under names like ''chaos theory'' (Gleick, '88), ''self-organization'' (Kauffman, '93; Camazine et al., 2003) and the ''sciences of complexity'' (Lewin, '92). It has even been suggested that this is the way forward for evolutionary theory (e.g., by Depew and Weber, '95), and in an extreme form, that all of natural science needs to be reframed in the algorithmic approach typical for self-organization research

---

[20] Schmalhausen's idea here was surely not to equate his theory to Simpson's, but to stress the Darwinian character of his concept. Timofeev-Ressovsky et al., ('75, p 148) used the terms ''centripetal'' and ''stabilizing'' selection synonymously.

(Wolfram, 2002). In this tradition, research along lines essentially similar to Schmalhausen's approach is being conducted, using theoretical tools not available to him, as well as modern computing power needed to run simulations. Schmalhausen would have looked favorably upon this development where, as Depew and Weber write in their Preface (1995), "…the Darwinian tradition is deepening and renewing itself be reconceiving natural selection in terms of the nonlinear dynamics of complex systems".

A research program that has been influenced by Schmalhausen's "Factors of Evolution" as well as by his work on salamander development and the book "The origin of terrestrial vertebrates", which appeared in English in 1968, is the integrative research on salamander biology conducted since the 1960s by David B. Wake and co-workers at UC Berkeley. Having started to teach a course on evolutionary biology at Berkeley in 1969, Wake was impressed by Schmalhausen's "insights and forward-looking ideas" on topics like reaction norms and phenotypic plasticity (D.B. Wake, pers. comm.[21]) Together with postdocs and graduate students, D.B. Wake has since investigated these issues using salamanders as his main "model system". Explaining "the fact that variation comes in discrete patterns, not just a smear of variation"[22] became a central topic in Wake's research program. Dave Wake has contributed significantly to making Schmalhausen's work more well-known internationally by urging the publisher to reprint "Factors of Evolution", for which he wrote a foreword (Wake, '86), by writing about Schmalhausen (Wake, '96) in the context of modern "evo-devo", and by his numerous papers and talks as well as through his teaching. His wife Marvalee H. Wake, as well as several of his postdocs and students (e.g., Stephen S. Stearns, James Hanken, Pere Alberch and Neil Shubin to mention just a few) have all been important for the development of different aspects of evolutionary developmental biology.

RÉSUMÉ

Based on Sewertzoff's evolutionary morphology, Schmalhausen created a theoretical system in which he synthesized selectionist evolutionary theory with genetics. Sewertzoff's evolutionary morphology was entirely incorporated into Schmalhausen's synthesis (Adams, '80). Due to his background as a morphologist Schmalhausen developed a holistic concept of the organism, which determined the specifics of his version of the "Modern Synthesis" and facilitated the development of the important concept of stabilizing selection. Schmalhausen coined this concept to explicate the role of selection in fluctuating but stable environments and to distinguish it from the dynamic selection operating in novel environments. Schmalhausen's stabilizing selection is a creative evolutionary force under certain circumstances, which leads to the establishment of new patterns of ontogenetic development. In the late works, based on the ideas of V.I. Vernadsky and V.N. Sukachev, Schmalhausen developed his concept of two forms of selection into a theory of evolution as a process of feed-back loops linking biogeocenoses, populations and individuals. Another leading evolutionary biologist from Russia, Nikolai V. Timoféev-Ressovsky, was thinking along similar lines, and supported the idea of biogeocenosis as an arena and a regulator of evolutionary processes. He wrote: "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., '75, p 249).

Schmalhausen's theory was a significant contribution to the research program initiated by Vernadsky which interpreted the biosphere as a self-regulating, evolving system. However, Schmalhausen also played a crucial role in the social history of Russian (Soviet) science. He became a key figure in the resistance against Lysenkoism in the Soviet Union. Schmalhausen successfully, and with great courage, resisted this obscurantism and was one of those who kept the Russian scientific tradition in genetics and evolutionary biology alive through this difficult period.

GLOSSARY OF SCHMALHAUSEN'S TERMINOLOGY

Allomorphosis—together with aromorphosis and telomorphosis (specialization), one of the major evolutionary directions (modi). A is adaptation proceeding without changes in the complexity of general morpho-physiological structures.

