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ORIGINAL PAPER

From molecules to the biosphere: Nikolai V. Timoféeff-Ressovsky's (1900–1981) research program within a totalitarian landscape

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Abstract Nikolai Vladimirovich Timoféeff-Ressovsky was one of the key figures in the Synthetic Theory of Evolution. Living and researching under what was arguably the two most powerful and cruel totalitarian regimes in human history, the Third Reich and the Soviet Union, Timoféeff-Ressovsky succeeded in developing an ambitious research program aiming to explain evolution on all major levels, from the molecular-genetic, the populational, and the biogeocenotic to the level of the entire Biosphere. Yet his scientific biography remains largely unwritten and his role under totalitarianism, especially in Nazi Germany, remains highly controversial. Here we approach the problem of his hypothetical cooperation with Nazi authorities examining both the crucial episodes of his biography and summarizing the development of his research program. We conclude that the key decisions he made reflected the specificity of his research program that was focused on the fundamental questions of evolutionary biology.

Keywords Timoféeff-Ressovsky · Evolutionary Synthesis · Nazi Germany · Molecular genetics · The Biosphere theory · Biogeocenosis · Radiobiology

This article is dedicated to the memory of Wolf-Ernst Reif, a pioneer of the rediscovery of the German Evolutionary Synthesis.

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Introduction

The biologist Nikolai Vladimirovich Timoféeff-Ressovsky (henceforth TR) is one of the most striking personalities in twentieth-century science (Paul and Krimbas 1992). On the one hand, his name stands for groundbreaking research in the fields of population genetics, radiation biology, evolutionary biology, and evolutionary developmental biology. On the other hand, he is still often associated with the propagation of eugenic ideas under National Socialism and the facilitation and military application of atomic energy under communism. Until very recently, studies of his life have been hindered by language barriers, the Cold War, and inaccessible archives. Materials discovered in the archives of the former East German Security Service ("Stasi") and FSB[1] as well as the latest investigations into the general context of the relationship between science and society sheds new light on TR's life and scientific achievements (e.g., Rokityansky et al.). Many episodes of TR's biography have been quite thoroughly reconstructed during the last decade. The questions that remain open are nevertheless significant. The question of why TR made no efforts to move to the USA from Nazi Germany is one of the crucial issues in his biography. In the field of theory, one of the most important questions is whether TR consequently developed a certain research program following an inner logic of this program or he simply followed the directives of the totalitarian regimes with which he was confronted throughout his entire professional life. We will approach these two interconnected questions in this article. We claim that, implicitly or explicitly, TR pursued the objective of creating a multi-level theory of evolution,

[1] FSB—Federal Security Service, contemporary Russian intelligence service, the successor of the KGB.

extending from molecular biology to biosphere theory. It is not our objective here to reconstruct TR's entire scientific biography; we will concentrate on its crucial episodes, paying most attention to his German period.

In addition, TR's scientific biography provides a good example for discussing the problem of the personal responsibility of a scientist toward society, including the question of the limits of personal responsibility. TR lived in Tsarist Russia as a child and was influenced by the Russian Revolution as a student. After he came to Germany, he experienced the deterioration of the Weimar Republic and the National Socialists' accession to power in 1933. This latter regime facilitated TR's most successful and original phase as a scientist, but also executed his son. Afterwards, TR experienced the most brutal excesses of Stalinism and Lysenkoism. During the so-called Khrushchev's Thaw (after the Soviet leader Nikita Khrushchev) TR was granted amnesty and during the Brezhnev era he participated in the reconstruction of Soviet genetics and in the expansion of the Soviet nuclear program. In 1988 the Soviet authorities turned down a request to rehabilitate TR. However, 3 years later a leading Soviet justice official announced that the accusations made against TR in 1946 were baseless. Ultimately, at the end of 1991, 10 years after his death and during Gorbachov's *glasnost*, TR was finally officially rehabilitated and became one of the most influential—one might even say canonized—historical figures in Russian science (Fig. 1).

Timoféeff-Ressovsky's early years in science

When Lenin died in 1924, a well-known brain researcher at the time, Oscar Vogt (1870–1959) of Berlin, was asked by the Soviet government to study Lenin's brain. During the investigation, Vogt asked the Soviets to send a young Russian geneticist to Germany so that he could work at Vogt's Kaiser Wilhelm Institute for Brain Research in Berlin-Buch. Nikolai K. Koltzoff (1872–1940), head of the research institute for experimental biology in Moscow, recommended a young supplementary research associate; this talented young researcher was TR.[2] Born on the 20th of July, 1900, in Moscow, TR studied biology there until the outbreak of the October Revolution, when he left university and joined the Red Army. In 1922 he returned to Moscow University, where he was taught the foundations of zoology, evolution, systematics, and the methods of comparative morphology. Of special importance, however, was his education in population genetics with Sergei S. Chetverikov (1880–1959) and his participation in the discussion club SOOR (abbreviation for "Joint Crying on Drosophila"), where TR received practical training in experimenting with *Drosophila* and was 'infected' by the SOOR's atmosphere of open discussions (Babkov and Sakanjan 2002, pp. 24–30). Through SOOR TR learned to work in a team on a scientific problem. The specificity of the method used was an open, exceedingly interdisciplinary, non-hierarchical (disregarding titles and achievements in science), informal, and intellectually aggressive discussion. It was this kind of intellectual aggressiveness that sometimes confused his German colleagues; thus, a German zoologist and evolutionary biologist Victor Franz noted: "Dealing with colleagues, he is often full of himself and arrogant in manner; in doing that he appears offensive, as I experienced myself."[3]

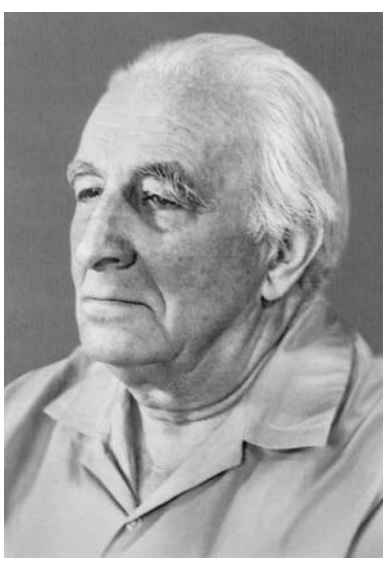

Fig. 1 N.W. Timoféeff-Ressovsky during his last years of his life (courtesy of Nauka press and Ivanov V.I. & Ljapunova N.A.)

Although TR had no formal academic degree (he finally received a Doctor of Science—Habilitation—in 1964), he moved with his family to Berlin in 1925, where he worked first as an assistant, and then, from 1931, as head of the genetics and biophysics divisions, and then in 1937 as director of an independent institute (formally: The Division of Genetics ["genetische Abteilung"]).

During this period, TR became well known, primarily due to his mutation research, which was based on atomic physics, and brought him early on into contact with young physicists. Perhaps the most famous result of this collaboration was the 1935 "three-man-work" with Max Delbrück (1906–1981), the Nobel Laureate for Physics in 1969, and Karl G. Zimmer (1911–1988). This publication showed that genes were molecules and inspired Erwin Schrödinger's (1887–1961) book, *What is Life*.

