



Remembering Professor Krishna K. Tewari (1937–2017): A Pioneer in Plant Molecular Biology

ABSTRACT

Professor Krishna K. Tewari (1937–2017) was a pioneer in plant molecular biology and biochemistry. He was a professor and served as the Chairman of the Department of Molecular Biology and Biochemistry at the University of California, Irvine, and was the founder-director of the International Centre for Genetic Engineering and Biotechnology, New Delhi, India. His research was focused on understanding the structure and function(s) of plant mitochondrial and chloroplast genomes, identification of aminoacyl-tRNA in the chloroplast genome, identification, and characterization of the large subunit of RUBISCO, chloroplast DNA polymerase, and topoisomerase I and II. Krishna Tewari also mentored and trained several young scientists. Here, Krishna's students, friends, and colleagues from the community of plant biology have put together a tribute commemorating his memory as a loving human being, a great leader and administrator, and above all an excellent plant biologist.



Figure 1: A photograph of Dr. Krishna Kumar Tewari (1990s). Source: Tewari family.

Krishna Kumar Tewari (Figure 1) was born on September 13, 1937, in a small village in Uttar Pradesh, India. He was the youngest of five children; he had an older brother and three sisters. His mother died when Krishna was only eight months old and he was cared for by his paternal grandmother. Krishna earned his B.Sc. in 1955 and M.Sc. in Biochemistry in 1957, both from the University of Lucknow, India. He then joined the research group of Professor Padmanabhan S. Krishnan in the Department of Biochemistry, University of Lucknow. He completed his Ph.D. in 1960, and then, for four years, he was a Lecturer at the same University. His early research was focused on the role of phosphates in the metabolism of fungi and plants.

In 1964, Krishna joined the laboratory of Professor Henry R. Mahler, of Indiana University, as a postdoctoral researcher and worked on yeast mitochondrial DNA. In 1966, he moved to the laboratory of Professor Samuel G. Wildman at the University of California at Los Angeles, where he had his first big breakthrough with the isolation of chloroplast DNA (cpDNA) from tobacco, published in *Science* [1]. After this, there was no stopping of top research in the field of cpDNA biology; see [2–6]. He

continued his studies on chloroplasts at the University of California, Irvine (UCI). For his outstanding & novel scientific contributions, he was appointed, in 1969, as an associate professor and promoted to professor in 1975. From 1979–1994, Krishna served as the Chairman of the Department of Molecular Biology and Biochemistry at UCI. He retired from there in 2005.

1. Krishna Tewari's research contributions

Krishna was the first to demonstrate that extrachromosomal genetic determinants lie within the chloroplast and have distinct characteristics from nuclear genomic material [1]. He demonstrated that cpDNA contains the complements of RNA from 70 S ribosomes but not the segments coding for RNA from 80 S cytoplasmic ribosomes [3]. Krishna was also able to isolate the DNA polymerase and DNA-dependent RNA polymerase from the tobacco chloroplast and provided unambiguous proof of its activity compared to the nuclear DNA polymerase [2]. Next, he showed that the cpDNA is not associated with histones in contrast to the nuclear DNA [4]. Krishna was also the first to show that mitochondrial DNAs from higher plants exist in the closed circular form [7]. Using the molecular hybridization techniques, he studied 70 S ribosomal RNA genes and showed that they are highly conserved and show little divergence between mono- and di-cotyledonous plants [8]. Krishna then focused on the mechanism of replication of cpDNA [9–13]. His other major contributions include identification of aminoacyl-tRNA in the chloroplast genome [14], identification and characterization of the large subunit of RUBISCO [15], cpDNA polymerase [16], plastid-specific topoisomerase I, and II [17–19] and a single-strand DNA-specific endonuclease [20]. Next, he studied the *in vitro* replication and identified the origin of replication sequences and other proteins, including a helicase likely associated with the replication in chloroplasts [21]. These contributions have left a lasting legacy of major discoveries in plant molecular biology and many fundamental facts about the chloroplast

genome.

Krishna mentored many students during his career who went on to have successful careers in science. He was a sought-after research leader and an administrator. In 1988, he was appointed as the founding Director of the International Centre for Genetic Engineering and Biotechnology (ICGEB), New Delhi, India, by Professor Irwin C. Gunsalus, then its Director-General. Since this center was established in 1983 by the United Nations Industrial Development Organization to help developing countries in the field of biotechnology, Krishna was very excited to have this opportunity to give back something meaningful to India, his country of origin. He put together a strong research team at the institute and cared very deeply about their well-being and success. He also initiated the Ph. D. program at ICGEB in collaboration with Jawaharlal Nehru University (JNU). After successfully establishing and leading it for ten years as its director, Krishna left ICGEB in 1998.

