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TRIBUTE

Remembering Navasard V. Karapetyan (1936–2015)

Nadezhda P. Yurina[1] · Vladimir O. Popov[1] · Alexander A. Krasnovsky Jr.[1] · Govindjee[2]

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Abstract Navasard Vaganovich Karapetyan (September 6, 1936—March 6, 2015) began his scientific career at the Bach Institute of Biochemistry of the Russian Academy of Sciences, Moscow, and was associated with this institute for over 56 years. He worked in the area of biochemistry and biophysics of photosynthesis and was especially known for his studies on chlorophyll *a* fluorescence in higher plants and cyanobacteria, molecular organization of Photosystem I, photoprotective energy dissipation, and dynamics of energy migration in the two photosystems. We present here a brief biography and comments on the work of Navasard Karapetyan. We remember him as an enthusiastic person who had an unflagging curiosity, energy and profound sincere interest in many aspects of photosynthesis research.

This tribute was read, edited and accepted by Thomas D. Sharkey, Associate Editor, Photosynthesis Research. He wrote: This is a nice tribute; it gives nicely a sense of Navasard as a wonderful person, and his importance to photosynthesis.

✉ Nadezhda P. Yurina
nyurina@inbi.ras.ru

Vladimir O. Popov
vpopov@inbi.ras.ru

Alexander A. Krasnovsky Jr.
phoal@mail.ru

Govindjee
gov@illinois.edu

[1] Bach Institute of Biochemistry, Research Center of Biotechnology of the Russian Academy of Sciences, 33, bld. 2, Leninsky Ave., Moscow, Russia 119071

[2] Department of Plant Biology, Department of Biochemistry, and Center of Biophysics & Quantitative Biology, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA

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Early life and education

Navasard (N.) Vaganovich (V.) Karapetyan was born in Leninakan (now Gyumri), Armenia, on September 6, 1936. He passed away on March 6, 2015, in Moscow, Russia. Both his father (Vagan Karapetovich Karapetyan; 1904–1974) and mother (Ofeliya Vagarshakovna Tovmasyan; 1913–2006) were biologists, and had come from Armenia to Moscow.

In 1953, after early education at the secondary school No. 7 in Moscow, Navasard entered the Department of Biology and Soil of the M. V. Lomonosov Moscow State University, and graduated in 1959. As a student of biology (specialization: physiology of plants), Navasard (Navik—to his many friends around the World) Karapetyan had the privilege of attending the course of photobiochemistry taught by Professor and Academician Alexander A. Krasnovsky, a world-recognized leader in biochemistry. (We note that this was the first course on this subject in the Soviet Union and Moscow University.) Inspired by lectures in this course, Karapetyan joined Krasnovsky's laboratory first, as a student, then later as his colleague. In our view, this decided the scientific fate of Navasard Karapetyan. His whole life was connected with research in photobiochemistry of photosynthesis and with the Bach Institute of the Soviet (Russian) Academy of Science, where he worked from 1957 until the last days of his life.

In 1963, N.V. Karapetyan received his Ph.D. degree (Candidate of Science) in biology, working on "The

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mechanism of primary process of photosynthesis", from the A.N. Bach Institute of Biochemistry of the Russian Academy of Sciences (RAS). And, in 1975, he obtained his habilitation (Doctor of Science) degree, from the same institute, for his work on "Light conversion of photosystems of photosynthetic organisms"; this research was devoted to the so-called "light reactions" of chlorophyll in evolutionarily different groups of photosynthetic organisms. As the main experimental tool, Karapetyan used measurements of photo-induced absorption and fluorescence changes of chlorophyll *a* in vivo under varying redox conditions affecting the state of electron transfer carriers. Later, for training PhD students (there were 8), he was awarded the title of Professor and from 1987 to 2015 he served as the Head of the laboratory of Chloroplast Biochemistry at the A.N. Bach Institute. In 1991, he became one of the laureates of the USSR State Prize for Science, which was awarded to the school of Academician Krasnovsky (A.A. Krasnovsky; Yu. E. Erokhin; V.B. Evstigneev (posthumously); N.V. Karapetyan; A.V. Klevanik; V.V. Klimov; and V.A.Shuvalov) for studies on the photobiochemistry of chlorophylls. Figure 1 shows Karapetyan in his office in 2015.

