## Unravelling the Mysteries of the Existence of Phototrophic Microorganisms. Elena Nikolaevna Kondratieva, a Full Member of the Russian Academy of Sciences (1925–1995)

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The present article is concerned with the biography and the scientific legacy of Academician Elena Nikolaevna Kondratieva. Special emphasis is placed on the implications of Kondratieva's activities in terms of history of science. In the Soviet Union (Russia), E.N. Kondratieva conducted comprehensive studies on the metabolism of phototrophic and, more recently, methylotrophic bacteria. Her work was of paramount importance not only for fundamental research but also for biotechnology. Kondratieva's contribution to microbiological education and promotion of microbiological knowledge should also be emphasized. She was the founder of a major school of thought within the Russian microbiological community. Being the President of the All-Union Microbiology Society and one of the leading microbiologists worldwide, she contributed significantly to the development of microbiological research in the Soviet Union and of scientific ties between the USSR and other countries. A versatile, talented person, Elena Nikolaevna also went in for equestrian sport and played an important role in its history in the Soviet Union (Russia). The present article contains the biographies of Elena Nikolaevna's parents: Nikolai Dmitrievich Kondratiev, a professor in economics, and Eugenia Davydovna Dorf whose life has not received sufficient attention in the literature yet. Kondratieva's scientific career is described in detail; her diploma paper and Candidate of Science dissertation are analyzed. Importantly, special emphasis is placed upon the history of relevant subfields of microbiology. They are associated with the history of the Microbiology Department of Moscow University (the work of Professor E.E. Uspensky, the founder of this department, and of his disciple Professor I.L. Rabotnova) and with the classical work of S.N. Winogradsky, the discoverer of chemosynthesis, and K. van Niel who elucidated the mechanism of bacterial photosynthesis. The main areas of research that were in Kondratieva's focus of attention are described. Much attention in this work is given to Kondratieva's educational activities, her role as the founder of a new scientific school, and her functions in the capacity of the President of the All-Union Microbiology Society (1975–1985). The scientific achievements of Kondratieva's disciples are discussed. This work makes use of a large number of reminiscences of people who personally knew Kondratieva. These reminiscences have not received sufficient attention yet in the literature; some of the archive data are quoted for the first time. Their authors supply interesting facts concerning Kondratieva's scientific career and her personal life.

*Keywords:* Elena Nikolaevna Kondratieva, Nikolai Dmitrievich Kondratiev, Russian Microbiological Society, history of microbiology, bacterial photosynthesis, autotrophs, methylotrophs, biotechnology.

"After all, scientific knowledge holds supreme value and has the power to uplift humankind's spirit"

N.D. Kondratiev

Elena Nikolaevna Kondratieva, a Full Member of the Russian Academy of Sciences, was an outstanding Russian microbiologist specializing in bacterial physiology and biochemistry (Fig. 1). Her entire scientific career was associated with Moscow State University which she entered as a student and where she finally held a Head of Department position. In the Soviet Union (Russia), E.N. Kondratieva conducted comprehensive studies on the metabolism of phototrophic and, more recently, methylotrophic bacteria. Her work was of paramount importance not only for fundamental research but also for biotechnology. Kondratieva's contribution to microbiological education and the promotion of microbiological knowledge should also be emphasized. She was the founder of a major school of thought within the Russian microbiological community. Being the President of the All-Union Microbiology Society and one of the leading microbiologists worldwide, she significantly contributed to the development of microbiological research in the Soviet Union and of scientific ties between the USSR and other countries. A versatile, talented



Fig.1. Elena Nikolaevna Kondratieva (date unknown, Archive of the Microbiology Department)

person, Elena Nikolaevna also went in for equestrian sport and played an important role in its history in the Soviet Union (Russia). To commemorate Kondratieva, posthumous All-Russian Symposia on Autotrophic Microorganisms, with participation of invited foreign scientists, have regularly been held at the Biology Department of Moscow State University.

Elena Nikolaevna was born on December 16, 1925 in Moscow. Her father, Nikolai Dmitrievich Kondratiev (1892–1938), was a gifted creative scholar — an economics professor whose fate proved to be tragic. Nikolai Dmitrievich was born in the village Galuevskaya of the Kostroma Region. His father, an engraver, was called Dmitry Gavrilovich Kondratiev; his mother's name was Lyubov' Ivanovna Kondratieva.

Nikolai Dmitrievich Kondratiev made it from a village parish school pupil to a graduate student of Law Department of the University of Saint-Petersburg (1914) and became a prominent specialist in the field of economics. Kondratiev's scientific achievements were widely acknowledged, and he played an extremely important part in the social life of Russia. After the February Revolution in 1917, he was Alexander F. Kerensky's secretary specializing in agriculture. Kondratiev was actively involved in preparing and holding the First All-Russian Meeting of Peasant Deputies' Soviets (Councils). He also participated in the Third Socialist Revolutionaries' Meeting, Subsequently, Kondratiev was elected the Deputy Food Minister, After moving to Moscow in 1918, Kondratiev was in charge of the Economic Department of the Agricultural Cooperation Council and the Central Society of Flax Breeders. He also was an appointed professor at the Cooperative Institute of the Petrov (Timiryazev) Agricultural Academy and worked in the capacity of the head of the Agricultural Economics Administration in the Agricultural People's Commissariate. Since 1920, he was the director of the Commercial Institute (Kondrat'ev, 1993). In 1923, Kondratiev designed the plan of the development of agriculture and forestry in Russia. The creation and implementation of this plan reflected an active social civic attitude of a scholar who predicted the tragic fate of Russian villages and tried to prevent it. Importantly, Kondratiev was familiar with the problems and issues faced by Russian villages.