2. Personal reminiscences by some of Krishna's friends

We present below the Reminiscences by Richard Kolodner, Brent L. Nielsen, Navin Khanna, Chalivendra C. Subbaiah, Amos Gaikwad, Narendra Tuteja, Sudhir K. Sopory, and Dharendra Kumar (one of the authors).

Richard Kolodner, Professor, UC San Diego, CA, USA:

I first met Krishna Tewari in the late 1960s when I was an undergraduate student at UCI. I later did undergraduate research in his laboratory and, in 1971, joined Krishna Tewari's lab as a graduate student at UCI in the Department of Molecular Biology and Biochemistry. It should be noted that what was Molecular Biology then was not what we think of as Molecular Biology now, as methods such as restriction mapping, DNA sequencing, cloning, and many others had not yet been invented. As a Ph.D. thesis project, Krishna suggested that I investigate the structure of the chloroplast genome using electron microscopy. Based on the work on mammalian mitochondrial DNA, he hypothesized that the chloroplast genome might have a circular DNA molecule. It was an extremely frustrating project that I mostly remember as an endless series of failed experiments. Regardless, Krishna was always there to encourage me to do the next experiment. Ultimately, I was able to visualize circular cpDNA molecules in the lysate of chloroplasts, and, at the time, these circular DNAs were the largest circular DNAs yet discovered. I then purified large amounts of intact cpDNA to characterize the structure and replication of cpDNA, and we published 14 papers (see selected references 6–7, 9–12). I learned many things about being a successful scientist from Krishna: key among these were that with hard work, I could succeed working on very difficult projects, not to be afraid of trying new methods, and move into new areas to advance my work. The confidence he imparted on me has helped me have a successful career. Krishna also encouraged me to have some fun, introduced me to many great scientists of the time, and Indian food, including mango pickles. This taught me to be comfortable interacting with scientists (who seemed unapproachable to someone as young as I was at the time). I am very thankful to have been able to work with Krishna.

Brent L. Nielsen, Professor, Brigham Young University, Provo, UT, USA:

I joined Krishna's lab in April of 1985 as a postdoc at UCI after completing my Ph.D. at Oregon State University, Corvallis, OR. My project was to purify and characterize cpDNA polymerase and other replication proteins, including topoisomerase and DNA primase. I was impressed with Krishna's ideas and motivation for research, and his ability to obtain significant funding. During my time at UCI, Krishna started going to India fairly often to help establish ICGEB. I remember working closely with other graduate students and postdocs in the Tewari lab, including Bob Meeker, V.K. Rajasekhar, Eric Sun, and Bor-Wen Wu. Some fond memories of personal interactions with Dr. Tewari and his family were at dinners at his home, where his wife, Dr. Sujata Tewari, would spend days preparing wonderful Indian food. After I moved to my first faculty position at Auburn University in Alabama, I returned to visit a couple of times and enjoyed visiting with Krishna. I especially enjoyed the retirement celebration for him, when many former students and postdocs returned and gave research talks, and we enjoyed a great dinner. After I moved to my current position at Brigham

Young University in Utah, my wife, youngest son, and I visited Krishna at his home in Irvine. Krishna was very friendly with our young son, who was impressed by Krishna's knowledge and experiences. My time in Krishna's lab was extremely helpful to me in preparing for a career as an academic scientist. He helped strengthen my love and appreciation for molecular biology and how it can help people in so many ways.

Navin Khanna, Arturo Falaschi Emeritus Professor, ICGEB, New Delhi, India:

I met Professor Krishna Tewari for the first time in 1988. I was then a postdoc at UC San Diego. He offered me a job at ICGEB, New Delhi, India, and guided me to set up a new Recombinant Gene Products Laboratory. Because of his timely support and encouragement, my laboratory developed high-performing yet affordable diagnostic kits for viral infections, such as HIV, Hepatitis B, Hepatitis C, and Dengue virus infections. We also collaborated on research involving the chloroplast transcription complex. My hero, Professor Krishna Tewari, had a way with people, and I miss him.

Chalivendra C. Subbaiah, Louisiana State University, Baton Rouge, LA, USA:

I first met Dr. Tewari when he visited my poster at the Indo-US Binational Symposium on Photosynthesis at JNU, New Delhi. My poster had described work on DNA-binding proteins induced in cyanobacteria and chloroplasts by DNA-damaging agents. Later, I got an opportunity to work with him on cpDNA replication at ICGEB. Dr. Tewari was as influential in understanding cpDNA replication and transcription as Dr. Arthur Kornberg was to E. coli DNA replication.