Research

Karapetyan's research centered on the photobiochemistry of plants and bacteria, with a focus on the protective mechanism of dissipation of excess absorbed light. He started from investigations on variable chlorophyll (Chl) *a* fluorescence in Photosystem II (PSII), as well as in PSI of plants (Karapetyan et al. 1963, 1973; Karapetyan 1977; Klimov et al. 1976). Later he worked with the structural organization of PSI complexes in cyanobacteria, origin of the long wavelength chlorophyll *a* forms in PSI and the role of these spectral forms in energy migration, charge separation, and dissipation of excess absorbed light (Shubin et al. 1992, 1993). Unlike higher plant PSI, cyanobacterial PSI is organized preferentially as a trimer of monomeric PSI units, enriched in long wavelength absorbing chlorophyll *a* whose spectral characteristics vary in different species of cyanobacteria. Developing the earlier concepts of Academician Krasnovsky, Karapetyan suggested that the long wavelength absorbing forms of chlorophyll *a* in PSI are aggregated chlorophyll molecules, which might have formed by interaction of pigments peripherally located on different monomeric units within the PSI trimers (Brecht et al. 2012; El-Mohsnawy et al. 2010; Karapetyan 2007, 2008; Karapetyan et al. 1999a, 2014; Schlodder et al. 2005, 2007, 2011, 2014).

Further, Karapetyan's research group focused on understanding the mechanism of non-photochemical quenching (NPQ) of long wavelength fluorescence of chlorophylls in cyanobacteria, which is due either to the formation of the cation radical or the triplet state of the reaction center Chl a of PSI (P700) (Shubin et al. 1991; Karapetyan et al. 1999b; Schlodder et al. 2005). Also, a new mechanism of OCP (orange carotenoid protein)—triggered quenching of phycobilisome fluorescence was studied in Karapetyan's laboratory (Karapetyan 2008; Rakhimberdieva et al. 2004, 2007, 2010).

Fig. 1 Navasard Vaganovich Karapetyan in his office, 2015. Photo from Bach Institute's archive

Collaborations

Karapetyan's collaborative spirit in research is shown by his work carried out with other groups of the A.N. Bach Institute, laboratories of the Lomonosov Moscow State University, of the Institute of Photosynthesis and Fundamental problems of Biology (Pushchino, Russia), and with several institutions in Germany (Plant Biochemistry, Faculty of Biology and Biotechnology of Ruhr-University-Bochum, Max-Volmer Laboratory for Biophysical Chemistry, Faculty of Chemistry, Technical University Berlin; Institut für Biophysik, J.W. Goethe Universität Frankfurt; Institute of Physical and Theoretical Chemistry, Tübingen University, among others). Further, Navasard Karapetyan had also served, for many years, as a visiting professor at the Max Planck Institute for Chemical Energy Conversion, Mulheim, Germany. In addition, he had collaborations at universities and research centers in France, Switzerland, The Netherlands and India.

Fig. 2 FEBS (Federation of European Biochemical Society) Conference, Moscow, 1984. *Left to right* Jan Amesz*, Alexander A. Krasnovsky*, Govindjee, Peter Böger, Helmut Metzner*, and Navasard Karapetyan* (*deceased). Photo from Bach Institute's archive

Fig. 3 Karapetyan discussing the conference program with colleagues in front of the portrait of A.N. Bach, 2003. *Left to right* Vyacheslav Klimov, Alexander Chibisov, Navasard Karapetyan and Vladimir Shuvalov, at the meeting dedicated to the 90th birthday of academician Alexander Krasnovsky. Photo from Bach Institute's archive

Fig. 4 Navsarad Karapetyan speaking at the Conference dedicated to the 100th birth anniversary of academician Alexander Krasnovsky. Standing next to him is J.W. Schopf. Standing on the far *right* is Vyacheslav Klimov asking a question. In the foreground (sitting): *Left to right* James (Jim) Barber, Robert (Bob) Blankenship and Govindjee. Photo from Bach Institute's archive

Fig. 5 Navasarad Karapetyan (*right*) with Nelli A. Ambartsumova (*left*) at their home in Moscow in August 2006. Photo provided by Matthias Rögner