In 1924, Kondratiev and his wife stayed abroad for a long time. They visited Germany, Great Britain, Canada, and the United States of America. It was in America that he met for the last time with Pitirim Alexandrovich Sorokin, a friend he had known since their studies at the school and the University. An eminent sociologist, Sorokin was forced to leave Russia in 1922 on board the notorious "Philosophers' Steamboat". In 1925, Kondratiev published the article entitled *Large-Scale Economic Cycles* that was to become a classical work in this field of science. It focused on the theory of economic cycles that subsequently were denoted as Kondratiev's cycles. The early 20's were Kondratiev's heyday in terms of carrier, success, and popularity. The rise was followed by a sharp decline. Kondratiev's views were severely criticized. The term "Kondratievshina" (following Kondratiev's example) was used for a long time as a synonym of the word *sabotage*. In 1928, Kondratiev was dismissed from his position. In 1930, he was falsely charged with membership in the "Peasants' Labor Party" and arrested. In 1932, he was sentenced to eight years of prison. He became an inmate of the Suzdal' Politisolator (political prison). On September 17, 1938, Kondratiev was executed by a firing-squad at Kommunarka near Moscow (Simonov, 1990). The scholar was completely exonerated in 1963 and, for the second time, in 1987.

Elena Nikolaevna's mother was Eugenia Davydovna Kondratieva (1893–1982). Her maiden name was Dorf. She was the daughter of David Yakovlevich Dorf, a village doctor and a public activist, and Tatiana Alexandrovna Plekhanova. Since her mother died while Eugenia was still very young, she was brought up by her father's close friends Mikhail Ivanovich and Maria Petrovna Lavrovs. Since her childhood, Eugenia used to be independent, hard-working, and strong-willed. She was very well educated and had a perfect command of several foreign languages. During World War I, she was working as a nurse, later as an interpreter, translator, shorthand writer, librarian, teacher, expert, desk clerk, and secretary for various organizations including medical institutions. During the whole course of her life, she was skilfully translating scientific literature that chiefly dealt with medicine and veterinary (Shaikin, Kliukin, 2014).

Eugenia Davydovna met Nikolai Dmitrievich in 1918 or 1919. They were working with the Central Society of Flax Breeders. Shortly thereafter (in 1920–1921), he married her. "Our meeting was not just a chance event", a romantic song with this title was dedicated by Kondratiev to his wife. The happy family life of N.D. and E.D. Kondratievs proved short-lived; it was interrupted by Nikolai Dmitrievich's arrest. However, Eugenia Davydovna cherished her love for Nikolai and remained devoted to him over the whole course of her difficult life. She did her best to improve his situation. She succeeded in providing him with a permission to do scientific studies while in prison, and she obtained books, food, and other essentials for him. She repeatedly visited him in the Suzdal political prison and in the hospital into which the seriously ill inmate was admitted. She courageously took the risk of keeping not only his letters written in the prison cell, but also the scientific manuscripts that were subsequently "deciphered" and copied by her. This was a heroic deed! The scientific work she saved saw the daylight many years later; it formed an important part of Kondratiev's scientific legacy. Eugenia Davydovna's life was quite long. She was an intelligent, educated, and kind person. Until the end of her life, she was staying with her daughter who she devotedly loved.

Elena Nikolaevna Kondratieva's had a difficult childhood. She was five when her father was arrested. She was stigmatized as the daughter of an "enemy of the people". During the whole course of her life, Elena Nikolaevna cherished her father's moving letters and the philosophical fairy tale in verse entitled *The Extraordinary Adventures of Shammi* that was written by N.D. Kondratiev (2004) in prison (Kondrat'ev, 2004). When the mother and the daughter learned in 1938 that Kondratiev was "sentenced to 10 years of prison and denied the right to correspond with his family", they did not know what this euphemism really meant. They recklessly hoped to meet

him again! In spite of the poverty and hardship faced by Elena Nikolaevna, she proved to be an excellent student (her school was located in the Malaya Dmitrovka Street). She was very well read. Together with many other school students, she was evacuated to the town of Molotov (Perm') in the autumn of 1941. In this town, she finished school and unexpectedly entered the Moscow Institute of Geodesy and Mapping that was also temporarily located in Molotov. This enabled her to continue her studies. After returning to Moscow, Elena Nikolaevna made the final decision with regard to her profession. In 1944, she entered the Biology & Soil Study Faculty of Lomonosov Moscow State University. She graduated from its Microbiology Department in 1949.

Elena Nikolaevna was still in her first year of study when the war was over. The Victory Day was celebrated, one of the most memorable days in her life (Rudakov, 1995). Elena was studying devotedly. Eminent scientists were teaching at the Biology Faculty, including D.A. Sabinin, A.S. Serebrovsky, E.S. Severin, V.N. Shaposhnikov, L.A. Zenkevich, S.I. Ognev, V.N. Beklemishev, and L.I. Kursanov. After the notorious meeting of the All-Union Academy of Agricultural Sciences in 1948, a number of faculty members had to quit the University. Soviet biology faced a hard time. For several days, the office of V.N. Shaposhnikov, the Head of the Microbiology Department, became suspiciously empty. However, the Department's life soon took its normal course again.