[2] According to the recommendation letter signed by Koltzoff, TR was at that time a supplementary associate ("vneshtatnyj sotrudnik") of the Institute and a teacher of the "worker's faculty": Babkov and Sakanjan (2002, p. 42).

[3] Archive of the Jena University (UAJ), Best. U, Abt. 10, Nr. 48.

No less important was his early contribution to evolutionary theory. As Ernst Mayr recalled, after he had come to the American Museum of Natural history in 1931, he began an intensive reading of literature on evolutionary theory, including TR's papers on geographic variation of genes distribution in the local populations of insects. In Europe TR played the same role, Mayr argued, as Dobzhansky did in the USA (Mayr 1993). TR, Mayr continued, was one of the factors determining the specificity of the continental synthetic movement. Yet TR's research program achieved its maturity toward the end of the 1930s.

Timoféeff-Ressovsky in the Third Reich

In 1932, TR spent several months in the newly established Cold Spring Harbor laboratory, sponsored by the Carnegie Foundation. The fact that TR was invited to the Cold Spring Harbor lab strengthened his position in Germany temporarily. However, the end of the Vogt era at the Brain Institute and the coming to power of a new director, Hugo Spatz (1936), made TR's situation precarious. Spatz expressed his views in a letter addressed to TR, where he claimed that the Division of Genetics was a "foreign body" within the Institute for Brain Research and recommended to TR that he should apply for a position at the KWI for Biology (KWIB). There was a position there, which remained vacant after the emigration of Jewish geneticist Richard Goldschmidt to the USA (Schmaltz 2005, p. 253). Yet the Director of KWIB, Fritz v. Wettstein (1895–1945), preferred Alfred Kühn. Kühn and Wettstein were both champions of cytoplasmic inheritance (e.g., Wettstein 1934) and it appears that TR's research program did not fit well into Wettstein's agenda.

In the middle of the 1930s, TR's American colleagues, worrying about TR's position in National Socialist Germany, offered him a position at the Carnegie Institution (via the Rockefeller foundation). In the summer of 1936, the Rockefeller foundation required an immediate answer. This offer from the USA, however, significantly strengthened TR's position in Germany and in June, 1936, Rudolf Mentzel, as a representative of the Ministry for Science and Education [*Reichsministerium für Wissenschaft, Erziehung und Volksbildung*], offered TR an independent budget within the KWI for Brain Research. As a result, TR turned down the offer from the USA. Considering the strengthening of national-socialists in all parts of German society and the mass emigration of German intellectuals, TR's decision appears enigmatic. Why did he stay in the totalitarian state, despite the growing evidence of its criminal nature?

Yakov Rokityanskij, based on the personal archive of Vassily Babkov, found a possible explanation of TR's decision. This is a note of a Rockefeller Foundation associate, G.M. Miller, who summarized TR's reasons for not moving to the USA (Rokityanskij 2003). Miller mentioned four reasons. First, TR felt responsible for his research group (five scientists and six technical assistants); second, TR thought that he would have much less technical assistance in the USA; third, his children, he argued, had already changed their cultural environment once, when moving to Germany; and, lastly, the prestige of a professor, he believed, was lower in the USA than in Germany. These arguments seem plausible, considering that around that time the *Kaiser Wilhelm Gesellschaft* (KWG) was an established scientific institution with a reputation as a hotbed for budding Nobel laureates.

Following his decision to remain in Germany, TR de facto became director of an independent research institute, the Division of Genetics, which was subordinated directly to the KWG. In the same year (1936), TR's Division obtained a minor neutron generator, a crucial device for the planned molecular-genetic experiments (Schmaltz 2005, p. 256). In this way, the German offer was much more attractive for TR, considering the experimental and interdisciplinary character of his studies, which implied expensive technical equipment and uniquely trained scientists.

Yet, hypothetically there was another possibility for TR to escape Hitler's regime: returning to the USSR. Indeed, in 1937 the Soviet Embassy strongly "advised" TR to return to Moscow. However, his teacher Koltzoff had already warned him in 1933 against an attempt to come back to the USSR. In 1937, political repressions was at its apogee, and a return would doubtlessly mean for him "the most terrible and complex way to commit suicide" as Koltzoff emphasized in his letter to TR (Babkov and Sakanjan 2002, p. 212). Predictably, TR turned down an "offer" from the USSR. The next year, National Socialist officials pressured TR to take German citizenship. This he refused, arguing that he was born Russian and that changing his citizenship was a serious decision, although it would make his life and work in Germany much easier.

Nevertheless, in 1938 TR became a scientific member of the KWG, a designation reserved for the Society's outstanding scientists. Two years later he was elected a member of the famous *Leopoldina Academy* in Halle. In these years TR achieved the peak of his scientific career in Germany.

Was Timoféeff-Ressovsky involved into the collaboration with the Nazi authorities?

After the *Perestroyka* in the Soviet Union, TR was not only rehabilitated but, due to the efforts of his biographers, became an icon of Soviet science. Despite the pressures of two totalitarian regimes, he became one of the leading figures in international science. Being an extremely charismatic personality and a talented narrator, TR gave his biographers the best chances for reconstructing his life story in terms of 'heroes' and 'villains.' A debate broke out between those who saw TR as a criminal[4] (Office of the General Military Prosecutor) or as an amoral person (Nikolai Dubinin) and those who claimed that TR met the highest ethical standards at all times.[5] Thus, in 1989 an influential Soviet geneticist Nikolai Dubinin (1907–1998) published a letter in a popular literary journal *Nash Sovremennik* accusing TR of amorality: "I always supported that Timoféeff's work in Germany between 1941 and 1945—when Germany invaded the USSR with the whole power of its military machine—was amoral." After the beginning of the Second World War, Dubinin continued, Timoféeff had a possibility to leave Germany, but he "stubbornly held on his place in Berlin" (quoted from Dubinina and Ovchinnikova 2006, p. 346).

The best example of a strictly pro-TR biography is the book of Babkov and Sakanjan. Here TR's German period appears as an attempt to preserve "islands of stability and decency" in the German scientific-cultural landscape (Babkov and Sakanjan 2002, p. 204). They emphasize that TR was one of the few scientists in Germany who helped individuals threatened and persecuted by the National Socialists: for example, he protected Soviet 'slave laborers' [Zwangsarbeiter]. The memoirs of his friend, the artist Oleg Zinger (1909–1997) are instructive in this respect. Zinger recalled that TR, though a totally "apolitical person," "was shocked by the 'inhumanity' taking place around [him]" (Zinger 1990). Being a person of action "Koljuscha [one of TR's nicknames—*auth*.] helped everyone and did everything he could! Berlin-Buch became an 'isle of life-saving' for the Soviet prisoner-of-war biologists, the French, the students etc.; Koljuscha somehow succeeded in settling all of them and protecting them from the authorities, from this awful Nazi, who made terrible things of which we were totally unaware at that time, although nobody believes us in this respect now." Zinger insists that none of them (TR's friends) were aware of Nazi crimes: "It was impossible at that time, in Germany, to gain an understanding of anything; there were Nazis somewhere, but we knew little about them" (Zinger 1990).