Navasard Vaganovich Karapetyan was one of the recognized leaders in photosynthesis research: he was frequently invited as a speaker, and served as a member of several organizing committees of international and national scientific conferences. In particular, in 2013, Karapetyan was appointed to co-chair the International Conference dedicated to the 100th anniversary of the birthday of his teacher, academician A.A. Krasnovsky. This conference, chaired by V.O. Popov, Director of the Bach institute and corresponding member of the Russian Academy of Sciences, took place at the Headquarters of the Russian Academy of Sciences during October 10–11, 2013. Figures 2, 3 and 4 show Karapetyan's photographs taken during different scientific meetings in Moscow. Three coworkers from his laboratory (Yulia Bolychevtseva, Irina Terekhova and Vladimir Shubin) wrote: "Navasard has left us with warm memories; he will remain an example of an energetic worker with true dedication to science and genuine enthusiasm in solving science problems for us."

Navasard Vaganovich Karapetyan leaves a legacy of more than 250 research papers and reviews in the field of biochemistry and biophysics of photosynthesis, a well equipped laboratory with qualified researchers. He is survived by his wife Nelli Avetisovna Ambartsumova, a teacher of music, and two sons Ruben (a molecular biologist) and Karen (a biochemist) and three grandchildren: Mikhail, Eduard and Nikita. Figure 5 shows Navik's

photograph with his wife Nelli, and Fig. 6 shows him at the Bolshoi theatre. We (and others; see below) will remember Navasard Vaganovich as an enthusiastic researcher, who dedicated most of his life to science.

Remembrances

Remembrances received, from others, are presented below (in alphabetical order).

Vyacheslav Klimov (Institute of Basic Biological Problems, RAS, Pushchino; klimov@rambler.ru)

Navik was my teacher as well as my friend. In 1967–1968, when I was a student of the Moscow State University (MSU), I worked for my diploma under his supervision, in the laboratory of academician Alexander Krasnovsky (at the A.N. Bach Institute of Biochemistry, Russian Academy of Sciences). It was Navik who had sparked my interest in the investigation of photosynthetic reactions of plants, using differential absorption and fluorescence spectroscopy. Later when I became a Ph.D. student at MSU (with A.A. Krasnovsky and N.V. Karapetyan as my supervisors), we constructed a set-up, which used a phosphoroscope available in Navik's group, and an additional modulated weak measuring light at a frequency that was used for measuring changes in the yield of chlorophyll fluorescence, upon illumination by actinic light of practically any spectral distribution and intensity (Karapetyan and Klimov 1971). This set-up must have been a prototype of pulse amplitude modulated (PAM) fluorometers, which appeared later.

These were really very exciting times! Together, we showed, for the first time, that the reaction centers of Photosystem II (PS II) (as well as of purple bacteria) remain photochemically active even after reduction (with dithionite) of the primary quinone electron acceptor, Q_A; we had observed this reaction via photoinduced decrease ($-\Delta F$) of chlorophyll a fluorescence (practically to the level Fo) (Karapetyan et al. 1971, 1973; Karapetyan and Klimov 1973). Since these negative photoinduced ΔF (and corresponding absorbance change, ΔA) reversed too slowly in the dark, and since this photoreaction had a low quantum yield, we, at that time, ascribed it to a "reductive photoinactivation" of PS II. Four years later, in 1977, we found the conditions (Eh of −200 to −400 mV) for the photoinduced ΔF (as well as the corresponding ΔA) to become completely reversible in the dark (Klimov et al. 1977). The analysis of these results led to the conclusion that these photoreactions are associated with reversible photoreduction of pheophytin acting as the primary electron acceptor in PS II reaction centers.

Jointly with Navik, we showed, for the first time, that PS I also has photoinduced ΔF and that this is related to reversible photooxidation of P700 (Karapetyan et al. 1973). I would like to emphasize again that Navik was for me not only a teacher, a senior colleague, but also a good friend, and an adviser in both science and life in general (Fig. 7).