The Microbiology Department occupied six small rooms of the Botanic Building of the University that is situated in the Mokhovaya Street. Its windows overlook the Herzen Street that has recently reacquired its historical name, Bolshaya Nikitskaya (Egorov, Keppen, Kolotilova, Kurakov, Osmolovskii, 2014; Nefelova, 2005). Lectures and practical classes were given and conducted in this building; the staff as well as postgraduate and undergraduate students also worked here. Elena Nikolaevna's diploma project was carried out under the guidance of Irina Leonidovna Rabotnova, an Associate Professor who later became a Full Professor. The project was concerned with the influence of redox conditions (aeration) on nitrogen binding by the cells of soil bacteria of the genus Azotobacter. The impact of physical and chemical conditions on microbiological processes was a traditional area of research at the Microbiology Department. It was associated with the name of the Department's founder, Eugeny Eugenievich Uspensky (1889–1938), who was a microbiologist and an algologist (Kolotilova, 2009). E.E. Uspensky promoted the development of several subfields of (i) soil microbiology by suggesting the use of Azotobacter as a model microorganism for determining soil's requirements with regard to fertilizers, and (ii) aquatic microbiology in terms of water purification in the Moscow water pipeline. Nevertheless, it was his contribution to research on the impact of physical and chemical environmental factors such as the redox potential and pH on metabolic processes that were of paramount theoretical importance. In 1938, Uspensky was arrested on false charges; on October 14, he was executed at the same place (Kommunarka) as Kondratiev.

For a long time, E.E. Uspensky's name was not mentioned in scientific literature but his area of research was further developed in the work of his followers, including I.L. Rabotnova, who have cherished their teacher's memory. In her diploma work, E.N. Kondratieva succeeded in determining the redox potential values that were optimal for nitrogen binding by *Azotobacter* and those that suppressed this process. The work was successfully presented, and the results obtained formed a part of the first scientific publication of Elena Nikolaevna. This was the first step in her scientific career (Rabotnova, Kondrat'eva, Nette, Arones, 1949).

<sup>&</sup>lt;sup>1</sup> Кондратьева Е.Н. Дипломная работа на тему: Влияние окислительно-восстановительных условий среды на фиксацию азота атмосферы азотобактером. — Руководитель: Работнова И.Л. (доцент). Московский Ордена Ленина Государственный университет им. Ломоносова. Биологический факультет. Кафедра микробиологии. Москва, 1949 г. 71 с. (Архив кафедры микробиологии МГУ).

Elena Nikolaevna continued her scientific research as a postgraduate student. The new research subject was suggested by the Department's Head, Full Soviet Academy Member Vladimir Nikolaevich Shaposhnikov (1884–1968). Shaposhnikov was K.A. Timirvazev's disciple and went down in history as the founder of "technical", i.e., industrial, microbiology that was based upon fermentation processes. He was awarded the second-degree Stalin Prize for the book Technical Microbiology (1948). The studies that were conducted by Shaposhnikov at the Microbiology Department were focused on microbial physiology; the emphasis was also placed upon physiological systematics and bacterial evolution. During the post-war period. the Department's area of research was considerably enlarged; it was supplemented with new subfields. One of them dealt with antibiotics-producing microorganisms. For a long period of time, this subfield was efficiently researched by Nikolay Sergeevich Egorov, who subsequently became the Department's Head (1967–1989). Another subfield was concerned with photosynthetic bacteria. It opened up new prospects for research on the biodiversity and metabolism of phototrophic microorganisms, the mechanism of photosynthesis and its evolution, and the "role of photosynthetic bacteria in the Universe" (paraphrasing K.A. Timiryazev's words concerning the "role of green plants in the Universe"). This subject was suggested by E.N. Kondratieva.

The history of the discovery of bacterial photosynthesis represents one of the most fascinating chapters of the history of microbiology. The lifestyle of the microorganisms forming visible pinkish spots on the surface of sludge or staining stagnant water bodies red remained mysterious for a long time. The first goal-directed studies were conducted in the 1880s. The outstanding Russian microbiologist S.N. Vinogradsky (1856–1953) was the discoverer of chemosynthesis, i.e. the bacterial capacity to exist at the expense of oxidation of inorganic substances, such as reduced sulphur, iron, and nitrogen compounds. Vinogradsky succeeded in precisely describing several genera of purple bacteria but failed to explain their metabolism<sup>2</sup>. His contemporary, the German scientist H.T. Engelmann, revealed phototaxis, i.e., light-induced motility, in purple bacteria. This provided indirect evidence for their capacity to carry out photosynthesis. However, no light-dependent oxygen evolution, which was considered the main criterion of photosynthesis, was ever detected in these bacteria. For more than three decades, scientists in various countries were continuing their research in this field; they were putting forward various sophisticated hypotheses and refuting them. It was only the Dutch researcher K. van Niel who for the first time established that purple (and also green) bacteria carry out a special type of photosynthesis that involves light-dependent oxidation of hydrogen sulfide and other reductants (electron donors). This generalized notion of photosynthesis as a redox process in which diverse substances can serve as electron donors became a new scientific paradigm, green plants-specific photosynthesis that results in oxygen evolution being just one of its variants. The paradigm facilitated further fruitful studies on photosynthesis<sup>3</sup>. However, very little attention was given in Russia to the metabolism of phototrophic bacteria, and Elena Nikolaevna actually had to start the research from scratch.

E.N. Kondratieva successfully carried out her post-graduate project within a limited period of time, meeting the official deadline for it. In 1953, i.e. three years after beginning the post-graduate studies, she produced an impressive dissertation that was over 200 pages long.

 $<sup>^2</sup>$  Additional sources: *Заварзин Г.А.* Три жизни великого микробиолога. Документальная повесть о Сергее Николаевиче Виноградском / под ред. и с коммент. Н.Н. Колотиловой. М.: Либроком, 2009. С. 29—54.