Interpretations like this are widespread in contemporary biographical reconstructions of TR's life.

At the same time, attempts to show that TR collaborated with Nazi officials also continue. Thus, very recently, the German historian of science Florian Schmaltz, offered a new account of TR's German period based on intensive archival research and opposed to the earlier investigations such as those by Hoßfeld (e.g., Hoßfeld 2001). Schmaltz proceeds from the assumption that German scientists of TR's format (de facto the head of a KWI institute), must have participated in the German scientific and social–political system to a significant extent. In his voluminous tome *Kampfstoff-Forschung*, Schmaltz devotes a chapter to investigations into TR's role in the Kaiser-Wilhelm Society's cooperation with the Nazi regime (Schmaltz 2005). He develops his argument by analyzing archival records, which reveal, for example, the details of TR's grant applications submitted to the *German Scientific Council* (DFG). The very character of the application process, Schmaltz argues, implied a scientist's own initiative to a significant extent. TR's Division of Genetics conducted, among others, respirator studies, which were undoubtedly of military significance. The same neutron generator which TR used for the fundamental investigations into the molecular structure of genes was ideally suited for testing the respirator filters using the method of isotopic markers. The structure and the equipment of TR's laboratory, as well as the expertise of its members, determined the very character of the research conducted in TR's Division. In this respect, the studies of the laboratory relevant to the army were not simply a result of the forced compromise with the social–political environment, but rather followed a sophisticated developmental pattern shaped by the interrelations of two actively interacting agents: science and society. This picture contradicts the received passive/proactive dichotomy implying a violent totalitarian society and an "asocial" scientist falling prey to the aggressive regime. In other words, in order to be integrated into the armaments research, there must have been a strong scientist's will to be integrated and to pool resources from the armament industry. According to Schmaltz, TR's Genetics Division demonstrated such a will.

Schmaltz distinguishes several stages in the Division's integration into the armament research. The first stage followed the dissociation of the Division from the KWI for Brain research. A new administrative structure gave TR more autonomy, while pushing him, at the same time, to a "closer cooperation with the institutions established by the Nazi regime, such as RFR[6] and the four-year-plan

[4] TR was accused for co-operation with the Nazi authorities and for contribution into the "completion of the military power of the fascist Germany," for example, Iljin and Provorotov (1989).

[5] E.g., official appeals and publications of his pupil Ivanov (1990). See also an official appeal to the Office of General Military Prosecutor: BStU, MfS HA IX/11 RHE25/87 SU. Bd. 119.

[6] RFR: Reichsforschungsrat was established in 1937 for the coordination of scientific studies. RFR had a clear emphasis on armament research, for instance, supported various the SS research projects.

bureaucracy [Vierjahresplanbürokratie]" (Schmaltz 2005, p. 289). TR was among those who succeeded in getting additional resources from the RFR. A member of his group, Karl Zimmer, undertook a research trip to Eindhoven (Philips), where he was trained to work with radioactive isotopes. This trip was financially supported by the RFR as well.

The next stage of integration began with the establishment, within TR's Genetic Division, of a branch office of the *Auergesellschaft* (1938). The head of the branch office became Hans-Joachim Born who, jointly with Zimmer, assembled the imported (from Holland, *Philips*) neutron generator. The generator remained the property of the *Auergesellschaft*. In 1939, the neutron generator was fully operational, and the process of integration entered into the third phase: the generator made it possible to conduct both radio-biological experiments and respirator filter studies. The cooperation of TR's Genetic Division with the armament relevant industry, Schmaltz concludes, was not of a sporadic character; on the contrary, it was a steady and constant cooperation based on the joint use of the neutron generator (Schmaltz 2005, p. 290).

Schmaltz's argument provides a good opportunity to analyze the very notion of "cooperation," which, in this case, will be closely coupled with the problem of personal moral responsibility.

One can distinguish three different aspects in the hypothetical involvement of TR and his Division with armament research. The first aspect is a structural one: the Genetic Division of KWI, as an autonomous scientific institution within the administrative structures of the Third Reich, was on its way to integrating itself into the preexisting system of relationships between science, industry, and political authorities. It is not surprising, however, that a successful research institution became integrated into this system as its constituting part. The sole fact of integration into the system does not necessarily mean that a scientific unit functions as an obedient instrument of a state power. The very nature of science provides it with autonomous fundamental targets. It is, for example, not just chance that the Evolutionary Synthesis developed along the same lines in all three relatively isolated countries: Germany, the USSR, and the USA.

The second aspect concerns the possible criminal character of the existing integration, if approached from the viewpoint of today's common values. The fact of the integration of a scientific institution into a given system of financial and structural stimuli does not routinely lead to any value judgment. Many institutions and economic units established by the NS regime or existing under this regime were ultimately incorporated into the post-war societies. Such industrial giants as *Osram*, *Krupp*, and the very system of KWI were all reintegrated into the liberal political–economical system in West Germany.

Ultimately, the third and final aspect concerns the personal responsibility of a scientist for being a part of a certain institution or social–political system, and for the decisions he/she makes. On this level, one can pose a question as to how somebody made use of the scientific and personal autonomy granted within an existing structure. This is also the level of possible moral accusations.

Considering the first aspect, a significant level of integration of the Genetics Division into the given institutional structure seems inevitable. The second and the third aspects, however, imply a question of scientific and personal responsibility within the field of choice. For TR's Division, the field of potential choices spread from participation in the atom project up to the eugenics experiments with humans (there is evidence that TR declined such suggestions). Within his field of choices, TR reduced the morally doubtful cooperation with the armament industry to a possible minimum. He personally can be reproached only for the participation in the respirator studies. There are no other reproaches which can be documented.

TR's Division was indeed involved into the respirator studies [Gasmaskenforschung], which was already well-known at the time of his rehabilitation.[7] In 1941 the journal *Angewandte Chemie* [*Applied Chemistry*] published his article based on a lecture given in Dresden on April, 5th 1941 (Timoféeff-Ressovsky 1941). In this article, TR examines the prospects of applying the neutron generator, and especially the indicator method based on the production of artificial radioactive isotopes, to various fields of biology and chemistry. Although the article concentrates on applying indicators in physiology, morphology, genetics, and microbiology, TR devotes a small paragraph to the utilization of the same method for testing the respirator filters. These 20 lines in fine print represent a minimum of possible compromises with an invisible co-author, the State. The same respirator example can be found in several other publications where TR appears as a co-author of Karl Zimmer and Hans Born (e.g., Born et al. 1941).

Beyond the respirator issue, there are no further documented accusations against TR. Furthermore, there is no evidence that TR embraced National Socialist ideology, supported the National Socialist regime, or even made racist remarks.

An ethical system is conceivable in which TR could be accused even for his modest collaboration with the Nazi institutions and for not preferring a research position in a liberal society. Yet, if developed, this ethical system would be incriminatory for the majority of scientists in the history of the twentieth century, insofar as they either collaborated with one of the multiple totalitarian regimes or contributed

[7] For example: *Priroda*, 1990, 9:81–84.

to well-known examples of the misuse of technology in the liberal world.

