Theory in Biosciences (2019) 138:73–88
https://doi.org/10.1007/s12064-019-00280-8

ORIGINAL ARTICLE

The reception of Haeckel in pre-revolutionary Russia and his impact on evolutionary theory

Eduard Kolchinsky[1] · Georgy S. Levit[2,3]

Received: 5 November 2018 / Accepted: 8 January 2019 / Published online: 7 March 2019

Abstract
The "German Darwin" Ernst Haeckel was influential not only in Germany, but in non-German-speaking countries as well. Due to the widespread use of German as a language of science in the Russian Empire along with growing Russian–German links in various scientific fields, Haeckel directly and indirectly influenced Russian intellectual landscape. The objective of the present paper is to investigate Haeckel's impact on Russian biology before the Bolshevik Revolution of 1917. We outline the transfer of Haeckelian ideas to Russia and its adaptation to a national research tradition. Haeckel's ideas influenced the most crucial Russian evolutionists such as brothers Alexander and Vladimir Kovalevsky, Ilya (Elias) Metschnikoff, Mikhail Menzbier (Menzbir), Karl Kessler, Andrei Famintzyn, and Konstantin Mereschkowsky. At the same time, Haeckel's speculative hypotheses and his attempts to convert Darwinism into a universal worldview by promoting monism found little support in biological circles of Russia. Russian biology grew as an empirical science having weak connections to "romantic philosophy" as German biology did. This, among others, explains the acceptance of Haeckel as a biologist and the rejection of Haeckel as a philosopher by crucial Russian evolutionists.

Keywords Ernst Haeckel · National scientific traditions · Russian biology · Phylogenetic tree · Biogenetic law · Eugenics · Anthropogenesis

Introduction

Ernst Haeckel (1834–1919) was one of the most influential evolutionary thinkers (Rieppel 2016, p. 12). Robert Richards even asserted that "more people at the turn of the century learned of evolutionary theory from his pen than from any other source, including Darwin's own writings" (Richards 2018). Haeckel's impact in Russia was of controversial nature though. From one side, he gained great influence over the Russian evolutionary thought and this can be observed during the recent 150 years. There was not a single branch of Russian evolutionary theory which escaped his impact. But many Haeckel's ideas were met with severe criticism and rejection. There are several examples of the strong influence of Russian biologists on Haeckel as well (Fig. 1).

Certain aspects of Russian evolutionary tradition can be traced back as far as to the early nineteenth or eighteenth century. Since there was a strong German influence on the early Russian transformism, Haeckel's methodology was not alien to Russian thinkers from the very beginning. At the same time, Russians were reluctant to accept Haeckel's scientific universalism (attempts to explain literally the whole universe by means of current science) and monist philosophy. Besides, Russian science developed under the strong ideological pressure including censorship of scientific publications (Levit et al. 2014).

German biology had its roots in romantic *Naturphilosophie* and was from the very first steps influenced by Goethean essentialism (Levit and Meister 2006; Levit et al.

This article is a contribution to the Special Issue Ernst Haeckel (1834–1919): The German Darwin and his impact on modern biology—Guest Editors: U. Hossfeld, G. S. Levit, U. Kutschera.

✉ Georgy S. Levit
georgy.levit@uni-kassel.de

Eduard Kolchinsky
ekolchinsky@yandex.ru

1 Saint Petersburg Branch of the Institute for the History of Science and Technology, Russian Academy of Sciences, Universitetskaia nab. 5, St. Petersburg, Russia 199037

2 Institute of Biology, University of Kassel, Heinrich-Plett-Strasse 40, 34132 Kassel, Germany

3 Biology Education Research Group, Jena University, Am Steiger 3, 07743 Jena, Germany

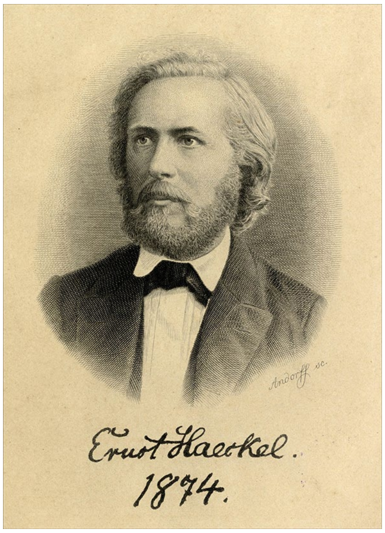

Fig. 1 Ernst Haeckel's portrait from: Ernst Haeckel, "The history of tribal development of organisms" (1879), p. 2 (Russian edition)

2015b). Russian biology tended to be more descriptive and empirically oriented. These tendencies predetermined a dichotomous view of Haeckel in Russia. Even within biology, the reaction to Haeckel's evidently speculative concepts such as *gastrea* hypothesis was rather negative.

Outside of biology, Haeckel's influence was determined by the political views of his readers. The pre-revolutionary Russia was the arena of fierce political struggle, and evolutionary theory was one of the most controversial issues. The publication of Haeckel's works in Russian has a dramatic history as they were often censored and prohibited, whereas revolutionary forces tried to use Haeckel's theories for their own benefits (for more details, see Kolchinsky, this volume).

The major objective of this paper is to demonstrate how the growing community of Russian evolutionary biologists adapted or rejected Haeckel's ideas. We concentrate on the time before the Bolshevik revolution as revolution completely changed the scientific, ideological, and educational landscapes. To do so, we begin with transformism to show the roots of early evolutionism. Then, we describe most crucial evolutionists and their reaction to Haeckel. One of the important indicators of his influence is the acceptance of terms he coined, such as "phylogeny," "ontogeny," "phylogenetic tree," "biogenetic law," and many others. The spread of the terms makes Haeckel's influence detectable even when his name did not explicitly appear in historical documents. It should be mentioned though that our analysis is only a first glance on the problem of Haeckel's reception in Russia as this topic remains to a significant extent unresearched and that we do not analyze anti-Darwinian resistance to the expansion of evolutionary biology.

The shaping of tradition: first steps toward evolutionism in the Russian empire

The Russian scientific biological community initially grew under strong German influence. Scientists like naturalist and medical doctor Georg W. Steller (1709–1746), botanist and geographer Johann G. Gmelin (1709–1755), botanist Joseph G. Kölreuter (1733–1806), pioneer of embryology Caspar F. Wolff (1734–1794) as well as the polymaths Peter Simon Pallas (1741–1811) and Karl Ernst von Baer (1792–1876) planted the seeds of the German scientific culture. Their immediate pupils such as Stepan Krasheninnikov (1713–1755), Ivan Lepekhin (1740–1802) and Vassilii Zuev (1754–1794) adapted both the problems to be studied and the ways these problems should be approached. Yet along with empirical approaches to issues such as species variability, they borrowed some bias toward broad theoretical generalizations, romantic *Naturphilosophie* and essentialism. The German influence on Russian science was also exercised via Russian scientists who studied in German lands and experienced German scholarly tradition from within. An additional factor of "German bias" in the early Russian biology was the German language culture of the Baltic states, which were part of the Russian Empire over 200 years. All this, along with the extensive use of the German language in the biological literature of the eighteenth and nineteenth centuries, had a significant impact on Russian transformism.

As already mentioned, one of the first influential German scholars in Russia was Peter Pallas. Pallas argued against "speculative" theories proposed by Georges-Louis de Buffon (1707–1788) and Carl von Linné (1707–1778) and systematically criticized the idea of unlimited species transformation (Pallas 1784; Kolchinsky 2005, 2007, 2011). Pallas' arguments were so substantial that they were even used by Russian anti-evolutionists of the post-Darwinian era, among others, against Haeckel (Brandt 1868). Paradoxically, Pallas can be also numbered among Haeckel's predecessors in the Russian speaking world. At the times when comparative anatomy still did not exist as a science, Pallas applied comparative methods to establish connections between various groups of animals. Pallas rejected the linear ladder of organisms and suggested a holistic approach to comparative studies considering structure and development of entire organisms by contrast to comparing merely their parts. Classifying "Zoophyta" (sponges and Anthozoa), he described 270 new species and came to conclusion that they are neither plants nor animals. As a consequence, he rejected a sharp distinction between animal and plant kingdoms and expressed this idea in a chapter with the telling title "Natura non facit saltus" (Pallas 1766, pp. 23, 24).

Looking for a visual representation of living nature, Pallas suggested representing plants and animals graphically as two tree trunks growing apart from *zoophyte* (although he himself made no such diagram). *Zoophyta* in this diagram is based directly on minerals serving as a soil for the entire organic world. Considering that Pallas proposed a treelike diagram of the living world, there were suggestions to interpret his tree as a "remote ancestor" of Haeckel's phylogenetic tree (Raikov 1969). Yet, in fact, Pallas used his tree just as a visual aid for classifying taxa within the conceptual space of the natural history and not for demonstrating evolution in time. There were no genealogical relations in this tree but rather an association with the mythological "tree of life" as a product of cosmogenesis and the very essence of the organic world. This conceptual connection between biological classification and the structure of the universe opened the way to understanding Haeckelian universalism.

The works of Christian Pander (1794–1865), Karl Ernst von Baer (1792–1876), and Karl Eichwald (1795–1876) were also within the scope of Haeckel's interests. Pander and Baer established general regularities of developmental processes of various groups of organisms to prove embryologically the common descent of all species within a certain type of organisms (von Baer 1828, p. 200). In other words, they supported the idea of transformation within a type, however, made no clear statements on mechanisms of transformation. With regard to transformation, von Baer combined rather incompatible approaches in his worldview, namely the naturphilosophical (*Naturphilosophie*) speculations and causal naturalistic analysis (Raikov 1961, pp. 413–438). The metaphysical elements, which can be interpreted as natural–philosophical, can be found even in the late 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).[1] 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 to the field of faith, and is responsible for the general design of the universe. Haeckel consequently criticized any teleology as he denied that "organisms harboured an *intrinsic* tendency toward improvement" (Richards 2008, p. 147). His concept of dysteleology [*Unzweckmässigkeitslehre*] was introduced to dispatch the ideas like *Zweckmässigkeit* from natural sciences.

On a more empirical level, Baer was one of the founders of developmental biology and one of the forerunners of Haeckel's biogenetic law. "Von Baer's law" claimed that features of the adult forms appear in a certain sequence during embryonic development and that this sequence corresponds to the hierarchy of systematic categories (e.g., family–genus–species), to which the individual belongs. 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), but both "laws" were coined within the same conceptual framework.