Aromorphosis—a crucial step in the morphophysiological progress which gives an organism significant evolutionary advantages like, e.g., the appearance of homeothermy in mammals.

---

[21] E-mail message to Lennart Olsson, August 17, 2005.

[22] E-mail message to Lennart Olsson, August 17, 2005.

Biocenosis—term coined by Karl Möbius (1877) meaning the totality of plants, animals and microorganisms occupying a certain biotope.

Biogeocenosis—term coined by V.N. Sukachev, who founded a new science "biogeocenology" ('44). Biogeocenosis is the sum total of biotic and abiotic elements (solar radiation, atmosphere, water, soil, etc.) organized in a relatively closed system of cycles. Phytocenoses have an especially important role in the identification of a B.

Biosphere—The first scientist to use the term "biosphere" in the modern sense was the Austrian geologist Eduard Suess (1831–1914). The first scientific and very influential concept of the biosphere was coined by the founder of biogeochemistry V.I. Vernadsky. As he puts it (Vernadsky, 1991, p 120): "The biosphere appears in biogeochemistry as a peculiar envelope of the Earth clearly distinct from the other envelopes of our planet. The biosphere consists of some concentric contiguous formations surrounding the whole Earth and called geospheres. The biosphere has possessed this perfectly definite structure for billions of years. This structure is tied up with the active participation of life, is conditioned by life to a significant degree and is primarily characterized by dynamically mobile, stable, geologically durable equilibria which, in distinction to mechanical structures are fluctuating quantitatively within certain limits in relation to both space and time".

Catamorphosis—general degeneration of an organism connected, for example, with the transition to parasitism. C is a process directly opposed to aromorphosis.

Endosomatic and ectosomatic organs—terms used by A.N. Sewertzoff. He labeled as ectosomatic organs that are functionally in direct contact with the environment (e.g., skin, teeth, eyes), 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.

Hypermorphosis—is an "overdevelopment" of an organism or its part (example: *Megaloceros*).

Hypomorphosis—is an "underdevepoment" of an organism due to failure to reach certain stages of ontogenesis exemplified by neoteny (Severtzov, '90, p 202).

Specialization—in some interpretations (Severtzov, '90) a general term for all forms of adaptive specializations covering telomorphosis, hypomorphosis, catamorphosis, and hypomorphosis.

Telomorphosis—adaptive specialization which leads the organism to become restricted to a narrow part of the environment (Dobzhansky, '86, p xvii).

Morphosis—non-heritable transformations induced by environmental changes and caused by disturbances of genetic activity. M can be experimentally induced, for example, by treating Drosophila larvae with X-rays.

Phytocenosis—a part of biogeocenosis composed of a plant community on a relatively homogeneous surface.

ACKNOWLEDGMENTS

Our research on the history of evolutionary biology is supported by the Deutsche Forschungsgemeinschaft (Ho 2143/5-2). We are thankful to Prof. Alexej S. Severtzov (Moscow University), and Prof. Brian K. Hall (Dalhousie University) for helpful comments on an earlier version of this paper, which was finished when LO was a visiting fellow at Harvard University, USA. We thank Olga Schmalhausen for checking the spelling of the names of I.I. Schmalhausen's ancestors. LO extends his thanks to the Friedrich-Schiller-Universität Jena for granting him a sabbatical leave in the summer semester of 2005. We thank Minka Kudrass for redrawing Fig. 3, and Dave Wake for taking the time to respond to our questions about how he has been influenced by I.I. Schmalhausen's ideas.

LITERATURE CITED

Adams MB. 1980. Severtsov and Schmalhausen: Russian morphology and the evolutionary synthesis. In: Mayr E, Provine WB, editors. The evolutionary synthesis: perspectives on the unification of biology. Cambridge, MA: Harvard University Press. p 193–228.

Arosevskij MG. 1994. Repressirovannaja nauka. St. Petersburg: Nauka.

Berg RL. 1996. Schmalhausen Ivan Ivanovich. In: Tort P, editor. Dictionnaire du Darwinisme et de l'évolution. Paris: Presses Universitaires de France. p 3825–3851.

Berg RL, Lyapunov AA. 1968. Predislovije. In: Berg RL, Lyapunov AA, editors. II Schmalhausen. Kiberneticheskije voprosy biologii. Novosibirsk: Nauka. p 5–13.