Timoféeff-Ressovsky in the Soviet Union

In the last weeks of the Third Reich, TR made every attempt to convince his friends and colleagues to remain in the Soviet occupation zone. However, his hope that the political situation in Berlin under the Red Army would change for the better was dashed after only a few months. The Soviet authorities began the deportation of scientists related to the German Atomic Project into the USSR. One of the deported scientists was a Russian-born nuclear chemist, member of the *Auergesellschaft*, and TR's friend Nikolaus Riehl (Riehl and Seitz 1993). Riehl and his staff, including their families, were conveyed to Moscow as early as July 1945.

TR was one of many scientists meriting forceful deportation/repatriation to be put to use in the Soviet atomic project and in related fields. He was arrested on September 13, 1945 and in July 1946 accused of anti-Soviet activity and refusal to return to the USSR in 1937 (*The Sentence of the Supreme Courte* in: Rokityanskij 2003, pp. 461–462). TR himself saw the reason of his arrest as a lack of coordination within the NKVD[8] structures (Timoféeff-Ressovsky 2000, p. 350). Soviet geneticist Valentin Kirpichnikov claimed in an interview to a historian of biology, Eduard Kolchinsky, that both the Interior Ministry and Igor Kurchatov's atomic research institutions made efforts to find TR in the NKVD system. Ultimately, he began working in "Kurchatov's system" and organized the only post-1948 genetic laboratory in the USSR[9]; however, at that time "nobody knew that TR is alive and resides in the USSR; this we found out only in 1953" (Kolchinsky 2003).

In the meantime, after a short stay in the Moscow transfer camp *Butyrka*, where TR met the future Nobel Prize Winner Alexander Solzhenitsyn (1946), he was interned in the GULAG (Russian abbreviation for 'The Chief Administration of Corrective Labor Camps and Colonies,' a system of forced labor camps). TR landed in one of the most dreadful camps, the Karaganda "death camp" (Karlag) in Central Kazakhstan. The humiliating conditions TR experienced in the camp, accompanied by chronic starvation, resulted in progressive blindness and in extreme memory loss. However, he was released after 107 days in Karlag and ultimately brought to a secret military research center *Sungul* in South Ural (Rokityanskij 2003), where he established a laboratory for radiation biology. The core members of his international and interdisciplinary research group "followed" him to Sungul: the biophysicist Karl Zimmer, the radiation biologist Alexander Catsch, the radiochemist Hans-Joachim Born, and the zoologist Sergej Zarapkin.

TR was released in 1951 and, in 1955, two years after Stalin's death, granted amnesty and moved to Swerdlowsk, where from 1955 to 1964 he built up a Division of Radiobiology and Biophysics within the biology institute connected to the Soviet Academy of Sciences and led numerous summer courses at the nearby experimental station on the Miassovo Sea. In 1964 he finally returned to the area around Moscow. In Obninsk, a 100 km from the capital, he founded a Division of Genetics and Radiobiology at the Institute for Radiology and until 1971 was also active at the Institute for Medical-Biological Problems of the Academy of Sciences in Moscow. TR died on March 28, 1981 in Obninsk.

During the long-lasting investigation, TR himself, his co-workers, relatives, friends, and colleagues were thoroughly interrogated by the Soviet Secret Service (NKVD). The interrogation acts from the KGB (and its predecessor organizations, MGB and NKVD) and the Stasi[10] shed an additional light on TR's research activity in Berlin, including hypothetical collaboration with the German authorities, and also help to explain his decision to remain in the Soviet occupation zone.

Of course there are problems inherent in sources like the protocol of an interrogation at the hands of Soviet officials, where scientists like TR and his German colleagues could be expected to say what they thought was in their best interests. However, when used cautiously and compared with other available sources, they can fill the holes in existing history and shed new light on old interpretations.

The transcripts of these postwar interrogations by the Soviet officials reveal that TR had not been involved in military research important for the German war effort. A kind of military research was done at his institute, but by his colleagues Karl Zimmer and Hans Born in conjunction with the Reich Research Council, the Air Force, and the Army. Zimmer provided his Soviet questioners with the most vivid account, but that was to be expected. A German, Zimmer did not have to fear being accused of treason for working for Germany. Moreover, his immediate future was secure in the sense that he was on his way to work on the Soviet atomic bomb.

According to Zimmer, research at TR's Institute under National Socialism included: investigating the biological effect of neutron radiation, measurements of the length and intensity of neutron radiation, methods for manufacturing radioactive elements, the artificial production of radium,

[8] NKVD—People's Commissariat of Internal Affairs, the Soviet secret service responsible, among others, for political repressions.

[9] 1948 is the year of apogee of Lysenkoism in the USSR.

[10] BStU, MfS HA IX/11, RHE 25/87 SU.

the effect of X-rays on the human organism, paints for the illumination of instruments in airplanes, using X-rays as a weapon against "enemy airplanes," the effect of cosmic radiation on pilots flying at high altitudes, and methods for protecting researchers from radiation.[11]

In an interrogation from October 24, 1945, Zimmer testified that, beginning in 1939 for the Brain Research Institute, and in 1942 for TR's Institute for Genetics, various types of war work were carried out, including work on "weapons of mass destruction," destroying enemy air forces with X-rays, which was a rather fantastic scenario. Born revealed additional incriminating information when he described radiation experiments on animals, on voluntary human subjects (including Born himself), and on two human corpses. Thus, Soviet officials found ample material to conclude that TR's institute had supported the German war effort. However, none of these resulted in an "invention" that was militarily significant or dangerous to humans.

The transcriptions of the interrogations of TR, Zimmer, and Born make it clear that the Soviet Security Service was mainly interested in military research or experiments with radium and uranium. The biophysical research under National Socialism was thereby supposed to benefit Soviet science.

The former East German archives also document the desperate struggle of a father, TR, fighting for the life of his son Dmitry. This was not, as sometimes has been claimed, an attempt to curry favor or to make contacts with leading National Socialists. Dmitry had been arrested by the Gestapo for attempted resistance to the National Socialist state. TR tried everything in order to free his son, including requests for help from leading SS officers, politically influential colleagues, and his superiors in the Kaiser Wilhelm Society. These efforts failed when Ernst Kaltenbrunner, head of the SS Security Service, rejected his request. In sum, none of the available documents from the Soviet period incriminates TR with armament research.

In 1987, TR's other son Alexei formally requested his father's rehabilitation. This effort was aided by Daniil Granin's 1987 book on TR (Granin 1987), something made possible by Gorbachov's policy of *glasnost*. A West German translation was published soon thereafter (Müller-Hill 1988), and in June, 1988, during the waning days of the German Democratic Republic, East German Communist officials considered whether an East German version of Granin's book should be approved.

In July, 1988, Soviet justice officials concluded their investigation of TR by rejecting the request for rehabilitation. Interpreting the scientific work done at TR's institute in the worst possible light and taking National Socialist directives that only work decisive for the war effort could continue at face value, the Soviet officials managed to argue that TR had worked on weapons of mass destruction for Germany. Moreover, in their view TR had committed treason by not returning to the Soviet Union, and by providing information to the Germans on Soviet scientific institutes.