Baer carried out his embryological research mostly during his Königsberg period (1817–1834). After having moved to St. Petersburg, he devoted himself to the anthropology, geography, and zoology as well as to geographical expeditions. 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). However, von Baer's idea of transformation as a causal and empirically describable process implicit within his "teleological evolutionism" (Kolchinsky 2007, p. 104) survived in the works of the later generations of developmental biologists and influenced, among others, Haeckel's Russian "counterpart" Alexander Kovalevsky (1840–1901).

Eichwald in his first paleontological works pushed forward the idea of progressive development of living forms from lowest to the highest, making a way to Haeckel's idea of progressive evolution from Monera to man (von Eichwald 1821). Guided by a transformist idea of the unity of plants and animals, Eichwald presented them as a "tree" rooting in the sea with the man as its crown (von Eichwald 1829–1831). Along with Pallas' tree and treelike diagrams of Baer, Eichwald's tree contributed to clearing the way for Haeckel's diagrams.

At the same time, one should be aware that transformism as well as *Naturphilosophie* was not especially welcomed in Russian academic circles. Only the first volume of Lorenz Oken's "Allgemeine Naturgeschichte für alle Stände" (1833–1841) was translated into Russian (Oken 1836) and became a devastating review in a popular Russian journal "Biblioteka dlia Chteniia" (Library for reading) (Senkovskii 1837). Under these circumstances, after moving to St. Petersburg and becoming members of the Russian academic community, Pander and Baer were cautious confessing to transformism, which was confined within a tight circle of elite scholars. Yet transformist ideas were not completely isolated from the rest of the society. For example, Eichwald was very much committed to teaching and, realizing the great interest of students to transformism and *Naturphilosophie*, he taught these doctrines at the University of Vilno (today: Vilnius, the capital of Lithuania) and at the Medical Surgery Academy in St. Petersburg.

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

In sum, before Darwin, transformism gained some foothold in Russia, but it did not belong to concepts, which determined biological discussions of the time.

At the mid-nineteenth century, a special interest to natural science captures many public figures of the political opposition to tsarist autocracy. Ivan Turgenev's famous novel "Fathers and Sons" (1862) captured this link between natural science and political views by addressing the problem of generations change in Russia. One of the major critics of the Nikolai the First's (1796–1855) autocracy, a writer and social philosopher Alexander Herzen (1812–1870) published in 1845/1846 in a popular literary journal "Otechestvennye Zapiski" (Domestic Notes) a philosophical essay "Letters on the Study of Nature." In this philosophical investigation, Herzen, among others, promoted the idea of "type" in morphology, which he correctly traced back to Johann Wolfgang von Goethe (1749–1832). Goethe's structuralism followed his concept of the morphological archetype (Williams and Ebach 2008, pp. 29, 30), which connected both the "high Church" (a fundamental inquiry into the most essential features of life and ultimately of the universe) and the "low Church" (empirical comparative studies of organic structures) principles. The archetype was, for him, an ideal structure (*Bauplan*) of an organism partly expressed in the basic elements of real organismic organization (Levit and Hossfeld 2017). Herzen credited Goethe with the success in making comparative anatomy into developmental biology: "The great Goethe was the first who introduced dynamics into the comparative anatomy and showed the way to reconstruct the organisms' architectonics in its origin and gradual development" (Herzen 1985, p. 384). As Haeckel considered Goethe along with Lamarck and Darwin as one of his most important predecessors, Herzen's emphasis on Goethe's comparative anatomy in a popular philosophical publication was a significant step toward preparing the public opinion for Haeckel's doctrine.

Darwin's theory of natural selection began spreading in Russia during a period of liberal reforms by Alexander II (1818–1881). The credibility of natural science continued to grow, and the link between science and liberal opposition to the tsarist autocracy became more and more evident. Scientific evolutionism turned into the center of political and religious discussions. The "Origin of Species" was on the verge of obtaining the status of a sacred script which could be either accepted or rejected in its entirety. For example, an extremely popular literary critic and leftist social thinker (revolutionary democrat) Dmitry Pisarev (1840–1868) published in the popular journal *Russkoje Slovo* [Russian Word] the voluminous paper *Progress in the Realm of Animals and Plants*, in which he made Darwin's *Origin* accessible, explaining it chapter by chapter. At the end of the paper, Pisarev concluded that "Darwin's theory was an urgent demand of our time" (Pisarev 1864). Pisarev briefly outlined the history of publication of the *Origin* and mentioned also Alfred Russel Wallace who, Pisarev claimed, "came close to Darwin's conclusions" (Levit and Polatayko 2013).

In conservative circles, Darwin's theory of evolution was labeled "blasphemous," "amoral," and politically dangerous. The authorities tried to prevent its influence on the broad audience by tolerating its impact on purely scientific publications (Kovalev 1959; Kharakhorkin 1960; Kolchinsky 2008). There were also more subtle attempts to resist the Darwinian version of evolutionary theory by appealing to the authority of Wallace. Wallace's major works were translated into Russian, and his major ideas were circulated by both scientists and public figures. At the same time, Wallace played a controversial role in Russian Darwinism and Darwin subsequently eclipsed Wallace in his influence on Russian evolutionary biology. Wallace's radical selectionism, as well as his controversial procreationist claims, predetermined his special place within the Russian intellectual landscape. Wallace's attitude toward anthropogenesis allowed some adherents of the Orthodox Church to produce a clash between two major figures within the Darwinian movement (Darwin himself and Wallace) and to construct arguments leading to what is known today as "scientific creationism" (Levit and Polatayko 2013). But the academic community was divided in relation to evolutionary theory as well. Many biologists from the Moscow University sharply criticized Darwinism (Samokish 2009; Manoilenko 2009).

Between 1859 and 1864, there were about 70 publications on the Darwinian theory in Russia, one-third of them included translations and paraphrases of foreign publications, most of which were German. Already first reactions to the new theory demonstrated that its interpretations ranked from what one would call today anti-Darwinism to strict selectionism (Kohn 1985; Glick 1988; Engels 1995; Junker and Hoßfeld 2009; Engels and Glick 2009; Glick and Shaffer 2014). Peter Bowler spoke in this respect about the "eclipse of Darwinism" (Bowler 1988, 1996), although the metaphor is not entirely accurate because there were several "Darwinisms" and it was unclear which one is the "correct" one right until the Modern Synthesis. Two major schools later labeled "old-Darwinism" and "neo-Darwinism" were represented by Haeckel along with his followers, on the one side, and Wallace with August Weismann along with their champions, on another side. "Old-Darwinians" followed Darwin's idea of multiplicity of evolutionary mechanisms (including neo-Lamarckian concepts), whereas neo-Darwinians were strict selectionists. For many biologists of the late nineteenth century and the beginning of the twenty-ninth century, "old-Darwinians" represented the proper, true Darwinian doctrine (Levit and Hossfeld 2006). Russia was a part of this early theoretical pluralism, and there was no straight road from Darwin to the Modern Synthesis as it is sometimes claimed by the champions of the view that Russia is "the second birthplace of Darwinism" (Kolchinsky 2014, pp. 255–296).

Talking about Russian biology as a part of the international scientific community, one should keep in mind a peculiarity of the knowledge transfer to Russia, namely its already mentioned German bias in the mid-nineteenth century. Just a few Russian scientists could read English, and the Russian scientific community learned Darwin's theory mostly from German translation published in 1860 and completed by a German paleontologist Heinrich Georg Bronn (1800–1862). As Sander Gliboff (2008) has demonstrated, for Bronn, who was intellectually shaped by the German ideal of *Wissenschaft* (pure and theory-oriented scholarship), Darwin's idea of natural selection was quite anthropomorphic and questionable. In Bronn's review of the *Origin* and in the comments accompanying the German translation (Bronn 1859, 1860), Bronn downplayed the connections between natural and artificial selection in favor of a general picture of organic history and diversity. On the level of scientific methodology, Bronn rejected Darwin's bias to historical narratives, which "evoked the image of the prescientific natural historian" (Gliboff 2008, p. 129). Most important, Bronn rejected gradualism and randomness of variation so characteristic for the Darwinian approach. These objections, Gliboff argued, were deeply rooted in Bronn's ideal of *Wissenschaft* and the commitment to explanations in terms of law and necessity. Although Bronn's translation and commentary was "better than its reputation," it was certainly colored by the differences in Darwin's and Bronn's worldviews and experiences including their "contrasting social roles as professional researcher and self-supporting gentleman" (Gliboff 2008, p. 152). Bronn's controversial translations of Darwinian terms (e.g., "favored" translated as "vervollkommnet" = "perfect") resulted from his attempts to make Darwinism understandable to his German peers. Bronn's language and definitions not only influenced Haeckel's initial understanding of Darwin, but also had a direct impact on the Russian scholarship. Even a Russian translation made by Sergei Alexanrovich Rachinskii (1833–1902) which was published in 1864 remained a minor channel of transferring Darwin's ideas compared to Bronn's German edition. But even Rachinskii's Russian translation of the *Origin* was influenced by Bronn's German edition as well. As a result, Russian translation of Darwin's terms was closer to Bronn's than to Darwin's (compare: Kolchinsky, this volume). The same terminology was used in the translation of Friedrich Rolle's (1827–1887) *Darwin's Lehre* (Darwin's Doctrine) (Rolle 1863) into Russian *Uchenie Darwina* (Rolle 1864). The book of the German paleontologist was the first monographic investigation into Darwin's theory available in Russian, which became widespread and appeared in several editions.

When a leading Russian evolutionist Climent Timiryazev (Timiriazev) (1843–1920) was writing his *Kniga Darwina: ego kritiki I kommentatory* (The Darwin's book, its critics and commentators) (published as a journal version in 1864 and then as a book in 1865), he appealed to Rachinskii's translation of Darwin (Timiryazev 1864, 1865). Timiryazev's book appeared to be the major source for learning Darwinism for the Russians for more than 50 years. In later works, he preferred to talk about "elimination or natural selection" and abandoned the "unhappy" metaphor of the "struggle for existence" (Timiryazev 1949, p. 27). Other biologists also began to interpret the "struggle for existence" in a more subtle way as an entire complex of ecological interactions and not as the literal "struggle for life."