<sup>&</sup>lt;sup>3</sup> Supplementary information: *Кондратьева Е.Н.* Фотосинтезирующие бактерии. М.: Изд-во АН СССР, 1963. С. 112-116.

The work was entitled *Carbon Assimilation by Purple Bacteria and their Development in Relation to the Ambient Redox Potential*<sup>4</sup>. It was evaluated by several reviewers. Taking into account cutting-edge research (conducted in the 1950s), Elena Nikolaevna produced a comprehensive literature review that dealt with the ecology, morphology, physiology, pigment composition, and systematic of purple bacteria as well as the methods of obtaining their pure cultures and the theory of bacterial photosynthesis — in comparison to green plant photosynthesis. From a pond in the Moscow Region, she isolated a purple bacterium that she identified as *Rhodopseudomonas palustris*. This bacterium was characterized in detail by Elena Nikolaevna. Special attention was given to the utilization of various organic substances by bacteria, which enabled her to delimit constructive and energy-producing metabolic processes. In the last chapter of the work, the impact of ambient redox conditions on the development of bacteria was discussed.

Elena Nikolaevna gradually brought together a group of talented undergraduate and, subsequently, postgraduate students. This made it possible to intensify their research and to develop new research areas.

In 1954, at the eve of the two hundred-year anniversary of Moscow State University, the biologists relocated to the new building of the Biology & Soil Science Faculty on the Lenin Hills. The spacious rooms and modern equipment provided new options in terms of scientific research. The Microbiology Department obtained new research devices, and it was E.N. Kondratieva who was the first to make a good use of a large part of them (Fig. 2). The progress of her research was also promoted by intense interaction with specialists in related fields including biochemists, biophysicists, geneticists, and chemists. This enabled developing a complex approach to her area of research. The results obtained provided an important insight into the metabolic diversity of phototrophic bacteria.



Fig. 2. Elena Nikolaevna Kondratieva using a photoelectric colorimeter in the 1960's (Archive of the Microbiology Department)

<sup>&</sup>lt;sup>4</sup> *Кондратьева Е.Н.* Фотоассимиляция углерода пурпурными бактериями и их развитие в связи с окислительно-восстановительным потенциалом среды: дис. ... канд. биол наук. М., 1953, 221 с.

The next stage of E.N. Kondratieva's scientific career was producing a sound monograph entitled *Photosynthetic Bacteria* (Kondrat'eva, 1963) that was presented by her as the Doctor of Science's dissertation. Even though this field of science has made great progress recently, her book is still of much interest today. It contains important data, useful references, and interesting facts.

The discussion of the main areas of Kondratieva's research should begin with emphasizing the fact that she created the first Russian collection of cultures of photosynthesizing bacteria and initiated systematic comparative research on them (Fig. 3). The purple sulfur bacterium *Ectothiorhodospira shaposhnikovii* isolated in 1959 and named in Academician V.N. Shaposhnikov's honor was one of the first strains in this collection. Year after year, the collection was enriched with new phototrophic bacteria belonging to various taxonomic groups, including representatives of purple sulfur (*Thiocapsa, Chromatium, Ectothiorhodospira*), purple non-sulfur (*Rhodobacter, Rhodomicrobium, Rhodopseudomonas, Rhodospirillum*), green sulfur (*Chlorobium*), and green non-sulfur (*Chloroflexus* and *Oscillochloris*) bacteria. Importantly, the photorophic bacteria that had been researched at the Department also included cyanobacteria that were investigated by M.V. Gusev, and unicellular algae.



Fig. 3. Elena Nikolaevna Kondratieva and Raisa Sergeevna Sumarukova setting up the Collection of Phototrophic Microorganisms in the 1960's (*Archive of the Microbiology Department*)

Comprehensive studies with each of the strains provided new scientific data. In the example of purple non-sulfur bacteria, studies were conducted concerning the flexibility of bacterial metabolism, the capacity to utilize a wide variety of organic substances during photosynthesis, and the ability to exist both in the light and the dark by switching from photosynthesis to aerobic or anaerobic respiration or fermentation. The energy-providing metabolism of phototrophic bacteria proved to be more variable than with most other microorganisms. This was of considerable interest because it provided an insight into the role of phototrophic bacteria in terms of evolution.

Comparative research on the carbon metabolism of sulfur and non-sulfur purple bacteria revealed significant differences among them with respect to the capacity to utilize and oxidize organic substances. Among these bacteria, the obligate phototroph *T. roseopersicina* is to the least extent capable of utilizing organic substances. It was established, with various bacterial species, that the mechanisms of transporting organic substances into the cells in the light and in the dark are different. These studies made it possible to elucidate the metabolic pathways that are used by phototrophic bacteria in order to utilize organic substances. It also became possible to address the question why obligate autotrophy, which is a general biological issue, exists.

Of paramount importance was the discovery that *T. roseopersicina* is capable of autotrophic growth in the dark at the expense of oxidizing sulfur compounds, i.e., of carrying out chemosynthesis (Kondratieva et al., 1976; Kondratieva, 1989). The capacity for chemosynthesis was later detected in a number of other purple bacteria.