The 1989 report by the East German Academy of Sciences, written during "*Die Wende*," the short transition between the old East German regime and the unification of Germany, was solicited by the East German Ministry of State Security and contributed decisively to TR's rehabilitation in the beginning of the 1990s. In sharp contrast to the preceding Soviet investigation, the Academy scientists reviewed the work actually done at TR's institute, set it in the context of the Third Reich, and gave him the benefit of the doubt. In sum, the Academy's expertise concluded that TR and his group followed a highly theoretical and fundamental research program hardly adaptable to the immediate military needs.

Timoféeff-Ressovsky's research program

One can distinguish three major directions in TR's scientific activities during the German period: evolutionary biology in general, molecular genetics, and developmental genetics. In the latter field he is best known for introducing the concepts of *penetrance* and *expressivity*,[12] reflecting correspondingly that "the rate expression (penetrance) and the degree and the form of manifestation (expressivity) of a gene depend on genotype it belongs to" (Blumenfeld et al. 2000). Following the lines of Valentin Haecker's (1864–1927) phenogenetics [*Phänogenetik*] TR conducted research on the "systemic regulation of the formation of phenotypic traits" (Ratner 2001). This work was paralleled by the investigations into the physical nature of the gene, which TR carried out applying the methods of radiobiology (e.g., Timoféeff-Ressovsky et al. 1935). TR realized the significance of the structural gene studies early on, among others, due to the insights of his teacher Koltzoff, who coined "the very idea of the template principle of biosynthesis at the Third Russian Congress of Zoology, Anatomy and Histology (Leningrad 1927)" (Blumenfeld et al. 2000). In their generalizing and voluminous book, *Das Trefferprinzip*, TR and Zimmer firmly stated that "gene mutation represent structural changes of the separate physic-chemical units." It is highly

[11] BStU, Archiv der Zentralstelle, MfS HA IX/11, RHE 25/87 SU Vol. 2a (UdSSR-Documents), p. 146.

[12] Harwood expressed doubts that these terms were coined by TR and appeals to the fact that Oscar Vogt employed the same terms (Harwood 1993, p. 55). However, Vogt used these terms with a totally different meaning and in a different field of biology. In fact, TR expressed these ideas already in 1925–1926 (Timoféeff-Ressovsky 1925).

probable, the authors continued, that genes are "huge molecules or micelles, which can create—alongside themselves—identical ones as well as specifically intervene into cell metabolism" (Timoféeff-Ressovsky and Zimmer 1947, p. 247). TR numbers, therefore, among the pioneers of molecular genetics and biophysics. His influence, in this respect, on Delbrück and Erwin Schrödinger is well-known. Yet it was only one of the scientific branches that he pioneered.

In 1938, at the thirteenth annual meeting of the German Society for Hereditary Research [*Deutsche Gesellschaft für Vererbungsforschung*] in Würzburg, TR made a significant step toward a consensus between geneticists and evolutionary biologists. This lecture significantly influenced contemporary discussion on the problem of evolution, for he concisely presented all of the essential and newest arguments for a genetic theory of evolution (Timoféeff-Ressovsky 1939) (Fig. 2).

During the late 1930s and 1940s, TR established a population genetics in Germany based upon the broad range of empirical data gained from both field research and laboratory research. He worked on the role of evolutionary factors, analyzed the role of recessive mutations, and

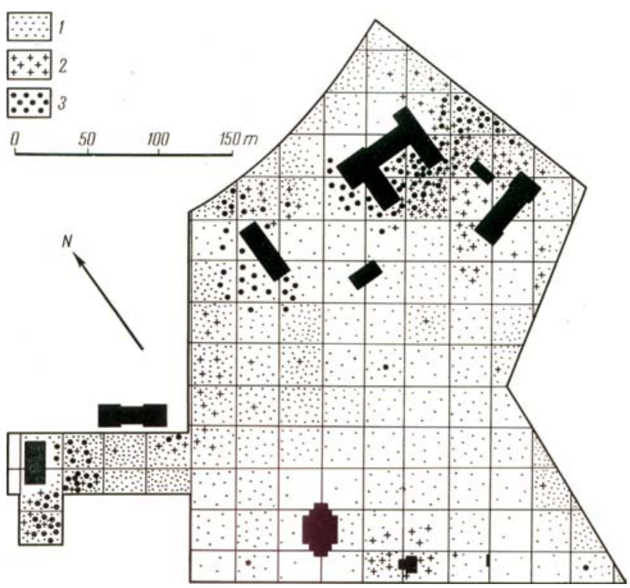

Fig. 2 TR's classical field studies on the geographic variability and systematics: The spatial distribution of *D. obscura* [. ˙], *D. funebris* [++], and *D. melanogaster* [• •] on a tenement in Berlin-Buch (summer of 1938). In the middle of each square a bottle with food was placed for 3–5 days; these bottles were inspected twice on each day, and the flies caught in them were counted and recorded; such experiments were repeated every 3–4 weeks during the whole season (original figure based on the data of Helena Timoféeff-Ressovsky). "These studies show that the regular activity-ranges in *Drosophila* are rather small, so that even small territorial fragmentations of the populations may result in partial isolation" (from: TR, *Mutation and geographical variation*. In: Huxley J. (ed.) *The New Systematics*. Oxford University Press, pp. 73–136)

discussed data and findings with colleagues from different areas of biology. TR, the "German Dobzhansky" (Hoßfeld 1998), was undoubtedly one of the architects of the Evolutionary Synthesis in the German-speaking world (Reif et al. 2000). He was the only evolutionary biologist included in both of the two major edited volumes that appeared in the early years of the evolutionary synthesis, one in English (Huxley 1940), the other in German (Heberer 1943). The latter certainly played the crucial role in the establishment of the Evolutionary Synthesis in the German lands, and, considering the weight of German science at the time, on the Continent. From this viewpoint, Timoféeff-Ressovsky was a central figure in discovering microevolutionary mechanisms, while Bernhard Rensch (1900–1990) took a lead in developing a Darwinian theory of macroevolution (Glass 1990; Vorontzov 1993, 2004; Hoßfeld 1998). It is worth noting that Rensch's conversion to a Darwinian took place under the significant influence of TR (Levit et al. 2008).

Just like Dobzhansky, TR pioneered experimental studies of genetic variation in wild populations of *Drosophila* (e.g., N. W. and H. A. Timoféeff-Ressovsky 1927). Beginning in the late 1920s, he investigated into the relative significance of various factors of evolution, approaching one of the most central issues of the Synthetic Darwinism. Dobzhansky, in his *Genetics and the Origin of Species*, highlighted several features of TR's research program that are especially important for evolutionary theory. First, TR has demonstrated that "the effects produced by a given mutation on viability are a function both of the environmental conditions and of the rest of the genetic structure of the individual" (Dobzhansky [1937] 1982, p. 20). Second, TR, in his works from the mid-thirties, did pioneering work determining the relative frequency of the different types of mutations by treating wild types of *D. melanogaster* with X-rays. He also devoted a great deal of attention to "the problem of mutability to and from a given allelomorph." TR, Dobzhansky concludes, has contributed to the new understanding "that the pace of evolution is not alike in all organisms," i.e., that "some group seem to possess an unlimited store of variation and evolve rapidly, while others are conservative and undergo no change during geological epochs" (Dobzhansky [1937] 1982, pp. 24, 37) (Fig. 3).

