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LETTER TO THE EDITOR

Forty years of research on the assembly and infection process of bacteriophage

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Abstract

This short biographical note was written as part of the lead-in material for a festschrift kindly organized for me on the occasion of my 70th birthday. The collection of articles assembled in this issue range within the spectrum of the topics covered in the special issue 'Multiscale structural biology—biophysical principles and practice ranging from biomolecules to bionanomachines.' Here I describe some of the high points of my 40 years of research science conducted in the USA, Switzerland and Japan. I also use this opportunity to express my sincerest thanks to my former colleagues and the very many contributors who so kindly contributed to this special issue.

I was admitted to the University of Tokyo in April 1968. The academic stream which I had chosen and for which I was accepted was Natural Science II, where not only mathematics, physics and chemistry, but also biology were required courses of study. I was originally not much interested in biology and wanted to pursue physics, but the biology lectures given by Prof. K. Maruyama were very interesting. I learned that there was a field called "biophysics" and gradually came to the conclusion that biophysics may be the direction to go. Two months after I had been admitted the university, there was a student strike, the so-called "Todai-Toso" or "Student Riot." At the University of Tokyo, the strike started when a student at the medical school got punished. There were no lectures. We students held meetings every day, discussed the problems and decided which direction/position we should take further. The strike went on, but some of the members of my class (including me) decided that we would like to study anyway, so we visited professors and asked for seminars. Professor Maruyama, an associate professor at that time, who was teaching introductory biochemistry to us, accepted our proposal and suggested that we meet in a seminar room once every week. These sessions were called "Rindoku seminars" and involved reading papers that he chose for us from Scientific American and which we then in turn translated sentence by sentence into Japanese. From time to time, he made comments on our translation and the contents. Among the papers which we read, I still remember one by Arthur Kornberg on DNA replication and another by Hugh Huxley on the "sliding theory" of muscle. In retrospect, these Rindoku seminars were an important moment which changed my future academic direction from physics to biological science. Prof. Maruyama emphasized that students who wish to study in biology should learn physics and chemistry. As I recall, it was not in the laboratory, but more likely in a pub near the campus that he often talked to us on his philosophy of science while drinking beer or "sake." I recall him often saying that when there is an "activity" in the body or in a cell, there must be some activity which counteracts it; he further added that that is something which one would not find in the physical sciences. Another notable remark was that "When you work on research, it is very important to choose the material. For example, if you want to work on muscle proteins, rabbit muscle would be the best, but if you like to work on the electrophysiology of muscle, you may want to choose the frog."

The strike was eventually over. The events taken as a whole were not beneficial for learning science, but they did give me the chance to think about social problems and the meaning of science which otherwise I would not have thought about.

During my fourth year of undergraduate studies, I was able to work in Prof. Maruyama's laboratory for the whole year

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where I studied the contraction of actomyosin fiber upon addition of ATP. To make the actomyosin fiber, we spread a concentrated actomyosin solution over the surface of a buffer solution in the Langmuir trough. The partially denatured actomyosin layer made fibers, and the generated force was measured under various conditions.

Before I entered graduate school, Prof. Maruyama moved to Kyoto University. In response to my inquiry as to where I should go, he suggested that I go to the laboratory of Prof. Haruhiko Noda who was a biophysical chemist. The title of my project for my Masters thesis was the kinetic aspects of actin polymerization. In that project I observed actin polymerization by measuring released ^{32}P-labeled phosphate and changes in flow birefringence upon polymerization. Some electron microscopy data of the time-dependent length distribution of actin filaments were measured by Dr. Kawamura, who also worked in the laboratory, and made available to me. The time-dependent length distribution was simulated by solving differential equations of polymerization by the Runge–Kutta–Gill method. The aim of my Master's project was to explain the mechanism of polymerization and depolymerization of actin.

At the time I started working in Prof. Noda's laboratory, Dr. Ikai had just come back from the USA and was an Assistant Professor. He had obtained his Master's degree in Prof. Noda's laboratory and then had gone to the USA where he obtained his Ph.D under the supervision of Prof. C. Tanford at Duke University. Conversations with Dr. Ikai awakened an interest in studying abroad for my Ph.D. Dr. Ikai mentioned that studying abroad as a student has a number of advantages over going abroad as a postdoc, including English development, a closer relationship with the professor of a major laboratory, as well as working with individuals in the academic world, many of whom would likely become friends for life. I wrote letters to Professors S. Timasheff, C. Tanford and K. Van Holde according to his advice. Based on their replies, I decided to go to Prof. Van Holde's laboratory at Oregeon State University (OSU), mainly because he indicated that I could get a scholarship there from the first year onward.

There was some financial problems to going abroad. My father had passed away in 1970 when I was a sophomore and as such I was not able to receive any financial support from my family. Dr. Ikai encouraged me to apply for a scholarship from the Japan Society for the Promotion of Science (JSPS). There was a fellowship for students who wished to study in the USA which was very competitive; students from all fields, including the humanities, were eligible to apply, and only 16 were to be selected—but I sent in an application anyway without very high expectations. It turned out that I was very lucky and was one of the 16 students selected; the fellowship paid for the tuition, travel costs as well as some living expenses for 1 year at OSU. I then finished my Masters course in Prof. Noda's laboratory in March 1974. As several months remained before I could leave for the USA, I stayed in the laboratory and carried out more experiments for publication. The results were published in *Biochimica et Biophysica Acta* in 1975 (Arisaka et al. 1974).