All these factors created a peculiar intellectual atmosphere in which Haeckel's ideas were transferred to Russia in the post-Darwinian but "pre-synthetic" times.

The attitude of leading Russian evolutionists toward Haeckel

The future Nobel Prize Winner Ilya (Elias) Metschnikoff (Mechnikov) (1845–1916) was ambivalent toward Haeckel. Metschnikoff was a close friend of Haeckel's Russian inspiration Alexander Kovalevsky and along with Kovalevsky, one of the most influential Russian evolutionists. In 1869, Metschnikoff published a summary of Haeckel's "Generelle Morphologie" (*GM*), where he accused Haeckel of being too speculative, tending toward premature generalizations and unnecessary novel terminology (Haeckel 1869, III–IV; more details in: Kolchinsky, this volume). Haeckel's major deserve young Metschnikoff saw in supporting evolutionism in consort with the general idea of unity and cognizability of nature. This was in line with a publicly displayed position toward Haeckel of other Russian evolutionists who usually avoided criticizing Haeckel in popular publications emphasizing instead his importance for the struggle against clericalism and conservatism.

In later years, Metschnikoff was quite straightforward in his criticism of Haeckel. In the voluminous "Review of the Question of the Origin of Species" (Ocherk voprosa o proizkhozhdenii vidov), first published in 1876, Metschnikoff devoted a lot of space to Haeckel (Metschnikoff 1950, pp. 31–209). Haeckel, according to Metschnikoff, trespassed the border between science and popular writing by trying to defend Darwinism and to make it into a universal and holistic theory. To do so, Haeckel replaced proper science with dilettantism and presented his views in the form of the *Naturphilosophie* so well known to Germans. The lack of data leads to the strengthening of the hypothetical and even "fantastical" sides of his doctrines. Metschnikoff saw Kovalevsky as a counterexample to Haeckel: "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" (1876, quoted from: Gourko et al. 2000, p. 90).

Haeckel appreciated Kovalevsky's work very much as well (Levit 2007). In his *Anthropogenie* Haeckel wrote: "The most significant germ histories in the recent time were those of Kovalevsky" (Haeckel 1874a, b, p. 49). It is astonishing in this respect that taken at face value Kovalevsky and Metschnikoff were mostly either indifferent or hostile toward Haeckel. In contrast to Haeckel and Darwin, there was no letter exchange between Kovalevsky and Haeckel. The Archive of the Ernst-Haeckel-Haus in Jena holds not a single letter to Haeckel, either from either Kovalevsky or 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 Kovalevsky's younger brother Vladimir (1842–1883) conducted his doctoral work under Haeckel's supervision (Uschmann 1956) and that the *Gastraea* theory was to a significant extent based on Alexander Kovalevsky's data. In the 185 letters from Kovalevsky to Metschnikoff, there are only 7 short mentions of Haeckel (Gaissinovich 1974). In the letter exchange (1867–1873) between brothers, Kovalevsky Haeckel is mentioned many times, although almost exclusively by Vladimir reporting about his experiences in Jena. Alexander mentioned Haeckel only once (and, again, quite critically) in reference to a potential scientific award for Metschnikoff, because "Haeckel got an award for a much poorer work on siphonophores" (Gaissinovich 1988, p. 240).

Another characteristic example is the attitude toward Haeckel of the already mentioned evolutionist and physiologist of plants Timiryazev. From one side, in the introduction to the second edition of "Charles Darwin and his Doctrine" he pointed out that it was one of Darwin's major credits that he involved such outstanding biologists as Ernst Haeckel, Thomas Huxley (1825–1895), Joseph Hooker (1817–1911), Charles Lyell (1797–1875), and Carl Vogt (1817–1895) in the evolutionary movement (Timiryazev 1949, 22). From another side, Timiryazev himself almost never directly cited Haeckel.

Mikhail Menzbir (1855–1935) was a professor of zoology and comparative anatomy and the "patriarch" of Russian Darwinism, who created the whole school of evolutionary thought. Menzbir's famous pupils included Alexej Sewertzoff (Severtsov) (1866–1936), who made important contributions toward a synthesis of Darwinism and evolutionary morphology, and a geneticist Nikolai Koltzoff (1872–1940). Menzbir, as well as Metschnikoff, appreciated Haeckel as an outstanding morphologist and propagandist of evolutionary theory and counted him as one of the most influential Darwinians along with Wallace, George Romanes (1848–1894) and Weismann. At the same time, Menzbir was ambivalent about Haeckel as well. For example, he wrote that Darwinism "in Haeckel's hands was significantly modified and not everything that Haeckel made in that direction can be judged positively" (Menzbir 1900).

The outlined attitudes of the Russian "apostles of Darwinism" toward Haeckel in general are characteristic but do not reflect the whole panoply of opinions because it was a time of a high diversity within evolutionary biology both in theories and in methods of proving these theories. Below, we overview more specific issues related to the perception of Haeckel in Russia.

The problem of factors of evolution and the reception of Haeckel

In a paper of 1909 "Charles Darwin and the semicentennial achievements of Darwinism," Timiryazev criticized all anti-Darwinian currents including mutationism, neo-Lamarckism, teleology, and panpsychism (Timiryazev 1949, pp. 245–248). Timiryazev did not mention Haeckel directly, but, considering Haeckel's Lamarckian bias and his panpsychism (the idea of "crystal souls" etc.), he seemed to embrace with this criticism Haeckel as well. Timiryazev was presumably not truly aware that Haeckel rejected teleology as incompatible with his monism and "denied, as did Darwin, that organisms harbored an intrinsic tendency toward improvement" (Richards 2008, p. 147). In another place, Timiryazev pointed out that the major mistake of neo-Lamarckians was the identification of variability with adaptability ("they forget that one does not follow from another") as an example of the Austrian botanist Richard Wettstein (1863–1931) shows. In the footnote to this argument, Timiryazev claimed that this confusion is characteristic for Haeckel as well (Timiryazev 1939, p. 121). At the same time, Timiryazev did not reject Lamarckism completely. He often favorably cited Haeckel's successor in Jena Ludwig Plate (1862–1937) who sought to combine Darwinian selectionism with moderate neo-Lamarckism (Levit and Hossfeld 2006). Timiryazev wrote, for example, that "only realistic [trezvyj] Darwinism gives Lamarckism its due place in science" (Timiryazev 1937, p. 131). Yet, as Richards correctly pointed out, Haeckel, like Darwin, "distinguished two general classes of variable traits," direct (Lamarckian) and indirect (random) (Richards 2008, p. 228). Both mechanisms were important for Haeckel, and he was criticized for this by neo-Darwinians. Timiryazev was not as strict of a neo-Darwinian as Weismann and admitted some direct environmental impact on the organism's heredity. He criticized neo-Lamarckians (and seemingly Haeckel as one of them) rather for exaggerating the scope of non-selectionist mechanisms in evolution, thereby diminishing the role of natural selection.

Another important figure in Haeckel's perception was Georg Karl Maria von Seidlitz (1840–1917). He was born in St. Petersburg to German parents and raised in Dorpat (Estonia), where he defended his doctoral degree in 1868 and thereafter taught various subjects including Darwinism. Seidlitz was in a letter exchange with both Darwin[2] and Haeckel.[3] His letter exchange with Haeckel suggests that he was strongly influenced by Haeckel's ideas quite soon after the publication of the *GM* (Haeckel 1866a). Thus, in a letter to Haeckel written in 1868 Seidlitz claimed that *GM* so strongly reflected his own "deepest monistic convictions" [innerste monistische Überzeugungen] that he felt a necessity to further elaborate his very own thoughts on the subject.[4] In the same years, Seidlitz became a member of the Leopoldina Academy in Halle, which is an indication of his early prominence in the German-speaking countries.[5] In 1871, he published arguably the best text book in evolutionary biology in pre-revolutionary Russia. The first edition of the book appeared in German in Dorpat, and the second in Leipzig in 1875 (Seidlitz 1871, 1875). In the first edition, Haeckel was mentioned several times. In Seidlitz' view evolutionary theory went via several major steps including Goethe's theory of transformation [Umwandlungstheorie], Lamarck's theory of adaption (Anpassungstheorie), and Haeckel's carbon theory [Kohlenstofftheorie], which is "as necessary for the justification of the natural selection theory [Selectionstheorie] as theory of natural selection for the explanation of adaptation- and transformation-theories" (Seidlitz 1871, p. 27). Under "carbon-theory," Seidlitz understood the idea that life processes can be explained by the physical–chemical properties of carbon. In this context, he saw Haeckel's major contribution to evolutionary biology in developing a (correct) causal theory of evolution as opposed to teleology and applying this causal principle to explanation of all evolutionary phenomena as opposed to Darwin, who, according to Seidlitz, applied it only to the principle of natural selection (Seidlitz 1871, p. 81). Besides, Seidlitz acknowledged Haeckel's priority in explaining the origin of life by proposing a monera hypothesis (Seidlitz 1871, p. 181). At the same time, Seidlitz heavily criticized Haeckel for supporting neo-Lamarckian principles: "Haeckel's indirect adaptions [indirecte Anpassung] as well as his directs adaptations [directe Anpassung] lead to the elimination of the theory of natural selection, back to the standpoint of the Lamarckian theory of adaptation" (Seidlitz 1871, p. 205).

It is astonishing that Haeckel's "laws of inheritance" presented in the *GM* were met with skepticism even by Russian neo-Lamarckians. For example, a well-known anatomist and popular science writer Peter F. Lesgaft (1837–1909), who published a voluminous paper on heredity, spoke about "Haeckel's laws" in rather moderate tones: "they are still insufficiently examined […] and, even, rejected by the majority of researchers" (Lesgaft 1889, pp. 119, 120). Narrowing down the scope of neo-Lamarckian mechanisms, Lesgaft affirmed that "neither abilities nor mechanical injuries and monstrosities can be inherited by the next generation" (Lesgaft 1889, p. 82).