Yet TR's mutation studies were only a fraction of his research program; his theoretical interests were much more inclusive. In one of his most important review articles, *Genetik und Evolution* (193-9a), TR discussed the importance of genetic constraints of variation and investigated the relative importance of various factors of evolution (Reif et al. 2000). In his seminal contribution to Heberer's *Evolution der Organismen*, which TR wrote jointly with Hans Bauer, approached the central issue of evolutionary

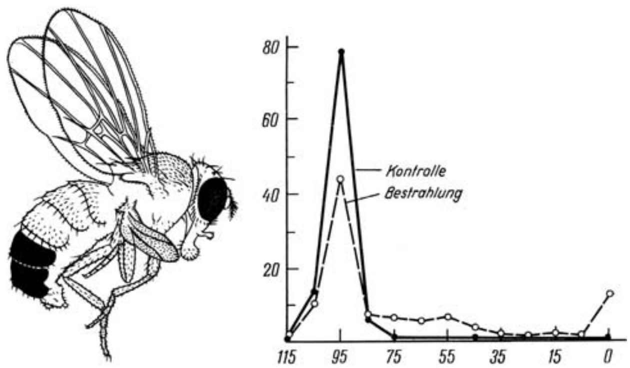

Fig. 3 "The mutation process is random and directionless" (Timoféeff-Ressovsky et al. 1975, p. 84): Timoféeff-Ressovsky illustrates this Darwinian thesis by two examples: *Left*: The mutation *tetraptera* of *D. melanogaster* as discovered by B.L. Astaurov (1927) is an example for a *Großmutation* (major mutation), which leads "to the occurrence of a character of another order" (Timoféeff-Ressovsky et al. 1975, p. 83). *Right*: The curve reflecting the minor mutations [*Kleinmutationen*] of relative vitality in *D. melanogater*. *Bestrahlung*—radiation; *Kontrolle*—control group. Abscissa: The number of males in the crossbreeding expressed in percent to the number of normal females. Ordinate: The percentage of corresponding crossings (control group = 837 individuals; the irradiated group = 868 individuals) (from Timoféeff-Ressovsky et al. 1975, p. 83)

theory, the relationships between micro- and macroevolution. The process of macroevolution, the authors argued, "escapes direct observation and analysis" (Baur and Timoféeff-Ressovsky 1943, p. 335). Yet, many evolutionary processes and elementary mechanisms can be reconstructed inductively proceeding from the micro-evolutionary observations. From this viewpoint Baur and TR analyze the most basic processes resulting in the origin of new races and species and, ultimately, arrive at the general discussion of factors and mechanisms of evolution. They conclude that mutations demonstrate all necessary features of the elementary material of evolution. Proceeding from the basic microevolutionary events one can come up to the most characteristic macroevolutionary trends like *Bergmann's rule*, although additional theoretical instruments such as auxiliary hypotheses may be necessary.

In sum, at the end of his German period, TR already possessed an explicit scientific methodology, which can be characterized by a combination of exact and elegant experiments made within the fundamental theoretical framework. In so doing, he continuously perfected his experimental techniques such as radiobiological methods, extending them to novel research fields. TR's scientific interests were concentrated around the most fundamental issues of evolutionary biology, biophysics, biochemistry, and genetics, which he approached by way of experiments integrated into a clearly constructed methodological agenda. In so doing, he demonstrated a remarkable tendency: he steadily elevated the level of generalizations, moving from molecules to macro-evolutionary trends. This tendency becomes even more evident in his post-German publications, although, and it is also an interesting feature, radiobiological methods remained his favorite research instrument.

In 1969 Timoféeff-Ressovsky published a concise text book on the theory of evolution together with N. N. Voroncov (Vorontzov) and A. V. Jablokov (German translation 1975). The authors already regarded macroevolution as a different research tradition requiring a multidisciplinary approach including comparative morphology, paleontology, embryology, genetics, ecology, biochemistry, and molecular biology. The mentioned representatives of this tradition include Huxley, Schmalhausen, Mayr, Rensch, Simpson, Takhtajan "and many others" (Timoféeff-Ressovsky et al. 1975, p. 66). In fact, TR's work extends the frames of any "tradition." At that time, his research program was explicitly directed toward an all-embracing theory explaining evolution on all basic levels of organization of living matter, from the molecular level to the biogeocenoses and the Biosphere (Tjurjukanov and Fedorov 1986). A harmonized model of micro- and macroevolutionary processes including ecological, biogeochemical, and global approaches would then form an interdisciplinary basis for an expanded theoretical system explaining all the levels. In other words, TR did not see the modern theory of evolution (in 1969/1975) as a rigid conceptual body, but rather as a dynamic complex of theoretical insights toward which he had worked at least since the early 1930s (Reif et al. 2000) and certainly can be regarded as one of the forerunners of *ecological developmental biology* (as defined in Gilbert 2009) and an '*expanded Synthesis*' (Kutschera and Nicklas 2004, 2008).

In the late Soviet period TR extended this approach to its possible limits, to the scale of the whole Biosphere. It is enough to throw a glance at TR's works of the late 1950s, 1960s, and 1970s to realize that in this period the concept of the biogeocenosis becomes the most central in his research program (Timoféeff-Ressovsky 1957, 1958, 1962a, b, 1968; Timoféeff-Ressovsky et al. 1957). This concept was coined by Vladimir Sukachov (1880–1967) in developing the idea of "natural zones" presented by Vassily Dokuchaev, who was a teacher of Vladimir Vernadsky (1863–1945), the founder of the Biosphere theory. *Biogeocenosis* describes the entire *biocenosis* taken together with its inert environment as a stable and self-regulating system. TR commented on it: "The biogeocenoses are dynamic systems, which at the same time can be in a state of dynamic equilibrium over quite a long biological time period (in the course of many generations of living beings residing in this biogeocenosis)" (Timoféeff-Ressovsky et al. 1975, p. 309). In this tradition, the biosphere is defined as the sum total of biogeocenoses. In contrast to the term "ecosystem," predominantly used in the

Western world, biogeocenosis comprises *all* biotic factors and all biotic dependencies in a relatively isolated system occupying clearly detectable zones (e.g., a pine forest or a swamp). TR explicitly and sharply contrasted the terms '*ecosystem*' and '*biogeocenosis*'. The 'ecosystem' is a "vague notion" covering, in practice, the idea of trophic chains of various levels of complexity. The biogeocenosis, by contrast, is an elementary, clearly empirically definable, self-regulating unit of the Biosphere (Timoféeff-Ressovsky and Abaturov 1970). He expressed these ideas with all possible clarity: "The biosphere in its entirety consists of more or less complex biotic and abiotic components, i.e., biogeocenoses. In other words, the biogeocenoses are the precise environments in which the evolutionary process of any group of living organisms takes place" (Timoféeff-Ressovsky et al. 1975, p. 249).