Fig. 6 Navasarad Karapetyan at the Bolshoi theatre in Moscow in September 2013 after the International Conference dedicated to the 100th birth anniversary of A.A. Krasnovsky. Photo provided by Matthias Rögner

Fig. 7 The Xth Congress on Photosynthesis, held in Montpellier, France, August, 1995. From *left to right* Vyacheslav Klimov, Vladimir Pyankov, Navasard Karapetyan, Gyozo Garab. Photo provided by Vyacheslav Klimov

Matthias Rögner (Ruhr-University Bochum; matthias.roegner@rub.de)

Navik Karapetyan was a frequent and distinguished guest, in my department, at the Ruhr-University in Bochum, Germany. We had a very fruitful as well as a very enjoyable collaboration on Photosystem (PS) I of cyanobacteria; most interesting results were obtained with *Spirulina platensis* and *Thermosynechococcus elongatus*. Our results on purified monomeric and trimeric PSIs from *Spirulina*, reconstituted into liposomes, led us to conclude that the long-wavelength chlorophyll *a* fluorescence band with a peak at 760 nm (F760) originates from PSI trimers, as it disappears when trimers disassociate into monomers; the latter was proven by increasing [$MgSO_4$] in the medium (Kruip et al. 1999). Further, using highly purified PSIs, from *T. elongatus*, we were able to isolate an intact monomeric PS1 complex, which preserves all the subunits and the photochemical activity of the isolated trimeric complex. We were able to conclude from these studies that dynamic equilibrium exists between the monomers and the trimers in the thylakoid membrane; further, we observed a good correlation between the higher activity of the trimers, under red light, and the presence of a long-wavelength form of chlorophylls, which, in turn, was dependent on the phase transition temperature of the lipids (El-Mohsnawy et al. 2010).

Speaking of the personal side of Navik, collaboration with him was always a pleasure, and most enjoyable due to his special sense of humor, and very special jokes. We show here a photograph of Navik with me (Fig. 8) and another with Alfred Holzwarth (Fig. 9), with whom he had collaborated in Muelheim, Germany (Karapetyan et al. 1999a).

Fig. 8 Navasarad Karapetyan at a dinner with Matthias Rögner in Moscow in August 2006 at a meeting in Pushchino. Photo provided by Matthias Rögner

Fig. 9 *Left to right* Navik's wife Nelli, Chavdar Slavov (a coworker of Alfred Holzwarth) Navasarad Karapetyan, and Alfred Holzwarth at Navik's home in Moscow in August 2006. Photo provided by Matthias Rögner

Navik not only had an outstanding knowledge of science, especially photosynthesis, but he was also a gourmet of food and loved and offered excellent drinks. The warm welcome and the excellent hospitality at his home by Navik and his family, in Moscow, were absolutely unique. No guest could ever forget his skillful variations of "toasts" when introducing his favorite vodka before starting a delicious Armenian dinner.

I end my remembrance of Navik by mentioning what he meant to the young researchers: He was extremely helpful to them, giving them detailed explanations and practical hints for their work, and this was because of his profound basic knowledge of the field of his research. We will all miss his friendly and stimulating attitude very much!

Eberhard Schlodder (Max-Volmer-Laboratorium Technische Universität Berlin; e-mail: Eberhard.schlodder@alumni.tu-berlin.de)

I do not only want to remember Navik as an excellent scientist, with whom I had worked for more than 15 years, but also as a very friendly and wonderful warm person. During our collaboration, a very nice personal relationship had developed and a wonderful friendship evolved. Yes, the research was a truly fruitful collaboration resulting in more than 11 joint publications. I remember his more-than-a week yearly visits to Berlin when he brought to us new ideas on interesting experiments. His research focused on the organization and function of long-wavelength (red/far-red-absorbing) chlorophylls in Photosystem I (PSI) of cyanobacteria, plants and algae (Witt et al. 2003). He provided us with preparations of monomeric and trimeric PSI complexes from *Arthrospira platensis*. During his stay in Berlin, he also visited us at home and we made many trips together in Germany; he also played with our children and was always interested in their development. Quite often he told us fascinating anecdotes from the history of the photosynthesis community. (I note that long before our

collaboration began, Navik had already attended, in 1968, the First International Congress on Photosynthesis, organized by Late Helmut Metzner in Freudenstadt, Germany.) We enjoyed Navik reminiscing about his experiences from his long-standing scientific career. Last but not the least was Navik's warm-hearted hospitality when we were invited to visit him at his home in Moscow. We miss you Navik.

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