Over the course of E.N. Kondratieva's scientific career, research on the mechanism of carbon assimilation by phototrophic bacteria was in the focus of her attention. During the studies with phototrophic bacteria, it was revealed that the Calvin cycle which is typical of all green plants and algae is not the only pathway used for autotrophic CO<sub>2</sub> assimilation. Various carboxylation processes that were revealed in phototrophic bacteria significantly contributed to our understanding of the diverse mechanisms that are used by phototrophs to utilize carbon dioxide. An important breakthrough was made in 1980 when carbon assimilation by the green sulfur bacterium C. limicola was investigated. R.N. Ivanovsky and N.V. Sintsov, who were E.N. Kondratieva's students, presented convincing evidence that carbon assimilation by green sulphur bacteria is not based on the Calvin cycle. Instead, it proceeds via the new pathway revealed in 1966 that is referred to as "the reverse citric acid cycle" ("the reductive tricarboxylic acid cycle"). A new bacterial enzyme, ATP-citrate lyase was detected; it is the key enzyme of this novel cycle (Ivanovsky et al., 1980a). Since then, E.N. Kondratieva has been considered one of the co-discoverers of the reverse citric acid cycle. This is emphasized in the review article on the history of the discovery of this cycle that has recently been submitted for publication. This article was produced on the initiative of another co-discoverer of the cycle, the prominent American scientist B.B. Buchanan (Buchanan et al., 2017, in press).

In the 1990's, research on  $\mathrm{CO}_2$  assimilation by the green filamentous bacterium  $\mathit{Cfl}$ . aurantiacus resulted in putting forward a new pathway of autotrophic  $\mathrm{CO}_2$  assimilation (Kondratieva et al., 1992). In addition, O.I. Keppen's studies on carbon metabolism in another green filamentous bacterium, O. trichoides, revealed the operation of the Calvin cycle in this species (Keppen et al., 1994). This gave grounds for classifying the bacterium into a new family.

At the turn of the XXI century, R.N. Ivanovsky's student A.I. Berg, revealed new mechanisms of utilizing acetate by purple nonsulfur bacteria and described new pathways of microbial CO<sub>2</sub> fixation. Therefore, comparative research on the physiology and carbon metabolism of phototrophic bacteria considerably enriched this field of science with new knowledge.

Elena Nikolaevna initiated the first studies on sulfur metabolism in phototrophic bacteria. The metabolism of sulfide, thiosulfate, and sulfur was studied in most details in the purple sulfur bacterium *Th. roseopersicina*, this work was regarded as classical. Sulfur metabolism enzymes were investigated for many years by E.N. Krasil'nikova.

Of considerable theoretical and practical importance was research on nitrogen fixation and molecular hydrogen production by phototrophic bacteria (Gogotov, Kondratieva, 1976). It was carried out under E.N. Kondratieva's guidance in Moscow State University (by Yu.V. Rodionov and N.V. Lebedeva) and at the Laboratory for Biotechnology and the Photosynthesis of Phototrophic Microorganisms in Pus chino (by I.N. Gogotov) that was set up with her

assistance. The research resulted in developing strategies of intensifying these processes and obtaining molecular hydrogen via bioconversion of solar energy. At the theoretical level, the mechanisms of regulation of nitrogen fixation in diverse bacteria were investigated in detail (Rodionov et al., 1986). The presence of an alternative, molybdene-lacking nitrogenase was established. The hydrogenase, the key enzyme of hydrogen metabolism, was purified and comprehensively characterized (Fig. 4). Currently, this area of research is being actively developed in Puschino under the guidance of Professor A.A. Tsygankov.



Fig. 4. An authorship certificate of E.N. Kondratieva and her coworkers: "*Thiocapsa roseopersicina* strain BBS-1, the producer of hydrogenase" (1976) (*Archive of the Microbiology Department*)

In sum, E.N. Kondratieva's studies with phototrophic bacteria represented an important contribution to research on photosynthesis in general; more specifically, the diversity of the characteristics of phototrophic microorganisms was demonstrated. The pathways of carbon, nitrogen, and sulfur metabolism were unraveled in a number of purple and green bacteria. The functioning of new pathways of autotrophic carbon dioxide assimilation was revealed, and the reasons for the obligate autotrophy of some bacteria were elucidated (Ivanovskii, 1999; 2010).

The scope of E.N. Kondratieva's research was gradually been broadening. In the 1970s, she was the first in Russia to initiate studies on the metabolism of C<sub>1</sub> compounds, such as methanol, formate, formaldehyde, and other methylated compounds in methylotrophic bacteria. This work provided foundations for the development of a number of self-contained subfields. One of them was associated with the investigation of enzymes that are involved in oxidizing C<sub>1</sub> compounds. This subject was in the focus of attention of the Enzymology Department of the Chemistry Faculty of Moscow State University that was headed by I.V. Berezin, a Full Member of the Russian Academy of Sciences, and later by S.D. Varfolomeev, a Corresponding Member of this Academy.

The second area of research deals with physiology and biochemistry of methylotrophs. It has been successfully developed under the guidance of her disciple Yu.A. Trotsenko, D. Sci. Biol., at the Institute of Microbial Physiology and Biochemistry of the Russian Academy of Science in Puschino. A new variant of the  $C_1$  compound assimilation pathway was revealed in his lab, and its key enzymes were isolated and investigated. It was at this Institute that the largest collection of cultures of methylotrophic bacteria isolated from various habitats including those existing under extreme conditions was set up in Russia. Methylotrophic bacteria have proved to be promising research subjects in terms of biotechnology; they are widely used for obtaining a number of practically important compounds.

The third subfield that is focused on the bioenergetics of methylotrophic bacteria, is further developing currently in Moscow State University under the guidance of a former Kondratieva's student, Professor A.I. Netrusov, the Head of Microbiology Department. To sum up, the pioneering studies of E.N. Kondratieva in the field of methylotrophic bacteria significantly contributed to our knowledge of the energy metabolism of such microorganisms (Ivanovsky et al., 1980b).