The controversies between Russian evolutionists and Haeckel concerning the struggle for existence comprised a significant segment of theoretical discussions. In the *GM*, Haeckel claimed: "The struggle for existence [translated as "Kamp ums Dasein," i.e., the struggle for being] or the wrestling for existence [das Ringen um die Existenz] or the struggle for life [Mitbewerbung für das Leben, Wettkampf um die Lebensbedürfnisse] […] is one of the greatest and most powerful natural laws, which directs the entire organismic world including humans and which acts universally and at any time among the eternally moving living organisms" (our translation from: Haeckel 1866b, pp. 231, 232). In contrast, Russian biologists supported the view that the struggle for existence is no more than an awkward metaphor. Daniel Todes even claimed that "few Russians shared Darwin and Wallace's respect for Malthus, and that many saw the struggle for existence as an infusion of the British enthusiasm for individualistic competition" (Todes 2009). We would like to emphasize though that Russian Darwinians (not to confuse with Russian mutationists, the champions of orthogenesis, symbiogenesis, and other representatives of the "alternative theories of evolution" (Levit et al. 2008) had no a priori aversion toward the very idea of the struggle for existence and rebelled against Haeckel's overemphasis on the competition model as well as against taking the metaphor to seriously. An example of an "anti-struggle-for-existence" theoretician is a botanist Andrei N. Beketov (1825–1902), who was a teacher of many botanists and physiologists of plants including Timiryazev, a symbiogeneticist Andrei Famintzyn (Famintsyn) (1835–1918), Ivan Borodin (1847–1930), and others. He had a great influence on the reception of Darwin in Russia. Beketov's major idea was the harmony of nature based on the ability of organisms to adapt in accord with environmental conditions (Beketov 1860). For him, organismic communities were well balanced in line with the ideas of Cuvier and Linné. There is little space for the Darwinian struggle for existence in his concept.

2 https://www.darwinproject.ac.uk/letter/?docId=nameregs/nameregs_4282.xml.

3 https://haeckel-briefwechsel-projekt.uni-jena.de/en/document/b_14848.

4 Letter of G. Seidlitz to E. Haeckel from 26th of March, 1868. EHH-Archive, Friedrich-Schiller-University Jena.

5 https://www.leopoldina.org/de/mitglieder/mitgliederverzeichnis/member/6629/.

In the view of brothers Kovalevsky the struggle for existence metaphor only impeded the understanding of evolution of higher animals. Metschnikoff in the review of *On the Origin* written in 1863 but published first in 1950 very critically approached both the struggle for existence and natural selection (Metschnikoff 1960, pp. 20, 269, 271, 273). At the same time, in later works such "Review of the Question of the Origin of Species" (1876) (after considering Darwin's arguments as well as the arguments of his opponents) Metschnikoff clearly stated that the struggle for existence is a complex phenomenon composed of four major elements: "(1) Competition between individualism of the same species; (2) competition between individuals of various species; (3) struggle between individuals of various species (e.g., between predators and herbivores); (4) struggle between living beings and their environments (cold, dry etc.)" (quoted from: Metschnikoff 1956, p. 129). It is easy to see that Metschnikoff puts the intraspecific struggle on the first place, although he indeed supported that the struggle for existence is a multifaceted phenomenon and was unhappy with Haeckel's bias toward competition metaphor.

One of the best examples of the "anti-competition model" approach gives the concept of the Rector of St. Petersburg University an ichthyologist and ornithologist Karl Kessler (1815–1881). Kessler was born in Königsberg, but his family moved to Russia when he turned seven. He went to school and attended the Department of Physics and Mathematics at St. Petersburg University (Sideleva 2017). Kessler offered a concept of mutual aid in evolution and awarded it with the rank of a law, which "was more important than the law which urges individuals to struggle with each other" (Kessler 1880, p. 124). Nevertheless, Kessler did not neglect competition model completely: "The need to find food, Kessler explained, stimulated struggle among organisms. But the need to defend themselves and reproduce led to cooperation" (Todes 1987). Mutual aid, according to Kessler, can weaken or completely exclude the intraspecific competition, but can eventually strengthen the interspecific struggle.

A champion of anarchism and traveler Petr Kropotkin (1842–1921) went even further. In his English book Mutual Aid: A Factor of Evolution (1907) Kropotkin claimed that the preferential survival of the best adapted to famines, the cold, droughts, and so on would lead to evolutionary regress, because individuals would survive being exhausted. From his viewpoint, the relationships within species were determined by harmony and all adaptations existed only to struggle with unfavorable climatic conditions and foes (Kropotkin 1907, c. 21).

At that time (the beginning of the twentieth century) due to translations of Darwin's works and the influence of brothers Kovalevsky, Metschnikoff, Menzbir, Alexei P. Pavlov (1854–1930) and especially Timiryazev, Russian evolutionary terminology was ultimately cleared of Bronn's impact. The critics of the struggle for existence as a major factor of evolution were directed mostly against Haeckel. Haeckel's views in the popular form were spread due to numerous translations of Wilhelm Bölsche (1861–1939) ("Entwicklungsgeschichte der Natur," "Das Liebesleben in der Natur," "Ernst Haeckel. Ein Lebensbild"). There was, however, a big difference between Bölsche's own views and Haeckel's theory, because sexuality (love) was for Bölsche the major engine of the universe whereas the Darwinian struggle for existence appeared only as a part of "erotic monism" (Ricci 2007, p. 38) and performing only a secondary role in evolution as a product of individualization of the higher animals and humans.

Russian biologists mostly escaped speculations about the inherited adaptability of organisms and tried to study the mechanisms of adaptive morphogenesis of animals and plants in empirical ways. Here are some examples. Beketov connected adaptive changes in a structure, form, size, coloring power, and position of leaves with the influence of environment, especially the direction and intensity of light (Beketov 1865). In later years, Beketov's ideas floated toward a more explicit Geoffroyism (neo-Lamarckian concept ascribing evolutionary change to the direct influence of the environment: Mayr and Provine 1998, p. 5) though, claiming that under the name of Darwinism various concepts are grasped giving more weight to abiotic factors in the struggle for existence (Beketov 1882). Timiryazev tried to experimentally prove functional connections between the green color of leaves (chlorophyll) and photosynthesis (Timiryazev 1897). Studying organismal protective properties, Metschnikoff in 1883–1892, first on medusas and then on other organisms, demonstrated that in animals with mesodermal tissues alien bodies will be destroyed by parenchymal cells which he labeled *phagocytes* (Metschnikoff 1898). This discovery ultimately led to the Nobel Prize in 1908. As we will show below, in 1882 he began to develop a theory of *phagocytella*, which was opposed to Haeckel's *gastraea* theory, which Metschnikoff, as already mentioned, held for too speculative (Metschnikoff 1950, pp. 271–471).

The "empirical bias" of Russian scholars was also observable in the interpretation of species. Although Haeckel is often accused in being a "determinist," Gliboff correctly argued that Haeckel rejected (sometimes "with great vehemence") mechanistic accounts of evolution (Gliboff 2012). The notion of "species" had for Haeckel, as well as for Darwin, no rigid definition. Haeckel arrived at the conclusion that practical determining of "species" relies predominantly on morphological differences (Haeckel 1866b, p. 332). The "physiological notion of species" defining species as a reproductively isolated unit was criticized by Haeckel as "there is no absolute difference between bastards (hybridi) and blendlings (spurii)" (Haeckel 1866b, p. 346). Russian scholars tried to combine the idea of species reality and discreteness with the concept of variability by conducting field studies. For example, Mikhail Menzbir championed the absence of rigid boundaries between species and varieties, the monophyletic nature of speciation along with a possibility of sympatric speciation, the heterogeneity of a species as a necessary condition for natural selection.

Besides, there were attempts to incorporate also further criteria of species above the purely morphological criteria championed by Haeckel. For example, Russian botanists began to consider geographical, physiological (reproductive), and biochemical criteria (Korzhinsky 1892; Komarov 1901; Pachoskii 1914), which allowed them to demonstrate polymorphism and holistic nature of species. One of the first advocates of polymorphism was Pyotr Petrovich Semenov-Tyan-Shansky (1827–1914) (Semenov-Tyan-Shansky 1910). Semenov-Tyan-Shansky defined intraspecific forms and suggested their hierarchy: species, geographical race (subspecies), phratry, and morph (incipient species).

Phylogenetic trees and major directions of evolution

Haeckel was arguably the first in the history of Darwinian biology, who suggested a "tree of life" as a model for visualization of the monophyletic evolution and a high species richness on Earth (Hossfeld and Levit 2016; Kutschera 2016). In *GM*, Haeckel published eight phylogenetic trees and divided all living organisms into three kingdoms—animals, plants, and protists. Haeckel claimed that evolution and development affected everything from inorganic matter (monads in the roots of a tree) to man (Hossfeld et al. 2017). In contrast to Darwin himself, Haeckel's objective was not only to visualize the principle of divergence, but to suggest phylogenetic trees illustrating the real phylogenetic relationships between certain organismic groups. In his later works, he continued to develop his initial ideas, but used his diagrams also to illustrate the degree of evolutionary progress including the evolution of mankind. Evolutionary progress [Vervollkommnung] had for Haeckel a status of law (Haeckel 1866b, p. 257). At the same time, Haeckel distinguished between the "progress law" and "divergency law" describing processes manifesting "neither progress nor regress" or even "definitely regress" (Haeckel 1866b, p. 258).

The latter idea was developed by Metschnikoff, who noted that evolution can proceed without heightening or lowering the level of organization by mentioning at the same time that such cases remain enigmatic from the viewpoint of natural selection. Andrei Famintzyn also distinguished (Famintzyn 1894) two kinds of progress embracing cases when organisms became more complex and cases when evolution proceeded without changing the level of organization. The greatest difficulty at that time was the lack of knowledge about real phylogenies.

Looking for parallelisms in the development of individuals, species and phyla [Stämme] Haeckel distinguished three stages in the genesis of all three "developmental series" (Hossfeld et al., this volume). Thus, the growth, restructuring, and degeneration in "biontic" (individual) development correspond to the early development [Aufblühzeit], blooming period [Blüthezeit], and decay of species and phyla (Haeckel 1866a, p. 361). Trying to explain these parallelisms, Haeckel came close to the concept of distinguishing morphophysiological and biological progress introduced by Alexei N. Sewertzoff (Severtzov) (1866–1936), whose research played a crucial role in the growth of evolutionary morphology worldwide (Sewertzoff 1914, 1925, 1931). A. N. Sewertzoff laid the foundations for a strictly Darwinian evolutionary morphology by proposing a concept of progress free of teleology, and a radically revised recapitulation theory (Levit et al. 2004, 2015a). Sewertzoff published an analysis of the concept of evolutionary progress as early as in his books in 1912 and 1914 (Sewertzoff 1912, 1914). Here, he articulated several ideas, which would later form the foundation of his theories, namely, that morphological evolution 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- and ecto-somatic that evolve in a correlated fashion (Levit et al. 2004). His revised theory of how phylogeny and ontogeny are related contributed significantly to the development of selectionist thinking. Sewertzoff claimed that *morphophysiological progress* does not necessarily coincide with biological progress, because, Sewertzoff reasoned, many biological forms show no or minimal morphological change over very long geological periods. For example, *Morphophysiological regress or degeneration* should not be confused with *biological* regress. Degeneration is a simplification, decrease or loss of certain functions and related structures, which may be caused by the transition to a sessile or parasitic mode of existence.