Amos Gaikwad, Scientist, Baylor College of Medicine, Houston, TX, USA:

My initial interaction with Dr. Krishna Tewari was at UCI when I joined the department as a postdoctoral fellow. It was pleasing to have candid conversations in Hindi with Dr. Tewari. He would often enquire about my family, research project, and if I needed any help in the process of my settling down at UCI. Later, I joined Dr. Tewari's group at ICGEB, New Delhi. I had fruitful, educational, and productive years working on the understanding of DNA replication in plants.

Narendra Tuteja, Senior Scientist, ICGEB, New Delhi, India:

It is indeed a great honor for me to write about my experience and wonderful association with Professor Krishna Tewari at ICGEB in Italy and then in India. In 1995, I joined ICGEB New Delhi to initiate research in plant molecular biology and conducted collaborative research on plant helicases with Dr. Tewari and we published the first report of purified helicase from plants [21].

Sudhir K. Sopory, Emeritus Senior Scientist, ICGEB, New Delhi, India:

I met Dr. Krishna Tewari personally, for the first time in 1996 at JNU, New Delhi. I already knew about his seminal contributions in the area of chloroplast biology, and my interests were on 'light signaling in higher plants' and I had also worked on phytochrome development of chloroplast in etiolated seedlings at JNU and on the regulation and turnover of thylakoid D1 protein at USDA. Our discussions were intense and highly enriching for me. Later, I decided to join ICGEB and held regular meetings with Dr. Tewari. With his suggestions, I decided to focus on areas that will also have biotechnological applications in agriculture. Soon, I was asked to head the Plant Molecular Biology Group at ICGEB. Our group published high-impact papers on plants under abiotic as well as biotic stress. Dr. Tewari had great insights and experience in Institute building. It is because of his thorough and in-depth knowledge of overall biology that ICGEB worked in many areas, other than just the plants. I consider it remarkable that Dr. Tewari provided critical feedback to every manuscript to be sent for publication from ICGEB. Dr. Tewari was also very particular that all the researchers should deliver the best talks. In fact, before making a presentation at the Scientific Advisory Committee of ICGEB, which usually had many top scientists from across the globe, including Nobel Laureates, he would review the presentation of each of the scientists. Being with him was a wonderful learning experience for me. I also had the privilege of being a co-author of a paper on topoisomerase II [19]. Dr. Tewari will be remembered for his contributions to the field of plant biology, for his mentorship abilities, and as an institution builder.

Finally, we end this section on reminiscences with remarks from one

of us (**Dhirendra Kumar**):

*I joined the plant molecular biology group at ICGEB as a research technician in 1990. Sometimes in 1993, my immediate supervisor, Dr. Sunil Mukherjee, told me that Dr. K.K. Tewari would like to meet me. I was told that he was impressed by the protein gels and western blots that I had generated for a research paper [20]. Shortly afterward, Dr. Tewari came to the lab, briefly chatted with me, and inquired about my future career plans. Later he encouraged me to pursue doctoral studies. Since, at that time, ICGEB did not have a Ph.D. program, I registered myself at the University of Lucknow under the supervision of Dr. Krishna Tewari and Dr. Hriday N. Verma. My research focused on the cloning and characterization of a gene encoding systemic resistance-inducing protein from *Clerodendrum aculeatum*. Dr. Tewari provided close supervision and ensured that I had all the resources needed to conduct my research at ICGEB successfully. For my thesis defense, he traveled with me from New Delhi to Lucknow (and even paid for my airfare). After completing my Ph.D., he encouraged me to seek a postdoctoral position. Soon, I got a positive response from Dr. Daniel F. Klessig to join his group at Rutgers University. Later, I moved with his group to Boyce Thompson Institute for Plant Research at Cornell University, Ithaca, NY. Dr. Tewari was a great mentor, very caring, and full of fun person. We all miss him.*

3. Epilogue

Krishna was a leading scientist and a very generous, kindhearted, fun-loving human being who had a lot of faith in others. He was a member of the International Plant Molecular Biology Association; Royal Institute of Chemistry (UK); Scandinavian Society of Plant Physiology; American Society of Plant Biology; The American Society for Cell Biology; and The American Society Biochemistry and Molecular Biology. His family, friends, and colleagues around the world remember him fondly.

On 17 March 2017, Krishna Tewari died at his home in Irvine, California. He is survived by his two sons, Krishnansu and Devansu. His family has established two graduate student awards in honor of Dr. Krishna K. Tewari and his wife, Dr. Sujata Tewari (1939–2000). These scholarships are given annually to one student from the Biological Sciences School and one from the School of Medicine at UCI (<https://www.bio.uci.edu/tewari-gift-brings-two-new-graduate-scholarships>). We are thankful to the Tewari family for providing us with his CV and his photograph.

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