E.N. Kondratieva provided important guidelines for biotechnological developments that were aimed at obtaining microorganisms that produce amino acids (aspartic acid, tyrosine, and dihydrohyphenylalanine) and enzymes (cholesterol oxidase, formate dehydrogenase, alcohol oxidase, nitrogenase, and others) and identifying active producer strains and developing methods of their breeding. M.B. Kupletskaya, Yu.V. Rodionov, E.V. Zakharova, and other staff members of the Microbiology Department were involved in this research.

E.N. Kondratieva was the author of over 200 scientific publications including two monographs (Kondrat'eva, 1963; Kondrat'eva, Gogotov, 1980) and four student manuals (Kondrat'eva, 1972, 1983, 1996; Kondrat'eva, Maksimova, Samuilov, 1989). She obtained eight authorship certificates. Under her guidance, 34 scientists were awarded the Candidate of Science degree (approximately equivalent to the Ph.D. degree). Eight scientists became Doctors of Science. Among the prominent researchers that were E.N. Kondratieva's students, the names of R.N. Ivanovsky, V.D. Samuilov, I.N. Gogotov, A.I. Netrusov, Yu.A. Trotsenko, N.N. Firsov, and V.D. Fedorov are to be mentioned (Fig. 5).

As an educator, E.N. Kondratieva played an important role in the history of Moscow State University. During the course of many years, she was giving excellent lectures on *General Microbiology* as well as on more specific subfields in microbiology such as *Photrophs* and



Fig. 5. Elena Nikolaevna Kondratieva and her coworkers in 1970's. From the left to the right, sitting: R.S. Sumarukova, R.N. Ivanovsky, I.V. Malofeeva; standing: E.N. Krasilnikova, V.D. Samuilov, E.N. Kondratieva, A.I. Netrusov, unknown (?), Yu.P. Petushkova, E.Z. Monosov (Archive of the Microbiology Department)

Chemolithotrophs and Methylotrophs. She conducted specialized seminars. Her lectures were attended by representatives of other departments and by numerous students of the Extended Education Faculty (EEF) who consulted her as a qualified expert.

Several term papers and diploma works were prepared under E.N. Kondratieva's supervision. The first student to carry out a diploma project under her guidance (in 1957) was V.D. Fedorov. Subsequently, he became a prominent ecologist and the Head of the Hydrobiology Department of the Biology Faculty of Moscow State University. He also became a member of the Soviet Writers' Union. He wrote the text of Moscow State University's anthem. Fedorov once asserted that it only "made sense to do the diploma work under Kondratieva" (Ramenskii, Ramenskaia, 2000). His work was concerned with the features of a new green sulfur bacterium (Shaposhnikov et al., 1960). It was established later that some of the unusual microorganisms investigated by him, such as *Chloropseudomonas ethylica*, actually represent coherent symbiotic systems that are composed of two bacterial species. This was a new stage in the development of microbial ecology.

Elena Nikolaevna was a thoughtful, tactful, benevolent, and, nevertheless, strict supervisor. Most of the students still remember how demanding the supervisor was with regard not only to the experimental data obtained by the students but also to the quality and the style of the work produced. Students had to spend much time and effort on rewriting the work. However, in the long run, this was useful for the students involved.

E.N. Kondratieva's undergraduate and, later on, postgraduate student V.D. Samuilov, who received his Candidate of Science degree in 1969, made a significant contribution to the development of microbial bioenergetics. After defending the dissertation, he engaged in monitoring the generation of an electrochemical proton gradient during photosynthesis in various groups of phototrophic bacteria by means of membrane-penetrating ions and "flat

membrane" systems. Importantly, Samuilov closely collaborated with professor V.P. Skulachev's team at the Interdepartmental Molecular Biology Laboratory, which enabled him to successfully defend the Doctor of Science dissertation in 1979. Subsequently, V.D. Samuilov's research team expanded its area of research. Drawing upon the notion of "technical microbiology" suggested by V.N. Shaposhnikov (E.N. Kondratieva's teacher), Samuilov concentrated on biotechnology. For several years, he was in charge of the Biotechnology Center of Moscow State University. He also co-authored the books *Biotechnology: Problems and Prospects* (1987) and *Technological Bioenergetics* (1995). More recently, Samuilov conducted studies on the mechanisms of immunity, particularly in plants, and paid special attention to the phenomenon of programmed cell death.

E.N. Kondratieva was the editor of a large number of books in microbiology, translated foreign guidebooks into Russian, and wrote chapters for prestigious international manuals (Kondratieva, 1965, 1979; Kondratieva et al., 1991). The information in her books and articles was presented in a clear, logical, and simple manner, because she put in very much effort while producing them.

The main stages of E.N. Kondratieva's scientific career can be summed up as follows: defending the Candidate of Science dissertation (1953); defending the Doctor of Science dissertation (1964), becoming a Full Professor (1967). In 1981, she was elected a Corresponding Member of the Academy of Sciences of the Soviet Union. In 1992, she was elected a Full Member of The Russian Academy of Sciences. E.N. Kondratieva worked at the Microbiology Department as a junior (1954) and a senior (1959) research scientist and then as a professor (1967–1989). Since 1980, she headed the Phototrophic Organisms Laboratory at the Microbiology Department that she had founded. In 1989–1995 she was the head of the Microbiology Department (Kondrat'eva Elena... 2004)<sup>5</sup>.