Russian paleontologists were actively involved into the phylogenetic studies pushed forward by Haeckel, although they escaped designing all-embracing phylogenetic trees concentrating on certain phyla. Best known in this respect is Haeckel's doctorate student (1871–1872) and one of founders of evolutionary paleontology Vladimir Kovalevsky (Davitashvili 1946, pp. 136–146; Todes 1978). V. Kovalevsky's position toward Haeckel was as ambivalent as that of his brother. In his letter to Alexander, he appealed to Carl Gegenbaur (1826–1903) more often than to Haeckel (Gaissinovich 1988). Vladimir's doctoral thesis (Kovalevsky 1873) was devoted to Darwin and not to his immediate supervisor Haeckel. Haeckel was even absent in the acknowledgements. At the same time, Kovalevsky's studies of even-toed mammals (*Hyopotamidae, Athracotherium, Entelodon*) were designed along the lines of Haeckel's research program (Kovalevsky 1950–1960). Their evolution was presented as a branching tree where branches developed parallel or went apart. Moreover, proceeding from Haeckel's ecological ideas Vladimir Kovalevsky laid foundations for paleoecology and tried to give a causal analysis of ungulates.

Abiogenesis and the polyphyly–monophyly controversy

In contrast to Darwin, Haeckel paid lots of attention to abiogenesis. In *GM*, he postulated the origin of life on Earth by way of *archegonia*, i.e., spontaneous generations of *monera* (most primitive structureless organisms) (Haeckel 1866b, p. 3). The initial occurrence of all phyla (Stämme) was polyphyletic: "The initial formation of phyla should be grasped in all cases as by way of archegonia, may be always as autogonia (not as plasmogonia)" (Haeckel 1866b, p. 367), i.e., the majority of cases, first phyla occurred directly from inorganic chemical substances (autogonia) and not from previously generated organic substances (plasmogonia).

Haeckel's hypothesis of spontaneous generation of living organisms in inorganic environments rich in carbon and nitrogen was adapted by an outstanding Russian botanist Vladimir Beliaev (1855–1911). In his talk at the Warsaw University, he presented an actualist thesis that life occurred under conditions similar to current processes (Beliaev 1893).

Timiryazev was also close to Haeckelian views on abiogenesis. Discussing neo-vitalism in 1913, he claimed that physics and chemistry intervene more and more into the processes which were previously seen as typical only for living organisms (Timiryazev 1949, pp. 356–376). He saw the disappearing of rigid boundaries between living and inert matter as an argument in favor of naturalist view on the origin of life. He proposed a picture of transition of a formless colloidal substance into organized structures ultimately evolving into living organisms (Timiryazev 1949, pp. 362, 363). However, neither Beliaev nor Timiryazev succeeded in creating an empirically based coherent theory of life origin.

Nevertheless, their claims contributed to the growth of experimental studies of abiogenesis in the early 1920s, the best known of which became the works of Aleksandr I. Oparin (1894–1980). In his book "The Origin of Life" (initially published in 1924), Oparin mentioned Haeckel in the chapter "Materialist theories of the life's origin" to acknowledge Haeckel's view that spontaneous generation is a "logical postulate of philosophical natural sciences" and to discuss his concept of abiogenesis quite in detail (Oparin 1941, pp. 48, 49). At the same time, Oparin classified Haeckel's views in general as naïve and "mechanistic" (Oparin 1941, pp. 48, 49). Oparin saw the major difficulty with Haeckel's theory in what Haeckel called *autogonia*, i.e., immediate emergence of living matter from inorganic structures.

Beginning in 1922, Oparin himself pushed forward a hypothesis proving the abiogenic origin of carbohydrates subsequently developing to protein-like structures and later colloidal systems able to a gradual enhancement of their organization by means of natural selection (Oparin 1924). Oparin enjoyed high scientific international reputation right until the age of molecular biology.

The representatives of the symbiogenesis theory coined in 1905–1907 by Andrei Famintzyn and Konstantin Mereschkowsky (Merezhkovsky) (1855–1921) supported the idea of polyphyletic evolution not only for the entire organic world, but also for separate kingdoms (Margulis 1970; Khakhina 1992; Kutschera and Niklas 2005; Levit and Krumbein 2007). Famintzyn expressed his views most fully in the paper of 1907 "On the Role of Symbiosis in Organisms' Evolution" (Famintzyn 1907). In this publication, Famintzyn claimed that the level of organisms' complexity in evolution increases not only by way of differentiation of organismic structures but also by way of "symbiotic unification of independent organisms into a living unit of a higher order" (Famintzyn 1907, p. 14). Famintzyn formulated this hypothesis proceeding from his long-standing research on spore formation by lichens, and investigations into the symbiotic relations of unicellular green and yellow algae with invertebrate species. He also studied plastids of sunflower seeds and sprouts as well as conducted experiments by cultivating chloroplasts in artificial mediums. Famintzyn saw the plant cell as a symbiotic complex, i.e., as a product of symbiosis of simple organisms.

In contrast to Famintzyn, who concentrated on empirical proofs of his theory, Mereschkowsky (1905, 1909) merged by his mind's eye two relatively independent concepts. The first one stated that any plant or animal cell is a combination of initially free living and very primitive individuals (symbiosis). This claim was based on studies of symbiotic nature of chromatophores. The second one was the theory of "two plasms," saying that all organic nature consists of two plasms differing in their properties. The first kind of plasm, called *micoplasm*, is characteristic for all bacteria and fungi (excluding phycomycetes), cyanobacteria as well as for chromatophores. All other plants and animals consist of *amoebaplasm*, although their cells include also micoplasm of nucleus and plastids. Mereschkowsky proposed that the initial bearers of micoplasm (bacteria) and amoebaplasm (monera) occurred independently of each other at different epochs in the history of earth. In the majority of cases, bacteria were digested by monera but in there were bacteria which created symbiosis with monera. This ultimately led to the occurrence of eukaryotes.

The theory of symbiogenesis required a revision of traditional phylogenetic schemes. In contrast to Haeckel, Mereschkowsky proceeded from the assumption that there are independent groups of organisms: prokaryotes and eukaryotes. Furthermore, only most primitive prokaryotes occurred independently and repeatedly, whereas all the rest and, especially, eukaryotes resulted from various symbiogeneses. This was a way to solve the problem of increasing complexity, which occupied Haeckel as well. Unfortunately, this exceptionally fruitful way of thinking found little support in Russia. One of the reasons for it was the dominance of Alexei Sewertzoff's school of evolutionary morphology.

In 1914, Sewertzoff attacked the advocates of polyphyletic theory of evolution (Sewertzoff 1914). Sewertzoff championed strict monophyly defined as an origin of the whole complexity of life from one protozoan species. The majority of evolutionists, Sewertzoff argued, share an intermediate position accepting the polyphyly of major taxa and monophyly of small taxa. He himself advocated monophyletism with divergence as a primary factor of evolution (Sewertzoff 1914, p. 81).

In general, there were not only pro-Haeckelian solutions to the polyphyly–monophyly issue in the pre-revolutionary Russia, but also non-Haeckelian approaches. The idea of polyphyletic evolution was tightly connected to speculative hypotheses on the origin of life.

The biogenetic law

The biogenetic law was central to Haeckel's evolutionary theory and extremely controversial at the same time: "When the concepts and terminology introduced by Haeckel did not suffice to answer the questions at hand, several biologists tried to supplement or replace the biogenetic law" (Hossfeld and Olsson 2003). Russian biologists played here a crucial role.

Soon after the publication of the "Origin" (Darwin 1859), Alexander Kovalevsky and Metschnikoff began their investigations into ontogeny of various animals without drawing large-scale phylogenetic trees, but concentrating on differences and similarities in embryonic development. First results of Kovalevsky were published to the moment of publication of Haeckel's *GM*. Kovalevsky demonstrated the common origin of vertebrates and invertebrates, and his results required serious corrections in Haeckel's trees. Already in his master thesis, Kovalevsky described common regularities characteristic for both invertebrates and vertebrates (Kovalevsky 1865). The boundaries between various "types" established by Cuvier, von Baer, and others crashed down. The similarity of embryogenesis in lancelets and vertebrates demonstrated the unity of two main animal groups. Haeckel concurred with Kovalevsky's findings and included lancelets and vertebrates into *Chordata* subdivided into *Acrania* and *Craniata* (Haeckel 1874a, b). Furthermore, studying ascidia, comb jellies, Oligochaeta, Arachnida, insects, and vertebrates, Kovalevsky demonstrated the similarity of early ontogenesis of ascidia with vertebrates and the presence of chorda in their larvae (Kovalevsky 1951, pp. 41–122). The similarity between double-layered lancelet larva and early ontogenesis of tunicate proved the monophyletic origin of the animal kingdom (Kovalevsky 1951, pp. 123–266, 387–432). Darwin recognized this discovery as an important contribution to evolutionary biology (Ghiselin 2009; Darwin 1908, p. 127). In a letter to his brother Alexander from Germany, Vladimir Kovalevsky pointed out several times that Haeckel was excited about Alexander's discoveries and that Alexander was more popular in Germany than in Russia (Gaissinovich 1988, pp. 50, 147). Gegenbaur was deeply impressed by Alexander Kovalevsky's works as well and even spent a sleepless night after reading his work on ascidia (Schtraikh 1940, p. 118).