Biogeocenology, the science of beogeocenoses, is methodologically closely connected to Vernadsky's biosphere theory. From the other side, TR continued, the biogeocenology belongs to the kind of studies defining the very basic biological structures on the "various levels of complexity in the biosphere" (Timoféeff-Ressovsky 1962b). In other words, he combines his molecular biological and biogeocenological studies on the basis of a common methodological platform. He distinguished four basic structural levels: genotypic, ontogenetic, evolutionary (speciation), and biohorological, i.e., the level of communities taken together with the inert environments and "performing the grandiose biogeochemical flow of matter and energy in the Biosphere." The latter (biohorological level), TR insisted, is the level on which evolution actually takes place. The biogeocenosis, in TR' terms, is an elementary (very basic) structure of the highest level of organization of life on Earth. In other words, TR's biogeocenology is a non-reductionist research program proceeding from the assumption that the elementary (non-reducible) evolutionary event is the circulation of energy and chemical elements within a biogeocenosis. These are specific for the populations of species composing an elementary biohorological unit (biogeocenosis).

Distinguishing the elementary structural units, TR emphasized, is a necessary prerequisite for an application of the mathematical apparatus to biological issues. It is also essential for the solution of strictly applied problems such as radioactive pollution of the biosphere and its regions.

TR's own contribution to biogeocenology was a novel branch of science, a radiation biogeocenology. Radiation biogeocenology implies a method of ionizing radiation radioactive isotopes for quantitative investigations into the structure of the biogeocenoses as well as the role of various species in the accumulation and distribution of the chemical elements within biogeocenoses (Fig. 4).

Hence, TR applied the same basic principles and even the same methods (for example, radiobiology) throughout his whole scientific life, consequently developing and completing this methodology. There is a clearly detectable logic in the evolution of TR's research program: a consequent increase of the level of explanation of evolutionary events or, in other words, making an explanation increasingly inclusive, so much so that the very notion of 'evolutionary biology' becomes too restrictive.

Fig. 4 Timoféeff-Ressovsky and the mathematician Alexei Ljapunov on the so called "gamma-field" in Miassovo (Southern Ural) in 1957, where they studied the impact of gamma-rays on plant communities. Courtesy of Nauka press and V.I. Ivanov & N.A. Ljapunova

TR himself emphasized, in this respect, that his way in science appears to be "remarkably logical". This is true considering that "his interest in certain problems was determined by the natural hierarchy of the levels of life organization" (Glotov 2000).

Conclusions

Both crucial episodes of TR's biography and his broad scientific interests can be explained as proceeding from his steady attempts to complete a certain research program, which became explicit in the late 1930s. The major idea behind this program was to connect molecular, developmental, evolutionary, and environmental processes within a comprehensible theoretical framework. It is remarkable that in his biophysical works of the German period, TR already appeals to Vernadsky's ideas (Timoféeff-Ressovsky 1942), which became crucial for his unifying research program in the Soviet period. The aspiration of his physicist friends (including Niels Bohr) toward an all-embracing physical theory may have played a paradigmatic role here. Further, TR's research program reflects the general and clearly detectable environmental bias in Russian-language evolutionary biology (Levit 2007). His complex, ambitious, and fundamental research program was the major factor determining the crucial episodes of his scientific and personal biography.

In any political situation, TR looked for the optimal conditions allowing him to conduct his scientific research at the highest level. Considering, that TR was involved in experimental molecular-genetic and radiobiological investigations, only a few countries with highly advanced and financed scientific institutions could provide him with the necessary research conditions. Further, a scientist of TR's format working not only experimentally, but approaching theoretical issues of the highest possible complexity, is expected to be tightly coupled with his cultural and scientific micro- and macro-environment along with unique equipment. All these factors taken together determined TR's decision to stay in Germany in 1936, despite the increasing nazification. TR's decision was certainly in contradiction to the deeds of other liberal intellectuals. The 1930s were marked by the massive emigration of the leading scientists to the Great Britain and the USA; about 15% of academic scientists left Germany. In 1937 one of the major scientific journals *Nature* was forbidden in Germany (Hoßfeld and Olsson 2007). It was a time of "packing bags" and TR could not be "unaware" of all these developments. His decision exposed him and his family to immediate danger.

The same motive prevented him from escaping the potential Soviet occupation zone. His intention was, with all probability, to preserve his institute and research group and prepare it for deportation to the USSR. And, again, he ran evident risks. Yet TR's decisions exactly followed his system of values, where science was at the top of the ethical hierarchy.

TR was not the only example for that kind of behavior. His older colleague and ideal, Vladimir Vernadsky, returned from Paris back to the totalitarian Soviet Union in 1926 because the liberal countries of that time could not support his large-scale research project in biogeochemistry. In both cases, science was seen not only as a 'profession,' but as a global force structuring natural and cultural landscapes. In one of his late articles, entitled *The Biosphere and Humankind* (Timoféeff-Ressovsky 1968) TR connects his hopes for solving planetary problems, as did Vernadsky, with the leading role of science. In other words, Science for TR was the highest priority determining his major decisions.

On a more general level, our overview of TR's scientific biography is in agreement with an inference made by Eduard Kolchinsky in his generalizing study of science under totalitarian regimes in Germany and Russia (Kolchinsky 2006; Levit and Hoßfeld 2007), that the scientific communities were ready to make a compromise with the totalitarian regimes expecting, in turn, financial support and non-intervention of the State in scientific affairs.

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References

Babkov VV, Sakanjan ES (2002) N.V. Timofeev-Ressovsky. Pamjatniki Istoricheskoj Mysli, Moscow

Bauer H, Timoféeff-Ressovsky NW (1943) Genetik und Evolutionsforschung bei Tieren. In: Heberer G (ed) Die Evolution der Organismen. Gustav Fischer, Jena, pp 335–429

Blumenfeld LA, Bogdanov YF, Ivanov VI, Lyapunova NA (2000) Pioneer of molecular genetics. Mol Biol 34(6):955–957

Born H, Timoféeff-Ressovsky NW, Zimmer K (1941) Anwendungen der Neutronen und der künstlich radioaktiven Stoffe in Chemie und Biologie. Umsch 45(6):2–6

Dobzhansky Th (1982) Genetics and the origin of species (Classics of modern evolution series). Columbia University Press, NY

Dubinina LG, Ovchinnikova IN (eds) (2006) Nikolai Petrovich Dubinin i XX vek (N.P. Dubinin and the 20th century). Nauka, Moscow

Gilbert SF (2009) Ecological developmental biology. Sinauer Associates, Sunderland

Glass B (1990) Timoféeff-Ressovsky NW. In: Holmes FL (ed) Dictionary of scientific biography, Vol. 18, Suppl. II. Scribner, New York, pp 919–926

Glotov NV (2000) Nikolai Vladimirovich Timofeeff-Ressovsky: a biologist's outlook. Russ J Ecol 31(4):220–223

Granin D (1987) Zubr. Novyj Mir, Moscow

Harwood J (1993) Styles of scientific thought. University of Chicago Press, Chicago & London

Heberer G (ed) (1943) Die Evolution der Organismen. Fischer, Jena

Hoßfeld U (1998) Dobzhansky's Buch "Genetics and the Origin of Species" (1937) und sein Einfluß auf die deutschsprachige Evolutionsbiologie. In: Rheinberger HJ, Weingarten M (eds) Jahrbuch für Geschichte und Theorie der Biologie 5. VWB, Berlin, pp 105–144