E.N. Kondratieva also engaged in social activities. Since 1966, she was the president of the Moscow Section of the All-Union Microbiological Society (AMS); in 1975–1985 she was the president of the AMS, and the society flourished during this period of time. Under her guidance, two AMS meetings were held. The Sixth and the Seventh Meeting took place in Riga (1980) and Alma-Ata (1985), respectively. The AMS was involved in organizing numerous large-scale scientific conferences and meetings dedicated to the anniversaries of prominent Soviet scientists, including the  $125^{th}$  anniversary of S.N. Vinogradsky (1981) and the  $100^{th}$  anniversary of V.N. Shaposhnikov (1984). Of paramount importance was the acquisition of the international status by the AMS International scientific symposia on *Microbial Growth on C*<sub>1</sub> *Compounds* (1977) and *Regulation of Microbial Metabolism by Environmental Factors* (1983) were held. The AMS became a part of the Federation of European Microbiological Societies (FEMS) in 1979.

Elena Nikolaevna worked in collaboration with an excellent team: the outstanding Soviet microbiologists L.V. Kalakutsky, G.A. Zavarzin, M.V. Ivanov, E.G. Afrikyan (Armenian Soviet Socialist Republic), M.E. Becker (Latvian Soviet Socialist Republic), and A.N. Ilyaletdinov (Kazakh Soviet Socialist Republic).

<sup>&</sup>lt;sup>5</sup> Supplementary reading: Елена Николаевна Кондратьева: Материалы к научной биографии. М.: МАКС Пресс, 2000. 40 с.; К научной биографии академика РАН Е.Н. Кондратьевой / сост. Колотилова Н.Н. М.: МАКС Пресс, 2015. 60 с.; *Лебедева Н.В.* Памяти Елены Николаевны Кондратьевой // Автотрофные микроорганизмы: 5-й Всероссийский симпозиум с международным участием. Москва, МГУ им. М.В. Ломоносова. Биологический факультет. 21—24 декабря 2015 г.: Материалы. М.: МАКС Пресс, 2015. С. 7—10.

The 1985 meeting in Alma-Ata turned out to be the last AMS meeting, Elena Nikolaevna's term of office was over, and the new AMS president Full Academy Member G.K. Skryabin started performing his functions. However, she still was enthusiastically involved in AMS activities. Her personal role was particularly important during the establishment of the Microbiological Society of the Russian Academy of Sciences (1992).

After the disintegration of the USSR, the Microbiological Society in Russia faced a serious threat. It has no functions to perform in the capacity of an "all-Union organization". Unlike all the other former Soviet republics with republican AMS sections. Russia lacked such a section. To establish a successor Microbiological Society in Russia, it was necessary to have the consent of all republican sections and thereupon to hold the Constituent Meeting of the Society. The meeting was scheduled for January 25–26, 1992. The Archives of the Russian Academy of Sciences contain the telegrams that were sent in January 1992 by the presidents of the Microbiological Societies of former Soviet republics (CIS member states)<sup>6</sup>. They agreed to consider the Russian Microbiological Society the successor to the AMS; many telegrams were personally sent to E.N. Kondratieva. Some telegrams arrived literally at the eve of the Meeting's opening day, and this stressful moment is reflected in the documents stored in the archives. The Constituent Delegates' Meeting of the Microbiological Society was held according to the schedule at the Institute of Microbial Biochemistry and Physiology (Pushchino). The decision was made to convert the AMS into the Microbiological Society of the Russian Academy of Sciences (MSRAS), to envisage the Microbiological Society as the AMS successor in the Russian Federation, to adopt the Society's Statutes, and to support the project of establishing an association (federation or confederation) of the microbiological societies of the independent states. Full Academy Member M.V. Ivanov was elected the President of the MSRAS, and Full Academy Member E.N. Kondratieva became one of the Vice-Presidents. In establishing the MSRAS, Kondratieva showed her courage, social activity, and patriotism.



Fig. 6. Elena Nikolaevna Kondratieva in 1980's (*Archive of the Microbiology Department*)

During the course of many years, E.N. Kondratieva was the President of the Scientific Council on Microbiology of the Russian Academy of Sciences and a member of the Scientific Methodological Council of the Ministry of Higher and Secondary Vocational Education of the USSR (Fig. 6).

Elena Nikolaevna's scientific and social activities were internationally acknowledged. She was elected a Vice-President of the Federation of European Microbiological Societies (FEMS) (1985–1988) (Federation of European Microbiological Societies, 1996), an Honorary Member of the microbiological societies of Germany and Great Britain, and a member of the editorial boards of the international scientific journals *Archives of Microbiology* (Germany, 1981–1989), *FEMS Letters* (Germany, 1988–1995), and *Anaerobe* (Germany, 1992–1995).

In 1970, E.N. Kondratieva was awarded a firstdegree Lomonosov Prize for her series of scientific publications on phototrophs. In 1979, she was awarded

<sup>&</sup>lt;sup>6</sup>Архив РАН. Ф. 1874. Оп. 1. Д. 146.

the Winogradsky Prize, the supreme prize for microbiologists in this country. In 1988, she received the State Prize of the USSR. E.N. Kondratieva was decorated with the *Znak Pocheta* (Badge of Honor) Order, the *Za Doblestnyi Trud* (For Valorous Labor, 1970), *V Oznamenovanie 100-Letiya so Dnya Rozhdeniya V.I. Lenina* (In Commeration of V.I. Lenin's 100<sup>th</sup> Anniversary, 1970), and *Veteran Truda* (Labor Veteran, 1985) Medals, and with the *Izobretatel' SSSR* (Honored Investor within the USSR) Badge.