Kovalevsky played for Haeckel a crucial role in relation to "*gastraea* theory" proposed by Haeckel in the "Kalkschwämme" (Calcarea) (Haeckel 1872). In the first volume of "Kalkschwämme," Haeckel wrote that already in 1867 his "phylogenetic studies became a highly welcomed confirmation in the, in-between published important embryological studies of Kowalevsky" (Haeckel 1872, p. 466).

Haeckel was convinced that Kovalevsky's results were in accord with the gastraea theory, although Kovalevsky was cautious about this inference. By contrast to Haeckel, Kovalevsky did not look for a hypothetical ancestor of metazoans, but rather described the early stages in their ontogenetic developments. His emphasis was on the unity of all processes of ontogenesis and on its structures. Kovalevsky never openly criticized Haeckel and even in letter exchange with Metschnikoff was always reserved (Poliansky 1955, pp. 60–61, 67, 107), although he was aware that double-layered organisms with big gastral cavity are a special adaptation (Kovalevsky 1951, pp. 390–401). Due to his work with *Coelenterata* (*Cnidaria* and *Ctenophora*), Alexander Kovalevsky was very aware that gastrulation was possible both by ingression and by invagination, and that Haeckel's theory is hardly applicable to the developmental processes in hydroid polyps. In other words, Kovalevsky 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 Kovalevsky admitted alternative paths of gastrulation without absolutizing one way as it was done by Haeckel.

Metschnikoff, in 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

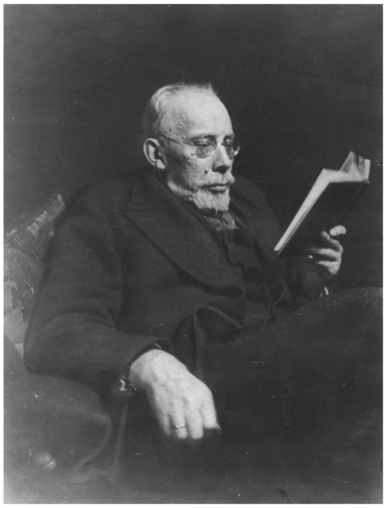

Fig. 2 Portrait of Alexei Nikolaevich Sewertzoff (from the Archive of A.S. Severtzov)

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 ameboid (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.

In Russian biology, Metschnikoff's theory of *phagocytella* was further developed by Vladimir N. Beklemishev (1890–1962), Aleksei A. Zavarzin (1886–1945), Aleksei A. Zakhvatkin (1905–1950), and Petr P. Ivanov (1878–1942). The rediscovery of *Trichoplax adhaerens* in the 1970s revived the controversy between Haeckel and Metschnikoff. Artemii V. Ivanov (1906–1992) even proposed a new domain *Phagocitellozoa* (Ivanov 1973). But irrelated to the question which of two hypotheses (*gastraea* or *phagocytella*) is closer to the modern science, there was a deeper methodological discrepancy between Haeckel and Metschnikoff. Metschnikoff, trying to be closer to empirical data, believed that in ontogenetic plasticity on all its stages, whereas Haeckel championed the palingenetic character of initial stages of ontogenesis and evolution by adding new characters by the end of it (Hossfeld and Olsson 2003) (Fig. 2).

A detailed theory of embryonic adaptations was suggested by Sewertzoff, who significantly revised Haeckel's biogenetic law by coining a theory of phylembryogenesis (Levit et al. 2004, 2015a). Sewertzoff's purpose was a radical revision of Haeckel's view on the relationships between ontogeny and phylogeny in order to rescue the very idea of recapitulation (Levit et al. 2004). 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 in Moscow (Sewertzoff 1910)—the term *phylembryogenesis* was coined 2 years later (Sewertzoff 1912). The last version of the theory can be found in the Russian editions of *Morphological Regularities…* (Sewertzoff 1939, 1949).

From his analysis of the history of the "biogenetic law," it is clear that Sewertzoff thought very highly of Fritz Müller's (1821–1897) approach to the problem of recapitulation (Levit et al. 2004). In Sewertzoff's opinion, Müller (1864, pp. 74–81) saw the problem of alterations in ontogenesis very clearly: "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 1874a, b, p. 5) but neglected the idea of an evolutionary impact of ontogeny on phylogeny. This idea survived in Germany mostly in the works of adherents to orthogenesis such as R. A. Kölliker (1817–1905).

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 1970). Sewertzoff himself acknowledged that he initially intended to prove that recapitulation is the proper method for phylogenetic studies. Investigations had shown, however, that the recapitulation of ancestral features was not a universal phenomenon and that it was detectable only in certain cases. This was in agreement with Sewertzoff's concept of progress, because according to his hypothesis the phylogenetically older forms are not necessarily more "primitive." Thus, the theory of phylembryogenesis could explain this phenomenon (Sewertzoff 1949, pp. 381, 396).

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 pupil Ivan Schmalhausen (1884–1963) 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, 357).

To answer this general question, Sewertzoff distinguished three basic modes of phylembryogenesis: anaboly, deviation, and archallaxis. *Anaboly*, i.e., changes to ontogeny by extension was supposed to explain "von Baer's law," which claims that features of the adult forms appear in a certain sequence during embryonic development and that this 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 it, i.e., "the pressing back of adult ancestral stages into the young stages of the descendants" (de Beer 1932). Sewertzoff stressed the difference between "von Baer's law" and Haeckel's recapitulation (Sewertzoff 1931, pp. 278, 279, 1949, p. 418). He maintained 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. *Deviation* is a departure from the usual course of ontogeny, which occurs in the middle stages. Sewertzoff adapted the term "middle stage deviation" from Haeckel's "scientific grandson" Franz (1927) (Hossfeld and Olsson 2003). In contrast to anaboly, "middle stage deviation" does not extend morphogenesis (Sewertzoff 1949, p. 429). Finally, *archallaxis* explains cases with no recapitulation at all. Briefly defined, archallaxis is an evolutionarily significant modification occurring in the earliest stages of ontogeny. 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).

In summary, the theory of *phylembryogenesis* ultimately separated the problem of recapitulation from Haeckel's "biogenetic law." Sewertzoff convincingly demonstrated 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, in that sense, into the Haeckelian explanatory paradigm broadly construed.

Conclusions

The significant German influence on Russian biology and the widespread of German as a language of science in Russia cleared the way for Haeckel's ideas. Yes, Haeckel's reception in Russia was highly ambivalent. From one side, he influenced literally all sides of evolutionary research in Russia. His ideas on the factors of evolution, speciation, the origin of life, and developmental processes were actively elaborated in Russia. One of the important indicators of his influence is the widespread of terms he coined, such as "phylogeny," "ontogeny," "phylogenetic tree," "biogenetic law," and many others.

From the other side, many influential Russian biologists heavily criticized Haeckel for being too speculative or modified his concepts to include them into their own research programs. There seem to be several methodological discrepancies between Haeckel and leading Russian life scientists. The first point can be labeled a revolt against Haeckel's universalism, i.e., his attempts to offer all-embracing "scientific" explanations driven by an aspiration to convert Darwinism into a universal worldview. This required from Haeckel to be radical, speculative, and universal even within the framework of evolutionary theory as can be exemplified by his all-embracing phylogenetic trees. Russian biologists such as Metschnikoff and Kovalevsky tried to avoid this kind of universalism and concentrated on quantifiable empirical tasks. In this way, Kovalevsky found a proof of the common origin of vertebrates and invertebrates, which Haeckel, again, adapted for his radical and speculative theoretical system.

The second (connected with the first) feature is the cool attitude toward Haeckel's "romantic connections" expressed, for example, in his refusal to principally distinguish living and inert matter (Richards 2008, pp. 11, 124). His ideas abiogenesis and early polyphyletic evolution inspired many biologists including Oparin, but their Russian versions were disconnected from Haeckelian monism, which "was rooted firmly in Romantic Jena" (Richards 2008, p. 124). Haeckel's version of monism found, in general, little support among Russian biologists (Levit and Hossfeld 2017).

The third feature was the radical modification of Haeckel's concepts to adapt them to an alternative theoretical landscape. The most characteristic example is Sewertzoff's theory of phylembryogenisis, which was a fundamental revision of Haeckel's biogenetic law, which claimed that phylogeny is a "mechanical" cause of ontogeny, yet without proposing any exact mechanism of ontogenetic evolution and without disclosing the ways of their *reciprocal* influence. Sewertzoff postulated various modes in which ontogeneses can evolve and thus demonstrated how ontogeny can alternate phylogeny. Another example is the growth of symbiogenesis theory in Russia, which echoed the Haeckelian idea of polyphyletic nature of the early evolution. At the same time, even these radical revisions ultimately contributed to the widespread of Haeckel's Darwinian evolutionism. Thus, Sewertzoff's phylembryogenesis and, especially, the concept of archallaxis (which was at the times of the Modern Synthesis adapted by Ivan Schmalhausen) contributed significantly to the Darwinian (selectionist) interpretation of the tempo of evolution and therefore to the triumph of Darwinism, which Haeckel so passionately propagated.

To sum up, in Russian biological circles one can observe a tendency to accept Haeckel as an empirical biologist and a prophet of Darwinism by rejecting his "philosophical," "universalist," or far too speculative hypotheses.

Acknowledgements We would like to thank Dr. Elizabeth Watts (Jena) for valuable suggestions. We extend our thanks to Dr. Thomas Bach (Ernst-Haeckel-Haus, Jena) for providing us with the letters of Georg Karl Maria von Seidlitz.