Camazine S, Deneubourg J-L, Franks NR, Sneyd J, Theraulaz G, Bonabeau E. 2001. Self-organization in biological systems. Princeton and Oxford: Princeton University Press.

Depew DJ, Weber BH. 1995. Darwinism evolving. Systems dynamics and the genealogy of natural selection. Cambridge MA and London: MIT Press.

Dobzhansky Th. 1937. Genetics and the origin of species. New York: Columbia University Press.

Dobzhansky Th. 1986. Foreword. In: Schmalhausen I.I. Factors of evolution. Chicago and London: The University of Chicago Press. p xv–xvii.

Dohrn A. 1875. Der Ursprung der Wirbelthiere und das Prinzip des Funktionswechsels: Genealogische Skizzen. Leipzig: Engelmann.

Dondua AK, Aleksandrov DA. 2002. International award of the St. Petersburg Society of Naturalists—Alexander Kowalevsky Medal. Russ J Dev Biol 33:324–325.

Gass GL, Bolker JA. 2003. Modularity. In: Hall BK, Olson WM, editors. Keywords & concepts in evolutionary developmental biology. Cambridge, MA: Harvard University Press. p 260–267.

Gilbert SF. 1994. Dobzhansky, Waddington, and Schmalhausen: embryology and the modern synthesis. In: Adams MB, editor. The evolution of Theodosius Dobzhansky. Princeton, NJ: Princeton University Press.

Ghilarov AM. 2006. The early history of ecology in Russia. In: Schwarz AE, Jax K, editors. Revisiting ecology, Vol. 1. Berlin: Springer (in press).

Gilbert SF. 2003. The morphogenesis of evolutionary developmental biology. Int J Dev Biol 47:467–477.

Gilbert SF, Bolker JA. 2001. Homologies of process and modular elements of embryonic construction. J Exp Zool B (Mol Dev Evol) 291B:1–12.

Gleick J. 1988. Chaos. Making a new science. London: Heinemann.

Gould SJ, Lewontin RC. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc R Soc Lond B 205:581–598.

Gulick JT. 1905. Evolution, racial and habitudial. Washington, DC: Carnegie Institution.

Hagemann R. 2002. How did East German genetics avoid Lysenkoism? Trends Genet 18:320–324.

Hall BK. 1998. Evolutionary developmental biology, 2nd edition. London: Chapman & Hall.

Hall BK. 2001. Organic selection: proximate environmental effects on the evolution of morphology and behaviour. Biol Phil 16:215–237.

Hoßfeld U, Olsson L. 2002. From the modern synthesis to Lysenkoism, and back? Science 297:55–56.

Hoßfeld U, Olsson L. 2003. The road from Haeckel. the Jena tradition in developmental morphology and the origins of evo-devo. Biol Phil 18:285–307.

Höxtermann E. 2000. ''Klassenbiologen'' und ''Formalgenetiker'' - zur Rezeption Lyssenkos unter den Biologen der DDR. Acta Hist Leopol 36:273–300.

Huxley J. 1942. Evolution: the modern synthesis. London: Allen & Unwin.

Jaroschevsky AA, editor. 1995. Perepiska Vernadskogo VI i Vinogradova AP. Moscow: Nauka.

Kaasch M, Kaasch J, Hoßfeld U. 2006. ''Für besondere Verdienste um Evolutionsforschung und Genetik''. Die Darwin-Plakette der Leopoldina 1959. Acta Hist Leopol (in press).

Kamshilov MM. 1974. O gipoteze zameny phenokopij genokopijami. In: Zavadsky KM, Gall JM, editors. Istorija i teorija evoliutzionnogo uchenija. Evoliutzionnyje vzgliady II Schmalhausena. Leningrad: AN SSSR. p 57–60.

Kauffman S. 1993. The origins of order. Self-organization and selection in evolution. Oxford and New York: Oxford University Press.

Kull K. 1988. Towards a constructive theory of phytocenology. In: Kull K, Ksenofontova T, editors. Perspektivy teorii fitocenologii (Perspectives in theory of phytocenology). Tartu: Academy of Sciences. p 11–18.