Hoßfeld U (2001) Im unsichtbaren Visier. Medhist J 36:335–367

Hoßfeld U, Olsson L (2007) Nature and Hitler. Hist J Nat. doi: 10.1038/nature06242

Huxley J (ed) (1940) The new systematics. Clarendon, Oxford

Iljin D, Provotorov V (1989) Kto Vy Doktor Timofeev-Resovskij? Nash Sovremennik, vol 11

Ivanov VI (1990) Net proroka v svojem otetschestve. Priroda 9:71–77

Kolchinsky EI (2003) Ryzar' nauki (The Knight of Science). Interview with V.S. Kirpichnikov. Repressirovannaja Nauka (Repressed Sci) 2:228–238, Nauka, Sankt-Petersburg

Kolchinsky EI (2006) Biology in Germany and Russia-USSR. Nestor-Istorija, Saint-Petersburg

Kutschera U, Nicklas KJ (2004) The modern theory of biological evolution: an expanded synthesis. Naturwissenschaften 91: 255–276

Kutschera U, Nicklas KJ (2008) Macroevolution via secondary endosymbiosis: a Neo-Goldschmidtian view of unicellular hopeful monsters and Darwin's primordial intermediate form. Theor Biosci 127:277–289

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

Levit GS, Hoßfeld U (2007) Review of "Biology in Germany and Russia-USSR". Hist Philos Life Sci 29(1):120–123

Levit GS, Simunek M, Hoßfeld U (2008) Psychoontogeny and psychophylogeny: Bernhard Rensch's (1900–1990) selectionist

turn through the prism of panpsychistic identism. Theor Biosci 127:297–322
Mayr E (1993) Timofeev-Ressovsky. In: Vorontzov NN (ed) NW Timofeev-Ressovsky. Nauka, Moscow, pp 178–179
Müller-Hill B (1988) Heroes and villains. Review of Daniel Granin's "Der Genetiker. Das Leben des Nikolai Timofejew-Ressowski, genannt Ur". Nature 336:721–722
Paul D, Krimbas C (1992) Nikolai V. Timoféeff-Ressovsky. Sci Am 266:86–92
Ratner V (2001) Timofeef-Ressovsky (1900–1981): twin of the century of genetics. Genetics 158:933–939
Reif W-E, Junker T, Hoßfeld U (2000) The synthetic theory of evolution: general problems and the German contribution to the synthesis. Theor Biosci 119(1):41–91
Riehl N, Seitz F (1993) Stalin's captive: Nikolaus Riehl and the Soviet race for the bomb. American Chemical Society and the Chemical Heritage Foundations
Rokityanskij J (2003) Timofeev-Ressovsky v Germanii I na Lubjanke. In: Rokityansky J et al (eds) Declassified "Aurochs": investigatory evidences in the case of N. W. Timofeeff-Ressovsky. Academia, Moscow, pp 6–162
Rokityansky J et al (eds) (2003) Declassified "Aurochs": investigatory evidences in the case of N. W. Timofeeff-Ressovsky. Academia, Moscow (in Russian)
Schmaltz F (2005) Kampfstoff-Forschung im Nationalsozialismus. Wallstein Verlag, Göttingen
Timoféeff-Ressovsky NW (1925) On the phenotypic expression of genotype I. Gene variation of radius incompletes in *D. funebris*. J Exp Biol (A 1) (3–4):93–142 (in Russian)
Timoféeff-Ressovsky NW (1939) Genetik und Evolution (Bericht eines Zoologen). Z Indukt Abstamm Vererblehr 76:158–219
Timoféeff-Ressovsky NW (1941) Einige chemisch-biologische Anwendungen der schnellen Neutronen und der künstlich radioaktiven Stoffe. Angew Chem 54(437):190–195
Timoféeff-Ressovsky NW (1942) Biologische Anwendungen des Zählrohres. Natwissenschaften 30(40):39–40
Timoféeff-Ressovsky NW (1957) The application of radiation and radioactive substances in experimental biogeocoenology. Bot J 42(2):161–194 (in Russian)
Timoféeff-Ressovsky NW (1958) Strahlungen und Strahlenquellen in der experimentellen Biogeozönologie. Sowjetwiss-Natwiss Beitr 4:361–399
Timoféeff-Ressovsky NW (1962a) On radiactive pollution of the biosphere and measures of the pollution control. Proc Inst Biol Ural Branch USSR Acad Sci 22:7–16 (in Russian)
Timoféeff-Ressovsky NW (1962b) Some problems in radiation biogeocoenology. Proc Inst Biol UF AN USSR (in Russian)
Timoféeff-Ressovsky NW (1968) Biosphere and humankind. Proc Obninsk Branch Geogr Soc USSR 1(1):3–12 (in Russian)
Timoféeff-Ressovsky NW (2000) Timoféeff-Ressovsky N.W. Istorii rasskazannyje im samim (The stories told by himself). Soglasije, Moscow
Timoféeff-Ressovsky NW, Abaturov JD (1970) Radioazionnaja biogeozenologija (Radiation biogeocenology). Proc Comm Obninsk Branch Geogr Soc USSR 2 [Doklady komissii obninskogo otdela geogr. obstchestva] (in Russian)
Timoféeff-Ressovsky NW, Timoféeff-Ressovsky HA (1927) Genetische analyse einer freilebenden *Drosophila melanogaster* population. Roux' Arch Entwick Org Bd 109, H 1, S 70–109
Timoféeff-Ressovsky NW, Zimmer KG (1947) Das Trefferprinzip in der Biologie. S. Hirzel Verlag, Leipzig
Timoféeff-Ressovsky NW, Delbrück M, Zimmer K (1935) Über die Natur der Genmutation und der Genstruktur. Nachr Ges Wiss Gött, Fachgruppe VI, NF 1:190–245
Timoféeff-Ressovsky NW, Poryadkova NA, Sokurova EN, Timoféeff-Ressovsky EA (1957) Works on the experimental biogeocenology I. Influence of the radioactive substances on the biomass and structure of terrestrial, soil and freshwater biocoenoses. Proc Lab Biophys Ural Branch Acad Sci USSR 9:202–250 (in Russian)
Timoféeff-Ressovsky NW, Voroncov NN, Jablokov AV (1975) Kurzer Grundriss der Evolutionstheorie. VEB Gustav Fischer, Jena
Tjurjukanov AN, Fedorov VM (1986) N.V. Timofeeff-Ressovskij: Biosfernyje razdumja. Verlag, Moscow (in Russian)
Vorontzov NN (ed) (1993) Nikolai Vladimirovitsch Timofeev-Ressovskij. Ocerki vospominanija materialy. Nauka, Moscow (in Russian)
Vorontzov NN (2004) Razvitije evoliutzionnykh idej v biologii (The development of evolutionary ideas in biology). KMK Press, Moscow (in Russian)
Wettstein Fv (1934) Über plasmatische Vererbung. Wiss Woche Frankf. 1
Zinger O (1990) Koljuscha: N. V. Timofeev-Ressovsky. Khimija i Zhizn 12:39–45