References

Beketov AN (1860) Harmony in nature, vol 30(1). Russkii vestnik, Moscow, pp 197–241 **(1–2:534–558; in Russian)**
Beketov AN (1865) Is there any reason to believe that the forms of plants adapted to the light? Estestvoispytatel 14:262–267 **(in Russian)**
Beketov AN (1882) Darwinism from the point of view of general physical sciences. Trudy St-Peterburgskogo obschestva estestvoispytatelei, 13, 1:92–110
Beliaev VI (1893) The primary origin. Tip. Warshawskogo universiteta, Warshawa **(in Russian)**
Bowler PJ (1988) The non-Darwinian revolution: reinterpretation of a historical myth. Johns Hopkins University Press, Baltimore
Bowler PJ (1996) Life's splendid drama. The University of Chicago Press, Chicago
Brandt FF (1868) Notes on the contents of the second and third divisions of my posts about sea corals. In: Trudy 1 s'ezda russkikh estestvoispytatelei, otdel zoologii, pp 211–215 **(in Russian)**
Bronn HG (1859) On the laws of evolution of the organic world during the formation of the crust of the earth. Ann Mag Nat Hist 4(3):175–184 **(4(20):81–90)**
Bronn HG (1860) Rezension von Charles Darwin "On the Origin of Species (London, 1859). Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde 112–116
Chernyak L, Tauber AI (1988) The birth of immunology: Metchnikoff, the embryologist. Cell Immunol 117(1):218–233
Darwin C (1859) On the origin of species by means of natural selection. John Murray, London
Darwin C (1908) Illustrated selected works, transl. V. Lepkovsky. Leningrad, Moscow **(in Russian)**
Davitashvili LS (1946) V.O. Kovalevskii. 1842–1883. Izdatel'stvo AN SSSR. Leningrad, Moscow
De Beer GR (1932) Book review: A.N. Sewertzoff "Morphologische Gesetzmässigkeiten der Evolution". Nature 3257(129):490–491
Engels EM (ed) (1995) Die Rezeption von Evolutionstheorien im 19. Jahrhundert. Suhrkamp, Frankfurt am Main
Engels EM, Glick TF (eds) (2009) The reception of Charles Darwin in Europe. Continuum, London
Famintzyn AS (1894) The nearest tasks of biology. Vestnik Europy 5:132–153 **(in Russian)**
Famintzyn AS (1907) On the role of symbiosis in the evolution of organisms. Zapiski Imperatorskoi Akademii Nauk 20(3):1–14 **(in Russian)**
Franz V (1927) Ontogenie und Phylogenie. Das sogenannte biogenetische Grundgesetz und die biometabolischen Modi. Abhandlungen zur Theorie der organischen Entwicklung, vol III. Springer, Berlin, pp 1–51
Gaissinovich AE (ed) (1974) Ill'ia Ill'ich Mechnikov. The letters (1863–1916). Nauka, Moscow **(in Russian)**
Gaissinovich AE (ed) (1988) Letter exchange between A.O. Kovalevsky and V.O. Kovalevsky. Correspondence 1867–1873. Nauka, Moscow **(in Russian)**
Ghiselin M (2009) Darwin: A reader's guide. California Academy of Sciences, San Francisco
Gliboff S (2008) H. G. Bronn, Ernst Haeckel, and the origins of German Darwinism. A study in translation and transformation. The MIT Press, Cambridge
Gliboff S (2012) Monism and morphology at the turn of the 20th century. In: Weir TH (ed) Monism: science, philosophy, religion, and the history of a worldview. Palgrave-Macmillan, New York, pp 135–158
Glick TF (ed) (1988) The comparative reception of Darwinism. University of Chicago Press, Chicago
Glick TF, Shaffer E (eds) (2014) The literary and cultural reception of Charles Darwin in Europe, vol 3–4. Bloomsbury Academic, London
Gourko H, Williamson DI, Tauber AI (eds) (2000) The evolutionary biology papers of Elie Metschnikoff Boston studies in the philosophy of science. Kluwer Academic Publishers, Dordrecht
Haeckel E (1866a) Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Deszendenz-Theorie, Bd I: Anatomie der Organismen. Reimer, Berlin
Haeckel E (1866b) Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformierte Deszendenz-Theorie, Bd 2: Allgemeine Entwickelungsgeschichte der Organismen. Reimer, Berlin
Haeckel E (1868) Natürliche Schöpfungsgeschichte Gemeinverständliche wissenschaftliche Vorträge über die Entwicklungslehre im Allgemeinen und diejenige von Darwin, Goethe und Lamarck in besonderen, über die Anwendung derselben auf den Ursprung des Menschen und andere damit zusammenhängende Grundfragen der Naturwissenschaft. Reimer, Berlin
Haeckel E (1869) The doctrine of organic forms, based on the theory of transformation of species. Compiled by Ernst Haeckel's work of "Generelle morphologie" under the editorship of Ilya Metschnikoff. A. Zalensky, St. Petersburg (in Russian)
Haeckel E (1872) Die Kalkschwämme. Eine Monographie, 3 Bde. Reimer, Berlin
Haeckel E (1874a) Die Gastraea-Theorie, die phylogenetische Classification des Thierreichs und die Homologie der Keimblätter. Jenaische Zeitschrift für Naturwissenschaft 8:1–58
Haeckel E (1874b) Anthropogenie oder Entwicklungsgeschichte des Menschen. Engelmann, Leipzig
Haeckel E (1904) Die Lebenswunder. Gemeinverständliche Studien über biologische Philosophie. Kröner, Stuttgart
Herzen AI (1985) Sochineniia. Mysl', Moscow **(in Russian)**
Hossfeld U, Breidbach O (2005) Haeckel Korrespondenz. Übersicht über den Briefbestand des Ernst-Haeckel-Archivs. VWB-Verlag, Berlin

Hossfeld U, Levit GS (2016) "Tree of life" took root 150 years ago. Nature 540(7631):38

Hossfeld U, Olsson L (2003) The road from Haeckel: the Jena tradition in evolutionary morphology and the origins of "Evo-Devo". Biol Philos 18(2):285–307

Hossfeld U, Watts E, Levit GS (2017) The first Darwinian tree of plants. Trends Plant Sci 22(2):100–102

Ivanov AV (1973) Trichoplax adhaerens—Parenchymula-liked animals. Zoologicheskii zhurnal 52(8):117–131 **(in Russian)**

Junker T, Hoßfeld U (2009) Die Entdeckung der Evolution: Eine revolutionäre Theorie und ihre Geschichte, 2nd edn. Wissenschaftliche Buchgesellschaft, Darmstadt

Kessler KF (1880) The law of mutual aid. Trudy St.-Peterburgskogo obshchestva estestvoispytatelei 11(1):124–136 **(in Russian)**

Khakhina LN (1992) Concepts of symbiogenesis: a historical and critical study of the research of Russian botanists. Yale University Press, New Haven

Kharakhorkin LR (1960) Charles Darwin and the tsarist censorship. Trudy Instituta Istorii estestvoznaniia i tekxniki 31:82–100 **(in Russian)**

Kohn D (ed) (1985) The Darwin heritage. Princeton University Press, Princenton, pp 731–752

Kolchinsky EI (2005) Zu den deutschen Vorläufern von Charles Darwin: Die Quellen des Transformismus in der russischen Biologie. In: Kästner I, Pfrepper R (eds) Deutsche im Zarenreich und Russen in Deutschland: Naturforscher, Gelehrte, Ärzte und Wissenschaftler im 18. und 19. Jahrhundert, vol 12. Shaker Verlag, Aachen, pp 273–285

Kolchinsky EI (2007) Biology in Germany and Russia: The Soviet Union under condition of social-political crises of the first half of the XX century (between liberalism, communism and national-socialism). Nestor-Istoriia, St. Petersburg **(in Russian)**

Kolchinsky EI (2008) Darwinism and Dialectical Materialism in Soviet Russia. In: Engels EM, Glick TF (eds) The reception of Charles Darwin in Europe, vol 2. Continuum, London, pp 522–552

Kolchinsky EI (2011) Peter Simon Pallas: a creationist or a pre-Darwinian evolutionist? (Long-standing debates about Pallas' evolutionary ideas). Stud Hist Biol 3:21–41 **(in Russian)**

Kolchinsky EI (2014) The unity of evolutionary theory in the 20th century divided world. Nestor-Historia, St. Petersburg **(in Russian)**

Komarov VL (1901) Flora of Manchuria. Gerol'd, St. Petersburg **(in Russian)**

Korzhinsky SI (1892) The flora of East European Russia and in its systematic and geographic relationships. Mikhailova and Makushina, Tomsk **(in Russian)**

Kovalev IF (1959) The persecution of the doctrine of Charles Darwin by tsarist censorship. Voprosy istorii religii i ateizma 7:410–421 **(in Russian)**

Kovalevsky AO (1865) The history of development *Anchiphioxus lanceolatus* or *Branchiostoma lubricum*. Tiblen i Ko, St. Petersburg **(in Russian)**

Kovalevsky VO (1873) Osteology *Anchitherium aurelianence*. Cuv. as a form which clarifies the genealogy of the horse *Equus*. Universitetskaia tipografiia, Kiev **(in Russian)**

Kovalevsky VO (1950–1960) A collection of scientific papers, 3 vols, Izdatel'stvo AN SSSR, Moscow **(in Russian)**

Kovalevsky AO (1951) Selected works. Izdatel'stvo AN SSSR, Moscow **(in Russian)**

Kropotkin PA (1907) Mutual aid as factor of evolution. Znanie, St. Petersburg **(in Russian)**

Kutschera U (2016) Haeckel's 1866 tree of life and the origin of eukaryotes. Nat Microbiol 1(8):16114

Kutschera U, Niklas KJ (2005) Endosymbiosis, cell evolution, and speciation. Theory Biosci 124(1):1–24

Lesgaft PF (1889) Heredity. Russkoe bogatstvo 11:68–120

Levit GS (2007) The roots of Evo-Devo in Russia: is there a characteristic "Russian tradition"? Theory Biosci 126(4):131–148

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 14:9–25

Levit GS, Hossfeld U (2017) Major research traditions in twentieth-century evolutionary biology: the relations of Germany's Darwinism with them. In: Delisle R (ed) The Darwinian tradition in context. Springer Nature, Cham, pp 169–193

Levit GS, Krumbein W (2007) Zur Diskussion der Symbiogenesetheorie unter sowjetischen Zoologen und Biologietheoretikern der ersten Hälfte des 20 Jh. In: Geus A, Höxtermann E (eds) Evolution durch Kooperation—Zur Entstehung der Endosymbiose-Theorie in der Zellbiologie. Reprints und Kommentare. Basilisken-Presse, Marburg an der Lahn, pp 477–503

Levit GS, Meister K (2006) The history of essentialism vs. Ernst Mayr's "Essentialism Story": a case study of German idealistic morphology. Theory Biosci 124(3–4):281–307

Levit GS, Polatayko SV (2013) At home among strangers: Alfred Russel Wallace in Russia. Theory Biosci 132:289–297

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 Part B MDE 302(4):343–354

Levit GS, Meister K, Hoßfeld U (2008) Alternative evolutionary theories from the historical perspective. J Bioecon 10(1):71–96