Levit GS. 2001. Biogeochemistry, biosphere, noosphere: the growth of the theoretical system of Vladimir Ivanovich Vernadsky (1863–1945). Berlin: VWB.

Levit GS, Hoßfeld U. 2005. Die Nomogenese: Eine Evolutionstheorie jenseits des Darwinismus und Lamarckismus. Ver Gesch Theor Biol 11:367–388.

Levit GS, Hoßfeld U. 2006. The forgotten ''Old Darwinian'' synthesis: the evolutionary theory of Ludwig H. Plate (1862–1937). NTM Int J Hist Ethics Nat Sci, Technol Med, 14 (in press).

Levit GS, Hoßfeld U, Olsson L. 2004. The integration of Darwinism and evolutionary morphology: Alexej Nikolajevich Sewertzoff (1866–1936) and the developmental basis of evolutionary change. J Exp Zool (Mol Dev Evol) 302B: 343–354.

Lewin R. 1992. Complexity. Life at the edge of chaos. Chicago and London: The University of Chicago Press.

Matsuda R. 1987. Animal evolution in changing environments with special reference to abnormal metamorphosis. New York: Wiley.

Mayr E. 1942. Systematics and the origin of species. New York: Columbia University Press.

Meister K. 2005. Metaphysische Konsequenz–die idealistische Morphologie Edgar Dacqués. N Jb Geol Paläont Abh 235: 197–233.

Mirkin BM. 1985. Teoreticheskije osnovy sovremennoj fitotzenologii. Moscow: Nauka.

Mirzoyan EN. 1983. Uchenije A. N. Sewertzova o glavnykh napravlenijakh evolutzionnogo prozessa. In: Mikulinskij SR, Poljanskij JI, editors. Razvitije evolitsionnoj teorii v SSSR (1917–1970s). Leningrad: Nauka. p 348–358.

Möbius K. 1877. Die Auster und die Austernwirthschaft. Berlin: Wiegandt, Hempel Parey.

Piliptchuk OJ. 2001. Ivan Fedorovich Schmalhausen (1849–1894). Moscow: Nauka (in Russian).

Plate L. 1913. Selektionsprinzip und Probleme der Artbildung. Ein Handbuch des Darwinismus, 4th edition. Leipzig and Berlin: Engelmann.

Pospelov DA, Fet JI, editors. 1998. Otcherki istorii informatiki v Rossii. Novosibirsk: NIZ IGGM SO RAN.

Regelmann J-P. 1980. Die Geschichte des Lyssenkoismus. Frankfurt a. M.: Rita G. Fischer Verlag.

Reif W-E, Junker T, Hoßfeld U. 2000. The synthetic theory of evolution: general problems and the German contribution to the synthesis. Theory Biosci 119:41–91.

Rensch B. 1947. Neuere Probleme der Abstammungslehre. Die Transspezifische Evolution. Stuttgart: Ferdinand Enke.

Roll-Hansen N. 2005. The Lysenko effect. The politics of science. New York: Humanity Books.

Schlosser G, Wagner GP. 2004. Modularity in development and evolution. Chicago and London: The University of Chicago Press.

Schmalhausen IF. 1879. Beiträge zur Jura-Flora Russlands. St.-Petersburg: l'Acad. Imper. des Sciences.

Schmalhausen II. 1907. Die Entwicklung des Skelettes der vorderen Extremität der anuren Amphibien. Anat Anzeiger 31:177–187.

Schmalhausen II. 1908. Die Entwicklung des Skelettes der hinteren Extremität der anuren Amphibien. Anat Anzeiger 33:337–344.

Schmalhausen II. 1917. On the extremities of Ranidens sibiricus Kessl. Rev Zool Russ 2:129–138.

Schmalhausen II. 1923. Osnovy sravnitel'noj anatomii pozvonochnykh. Moscow-Petrograd: GIZ.

Schmalhausen II. 1937a. Anton Dohrn i ego rol v razvitii evolutsionnoj morphologii. In: Dohrn A, editor. Prinzip smeny funktzij i proiskhozhdenije pozvonochnykh. Moscow: Biomedgiz. p 9–78.

Schmalhausen II. 1937b. Znachenija individualnykh korreljatzij v evulutzii embryiona. Pratzi Naukovodoslidnogo Institut Biolog 1:7–31.