It was while a student, that Elena Nikolaevna took up equestrian sport, and interest that strongly influenced her throughout her entire life (Fig. 7). She became especially accomplished in its most sophisticated type called dressing-out (*haute école*). Elena Nikolaevna trained at the Amateur Sports Society called *Nauka* (Science) and later, since 1955, *Burevestnik* (Stormy



Fig. 7. Elena Nikolaevna Kondratieva. Horseback riding (date unknown, Archive of the Microbiology Department)

Petrel) under the guidance of the Society's founder, the gifted horseman and coach Mikhail Sergeevich Ivanov (1904–1985). His teacher was Marshal M.S. Budenny. Three times she succeeded in becoming the USSR champion in triathlon. She was a USSR Master of Sports, an international-level umpire in dressing-out and a member of the USSR Equestrian Sport Federation. It is thanks to equestrian sport that E.N. Kondratieva could travel abroad as an umpire (her first trip was to Aachen in 1970). Elena Nikolaevna worked in this capacity during many championships, including those for the World Cup and the cup of Europe; she was an umpire at the Olympics in Moscow (1980), Los Angeles (1984), and Seoul (1988) (Netrusov, 2010). Going in for sports helped her attain new successes, strengthen her willpower, organization, discipline, and persistence. Sports also improved her physical shape, enabling her to stay slim, elegant, young, and vigorous. It is no accident that reminiscences concerning Elena Nikolaevna often emphasize her quick light gate and big, bright, flashing eyes (Nefelova, 2005). Both photographs and oil paintings of Elena Nikolaevna clearing a hurdle on horseback depict this image that was copied on picture cards and the cover page of the Ogonek magazine (1954, No.7). A similar picture has for many years been decorating the three gyms-containing building in Moscow University.

Elena Nikolaevna always cherished the memories of the tragic fate of her father. After his final exoneration (1987), she made much effort to immortalize his name. She participated in organizing Kondratiev's International Foundation. E.N. Kondratieva also was a member of the Commission for N.D. Kondratiev's Scientific Legacy. She prepared for publication his manuscripts that had been kept by the family for more than fifty years. Presently, the work of N.D. Kondratiev, "the greatest scholar of the 20th century in the field of economics" (Kuzyk, Iakovets, 2004), enjoy the popularity they deserve. To a large extent, this has been the result of Elena Nikolaevna's efforts.

It seemed that Elena Nikolaevna's energy was inexhaustible, thus many were surprised when she became seriously ill and passed away on April 26, 1995. She was buried at the Vagan'kov Cemetery.

The name of the Full Academy Member E.N. Kondratieva is very popular in Russia. She lives on in the work of her students and followers; both Russian and foreign microbiologists and scholars in history of science consult her scientific work (Olson et al., 1996). To commemorate Elena Nikolaevna's achievements, the Academic Council of Moscow State University has decided to provide the most meritorious students of the Biology Faculty of Moscow State University with the Kondratieva Stipend. Once in five years (in 1996, 2000, 2005, 2010, and 2015), the Biology Faculty has been holding All-Russian Scientific Symposia on *Autotrophic Microorganisms* (with participation of foreign scientists) to commemorate the Full Russian Academy of Sciences Member Elena Nikolaevna Kondratieva. During the Fifth Symposium (2015) conducted in E.N. Kondratieva's honor, a memorial plate with her name was placed in the building of the Biology Faculty of Moscow State University (Kolotilova, Netrusov, 2016).

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## Постигая тайны существования фототрофных микроорганизмов. Академик РАН Елена Николаевна Кондратьева (1925–1995)

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Настоящая статья посвящена биографии, научному наследию и историко-научному значению деятельности академика Елены Николаевны Кондратьевой (1925–1995). В нашей стране Е.Н. Кондратьева стала основоположником всестороннего изучения метаболизма фотосинтезирующих, а затем и метилотрофных бактерий. Ее труды имели значение для развития не только фундаментальной науки, но и биотехнологии; необходимо также подчеркнуть вклад Елены Николаевны в развитие просвещения и популяризации микробиологии. Е.Н. Кондратьева основатель крупной отечественной научной школы микробиологов. Президент Всесоюзного микробиологического общества, один из лидеров развития микробиологии, она внесла большой вклад в организацию этой науки в нашей стране, а также в развитие научных связей между СССР и другими странами. Многогранно одарённый человек, Елена Николаевна оставила заметный след в истории отечественного конного спорта. О высокой гражданской позиции свидетельствует её активное участие в создании Международного фонда Н.Д. Кондратьева и реабилитации имени репрессированного учёного. В статье приведены биографические сведения о родителях Е.Н. Кондратьевой: профессоре-экономисте Николае Дмитриевиче Кондратьеве и Евгении Давыдовне Дорф, чья биография до сих пор слабо освещена в литературе. Описан жизненный путь Е.Н. Кондратьевой и её становление как учёного, проанализированы её дипломная работа и кандидатская диссертация. При этом авторы обращают внимание на историю научной проблематики, связанную как с историей кафедры микробиологии Московского университета (работы основателя кафедры профессора Е.Е. Успенского и его последовательницы профессора И.Л. Работновой), так и с классическими работами С.Н. Виноградского (открытие хемосинтеза) и К. ван Ниля (объяснение сущности бактериального фотосинтеза). Охарактеризованы основные направления дальнейшей научной деятельности Е.Н. Кондратьевой. Заметное место в работе уделено Е.Н. Кондратьевой как педагогу и основателю научной школы, как президенту Всесоюзного микробиологического общества (1975–1985), а также научным судьбам её учеников. В статье использовано большое количество малоизвестных воспоминаний о Е.Н. Кондратьевой, обогащающих представление о ней как учёном и человеке, ряд архивных данных вводится в научный оборот впервые.

**Ключевые слова:** Елена Николаевна Кондратьева, Николай Дмитриевич Кондратьев, Российское микробиологическое общество, история микробиологии, бактериальный фотосинтез, автотрофы, метилотрофы, биотехнология.