Levit GS, Levit I, Levit GS, Hossfeld U, Olsson L (2014) Creationism in Russia and its neighbors. In: Blancke S et al (eds) The history of Creationism in Europe. Johns Hopkins University Press, Baltimore, pp 162–179

Levit GS, Hossfeld U, Olsson L (2015a) Adolf Naef and Alexei Sewertzoff: revising Haeckel's biogenetic law. Hist Philos Life Sci 36(3):357–370

Levit GS, Reinhold P, Hossfeld U (2015b) Goethe's "Comparirte Anatomy" as a foundation for the growth of theoretical and applied biomedical sciences in Jena. Theory Biosci 134(1–2):9–15

Manoilenko KV (2009) Pros and cons: the attitude of honoring the memory of Charles Darwin in 1909. Stud Hist Biol 1(1):103–107 **(in Russian)**

Margulis L (1970) Origin of Eukaryotic cells. Evidence and research implications for a theory of the origin and evolution of microbial, plant and animal cells on the Precambrian earth. Yale University Press, New Haven

Mayr E, Provine W (eds) (1998) The evolutionary synthesis: perspectives on the unification of biology. Harvard University Press, Cambridge

Menzbir MA (1879) Prosimians. Priroda i okhota 3(8):59–67 **(in Russian)**

Menzbir MA (1885) Advances in biology and in similar sciences. Russkaia mysl 4(2):37–70 **(in Russian)**

Menzbir MA (1897) Ceylon's Vedda and the fossils of humanoid creatures from the island of Java (Zooanthroponosis essay). Russkaia mysl 8(3):129–163 **(in Russian)**

Menzbir MA (1900) The main representatives of Darwinism in Western Europe. Ernst Haeckel Russkaia mysl 6(2):1–17 **(in Russian)**

Mereschkowsky C (1905) Über Natur und Ursprung der Chromatophoren im Pflanzenreiche. Biol Zentralbl 25(18):593–604

Mereschkowsky KS (1909) The theory of two plasmas as the basis of symbiogenesis, a new doctrine about the origin of organisms. Tipografia Imperatorskogo Universiteta, Kazan

Metschnikoff II (1878) The Struggle for existence in a broad sense. Vestnik Evropy 7:9–47 **(8:437–483; in Russian)**

Metschnikoff II (1898) The immune system. P.P. Soikin, St. Petersburg **(in Russian)**

Metschnikoff II (1946) Pages of memories. Izdatel'stvo AN SSSR, Moscow **(in Russian)**

Metschnikoff II (1956) Selected works. Uchebno-Pedagogicheskoje Izdatelstvo, Moscow **(in Russian)**
Metschnikoff II (1950) Selected biological works. Izdatel'stvo AN SSSR, Moscow **(in Russian)**
Metschnikoff II (1960) Akademicheskoe sobranie sochinenii, vol 4. Izdatel'stvo AN SSSR, Moscow **(in Russian)**
Müller F (1864) Für Darwin. Wilhelm Engelmann, Leipzig
Oken L (1836) Lorenz Oken's works, translated from German. General natural history for all classes [vseobschaja estestvennaja istorija dlya vsekh sostojanij], vol 5. Zoologija, Sankt-Petersburg
Oparin AI (1924) Origin of life. Moskovskii rabochii, Moscow **(in Russian)**
Oparin AI (1941) Origin of life on earth. Leningrad: The Academy of Sciences, Moscow **(in Russian)**
Pachoskii IK (1914) Kherson's flora. S.N. Ol'khovikova and S.N. Khodushina, Kherson **(in Russian)**
Pallas PS (1766) Elenchus zoophytorum sistens generum adumbrationes generaliores et specierum cognitarum succinctas descriptiones cum selectis auctorum synonymis. Petrum van Cleef, Hagae Comitum
Pallas PS (1784) Memoire sur la variation des animaux; Premiere partie, lue ál' Assemblee publique du 19 September 1780, en presence de Msgr. Le Prince Royal de Russe. Acta Acad Sci Imrerialis Petropolitanae 2:69–102
Pisarev D (1864) Progress in the realm of animals and plants. Russkoje Slovo 4:1–52 **(in Russian)**
Poliansky II (ed) (1955) The A.O. Kovalevsky's letters to I. I. Metschnikoff. Izdatel'stvo AN SSSR, Moscow **(in Russian)**
Raikov BE (1950) Comments to K.E. von Baer's biography. In: Baer KM (ed) Avtobiographija. Izdatel'stvo AN SSSR, Moscow **(in Russian)**
Raikov BE (1961) Karl Baer, his life and works. Izdatel'stvo AN SSSR, Moscow **(in Russian)**
Raikov BE (1969) German biologists-evolutionists before Darwin. Izdatel'stvo AN SSSR, Leningrad **(in Russian)**
Ricci F (2007) Ritter, Tod und Eros: die Kunst Elisar von Kupffers (1872–1942). Böhlau Verlag, Weimar
Richards RJ (2008) The tragic sense of life: Ernst Haeckel and the struggle over evolutionary thought. The University of Chicago Press, Chicago
Richards RJ (2018) Ernst Haeckel: a dream transformed. In: Harman O, Dietrich MR (eds) Dreamers, visionaries, and revolutionaries in the life sciences. University of Chicago Press, Chicago
Rieppel O (2016) Phylogenetic systematics: Haeckel to Hennig. CRC Press Publisher, Boca Raton
Rolle F (1863) Charles Darwins Lehre von der Entstehung der Arten im Pflanzen- und Thierreich in ihrer Anwendung auf die Schöpfungsgeschichte dargestellt und erläutert. Joh. Christ. Hermann'sche Verlagsbuchhandlung, Frankfurt am Main
Rolle F (1864) Charles Darwin's doctrine on the origin of species in the plant kingdom and the animal kingdom applied to the history of the world creation world creation. M.O. Wolf, St. Petersburg **(in Russian)**
Samokish AV (2009) Charles Darwin and the Imperial Academy of Sciences. Documentary evidence. Stud Hist Biol 1:95–103 **(in Russian)**
Schmalhausen II (1969) Problemy darwinizma. Nauka, Leningrad **(in Russian)**
Schtraikh S Ia (1940) From the correspondence of the brothers Kovalevsky. Sovetskaia Nayka 7:99–120
Seidlitz GV (1871) Die Darwin'sche Theorie. Elf Vorlesungen über die Entstehung der Thiere und Pflanzen durch Naturzüchtung. Mattiesen, Dorpat
Seidlitz GV (1875) Die Darwin'sche Theorie. Elf Vorlesungen über die Entstehung der Thiere und Pflanzen durch Naturzüchtung. 2. Vermehrte Auflage. Wilhelm Engelmann, Leipzig
Semenov-Tian-Shansky AP (1910) The taxonomic boundaries of the species and its subdivisions/Zapiski Imperatorskoi Akademie nauk 25.1:1–29 **(in Russian)**
Senkovskii OI (1837) Literary chronicle. Libr Read 14:74–76 **(in Russian)**
Severtzov AS (1970) On the evolution of ontogenesis. J General Biol 31(2):222–235
Sewertzoff AN (1910) Evolution and embryology. Tipografiia Moskovskogo Universiteta, Moscow **(in Russian)**
Sewertzoff AN (1912) Essays on the theory of evolution. Individual development and evolution. Tipografiia universiteta imeni Vladimira, Kiev **(in Russian)**
Sewertzoff AN (1914) Modern problems of evolutionary theory. Nauka, Moscow **(in Russian)**
Sewertzoff AN (1925) The main directions of the evolutionary process. Izdatel'stvo AN SSSR, Moscow **(in Russian)**
Sewertzoff AN (1931) Morphologische Gesetzmäßigkeiten der evolution. Gustav Fischer Verlag, Jena
Sewertzoff AN (1939) Morphological patterns of evolution Izdatel'stvo AN SSSR. Moscow **(in Russian)**
Sewertzoff AN (1949) Sobranije sotchinenij, vol 5. Izd. Akad. Nauk, Moscow **(in Russian)**
Sideleva VG (2017) Contribution of Karl Fedorovich Kessler (1815 – 1881) to fish systematics and faunal research. J Ichthyol 57(3):473–483
Timiryazev KA (1864) The Darwin's book, its critics and commentators. Otechestvennye Zapiski Note 155:880–912 **(156:650–685; 157:659–682; in Russian)**
Timiryazev KA (1865) A brief essay of the Darwin's theory of Darwin. Typ. AA. Kraewskii, St. Petersburg **(in Russian)**
Timiryazev KA (1897) Plant and solar energy. Grosman and Knebel, Moscow **(in Russian)**
Timiryazev KA (1937) Darwinism and selection. Ogiz-Selkhozgiz, Moscow **(in Russian)**
Timiryazev KA (1939) Selected works, vol 8. Sel'khozgiz, Moscow **(in Russian)**
Timiryazev KA (1949) Selected works, vol 4. OGIZ-Sel'khozgiz, Moscow **(in Russian)**
Todes DP (1978) V.O. Kovalevskii: the genesis, content, and reception of the paleontological works. Stud Hist Biol 2:99–165
Todes DP (1987) Darwin's Malthusian Metaphor and Russian Evolutionary Thought, 1859–1917. Isis 78(294):537–551
Todes DP (2009) Global Darwin: contempt for competition. Nature 462:36–37
Turgenev I (1862) Fathers and sons. Tipografija Gracheva, Moscow
von Baer KE (1828) Über Entwickelungsgeschichte der Thiere. Beobachtung und Reflexion, vol 1. Bornträger, Königsberg
von Baer KE (1864) Reden, gehalten in wissenschaftlichen Versammlungen und kleinere Aufsätze vermischten Inhalts, Th. 1 Reden. Schmitzdorff, St. Petersburg
von Eichwald KE (1821) Ideen zu einer systematischen Oryktozoologie oder über verändert und unverändert ausgegrabene Thiere. Mietau, Steffenhagen
von Eichwald KE (1829–1831) Zoologia Specialis. Josephi Zawadskii, Vilnae, pp 1–3
Williams DM, Ebach MC (2008) Foundations of systematics and biogeography. Springer, New York
Uschmann G (1956) Die Promotion von W.O. Kowalevsky in Jena, ein Beitrag zur Geschichte der evolutionistischen Paläontologie. EHH, G. Uschmanns Nachlass: B. 11, 15–17 [Hefter: Vorträge III]