Schmalhausen II. 1938. Organizm kak tseloje v individual'nom i istoricheskom razvitii. Leningrad: AN SSSR.

Schmalhausen II. 1939. Puti i zakonomernosti evoliutzionnogo protsessa. Moscow- Leningrad: AN SSSR.

Schmalhausen II. 1946a. Problemy Darwinizma. Moscow: Sovetskaja Nauka (2nd edition: 1969).

Schmalhausen II. 1946b. Faktory Evoliutzii. Moscow-Leningrad: AN SSSR. (2nd edition: 1968).

Schmalhausen II. 1949. Factors of evolution: the theory of stabilizing selection. Philadelphia: Blakiston Co. (reprinted in 1986 by Chicago University Press).

Schmalhausen II. 1968. The origin of terrestrial vertebrates. New York: Academic Press.

Schmalhausen II. 1969. Problemy Darwinizma. Leningrad: Nauka.

Schmalhausen II. 1974. Evolutzija faktorov evolutzii i ee dvizhustchije sily. Plan. In: Zavadsky KM, Gall JM, editors. Istorija i teorija evoliutzionnogo uchenija. Evoliutzionnyje vzgliady II Schmalhausena. Leningrad: AN SSSR. p 5–9.

Schmalhausen II. 1983. Izbrannyje trudy. Puti i zakonomernosti evoliutzionnogo prozessa. Moscow: Nauka.

Schmalhausen II. 1990. Voprosy darwinisma. Neopublikovannyje raboty. Moscow: Nauka.

Schmalgausen OI. 1988. Ivan Ivanovich Schmalhausen (1884–1963). Moscow: Nauka (in Russian).

Severtzov AS. 1990. Directionality of evolution. Moscow: Moscow University Press (in Russian).

Severtzov AS. 2004. O prichinakh evolutzionnogo stazisa. Zool Zh 83:927–935.

Simpson GG. 1944. Tempo and mode in evolution. New York: Columbia University Press.

Sobolev SL, Kitov AI, Lyapunov AA. 1955. Osnovnyje tcherty kibernetiki. Vop Filos 4:136–148.

Sukachev (Sukatschow) VN. 1944. O prinzipakh geneticheskoj klassifikatzii v biogeotzenologii. Zh Obtschei Biol 5:213–227.

Sukatschow WN. 1969. Die Struktur der Biogeozönosen und ihre Dynamik. In: Laitko H, editor. Struktur und Formen der Materie. Berlin: Dt. Verl. der Wiss.

Sytnik KM, Apanovich EM, Stoiko SM. 1988. Dejatel'nost' Vernadskogo na Ukraine. Kiev: Naukova Dumka.

Timoféev-Ressovsky NW. 1961. O nekotorykh prinzipakh klassifikatzii biohorologicheskikh edinitz. Trudy AN SSSR. Ural Institute of Biology. Vop Klassifikatzii rastitelnosti 27: 23–28.

Timoféev-Ressovsky NW, Vononcov NN, Jablokov AN. 1975. Kurzer Grundriss der Evolutionstheorie. Jena: Gustav Fischer Verlag.

Vernadsky VI. 1926. Biosfera. Leningrad: NHTI.

Vernadsky VI. 1965. The chemical structure of the biosphere of the earth and of its environment. Moscow: Nauka (in Russian).

Vernadsky VI. 1991. Scientific thought as a planetary phenomenon. Moscow: Nauka (in Russian).

Waddington CH. 1953. Genetic assimilation of an acquired character. Evolution 7:118–126.

Waddington CH. 1975. The evolution of an evolutionist. Ithaca, NY: Cornell University Press.

Wake DB. 1986. Foreword, 1986. In: Schmalhausen I.I. Factors of evolution. Chicago and London: The University of Chicago Press. p v–xii.

Wake DB. 1996. Schmalhausen's evolutionary morphology and its value in formulating research strategies. Systematic Biology as an Historical Science. Memorie della società Italiana di scienze naturali e del museo civico di storia naturale di Milano, Volume XXVII, Fascicolo I: 129–132.

Wolfram S. 2002. A new kind of science. Champaign, IL:Wolfram Media.

Zherikhin VV. 2003. Izbrannyje trudy po paleoekologii i phylozytogenetike. Moscow: KMK.