I departed from Haneda Airport in July 1974 for San Francisco. It was the first flight of my life. The first destination was Austin, Texas, because JSPS had arranged for all 16 recipients of the fellowship to go to somewhere different from the final destination, i.e. the respective graduate school, to improve our ability to communicate in English and to give us the chance to learn some aspects of American culture that foreign students should be aware of. For example, I remember the instructor saying that it was not considered intrusive or impolite to talk about religion with a host family, but it was not wise to talk about politics. It was a very hot summer, but I enjoyed my 6-week stay in Austin and the the special English course. During the English course, we visited several places, including the capital building of the State of Texas and NASA in Houston. After the course, I visited a couple of friends, Kazuo Sutoh and Hiroshi Mizutani, who lived on the East Coast. At that time, Kazuo had a postdoc position at Johns Hopkins University where he was doing research on myosin in the laboratory of Prof. William Harrington and Hiroshi was a Ph.D. student studying the origin of life under the guidance of Prof. Cyril Ponnamperuma at the University of Maryland. Both were former students of Prof. Noda. After the visit, I flew over the continent to the West Coast and arrived in Corvallis, Oregon at the end of September and met Prof. Ken E. Van Holde. The rainy season was just about to start.

Prof. Van Holde offered me two research options for my Ph.D project, namely, chromatin or hemocyanin. After some consideration, I chose hemocyanin because I thought it may give more quantitative results; however, I also recognized that I did not have courage to immediately jump into the very competitive field of chromatin biology. To obtain hemocyanin from the shrimp, *Calianassa californiensis*, I went to the west coast of Oregon, close to the OSU marine biological station, with a couple of friends once or twice every month, which was quite nice. Hemocyanin was easy to purify by a one-step gel filtration process. It exists in the hemolymph at a concentration of approximately 60 mg/mL in a rather pure form, and a major contamination protein was easily removed by size-exclusion chromatography.

I collected oxygen-binding data of hemocyanin using a tonometer connected to a quartz cell to allow measurement of the absorbance change. The oxygen-binding properties depended on pH and Mg^{2+} ion concentration. In turn, pH and the Mg^{2+} concentration also affected the association state of hemocyanin, which I measured by sedimentation velocity. The association of hemocyanin was in dynamic equilibrium between the hexamer (we called it a monomer) and 24-mer (we called it a tetramer). After 1 year of experiments, I had collected a sizable amount of oxygen-binding data and subunit

association–dissociation data. However, I then faced the problem of how to co-relate the two kinds of data. Although puzzling out this dilemma took awhile, at some point I remembered John Schellman's paper on "Macromolecular binding" which had appeared in *Biopolymers* a couple of years earlier (Schellman 1975) in which he related the dimer–tetramer association equilibria of hemoglobin and oxygen binding. When I first read the paper more than 1 year earlier, I was not able to understand the details of the theory, but now I could! I was very excited and immediately started applying the theory to my hemocyanin system. I was very happy because all of a sudden I thought I understood what was happening in the system. I also understood what J. Wyman meant by "linked functions." When I told Ken about it, he also got very excited and told me to start writing my Ph.D. thesis. The work was ultimately published in the *Journal of Molecular Biology* (Arisaka and Van Holde 1979).

It was on June 21, 1977 that I was granted a Ph.D. degree at the commencement ceremonies of OSU. My future wife, Hiroko, whom I had met in Corvallis and was to marry in the coming September, came over from Japan to see me and to celebrate my achievement. A year or so earlier, I had discussed with Dr. Wolfgang Weischet, a postdoc in Prof. Van Holde's laboratory, the possibility of obtaining a postdoc position in Europe. He had obtained his Ph.D. at the Biocenter of the University of Basel and recommended me to Prof. Jürgen Engel at the Department of Biophysical Chemistry. I wrote a letter to Prof. Engel to convey my wish to work in his laboratory and was surprised to receive his positive answer right away. Later, I learned that Prof. Engel liked and respected Ken Van Holde and that also a talented former Japanese postdoc currently working in Prof. Engel's laboratory, Dr. Hiroshi Maeda, supported my application; the support of both these men most certainly played a major role in obtaining the postdoc. Before going to Switzerland, I had a chance to participate in the physiology course of the Marine Biological Laboratory in Woods Hole, which Prof. Van Holde had organized for that year. That was a wonderful course. After the course was finished, I went back to Japan to marry Hiroko and we then went to Basel together.

It was at the end of September 1977 that we arrived in Basel. The Department of Biophysical Chemistry was on the sixth floor. Prof. Jürgen Engel had been working on collagen and actin, which polymerize to form long fibers. Before I arrived in Basel, I was thinking about going back to the muscle field, but he mentioned that I could work on either actin or the tail sheath protein, gp18, of phage T4, which they had recently started to work on. The phage project sounded very interesting, mainly because it was something which Max Delbrück worked on, but also because it looked more alive than protein molecules or protein oligomers to me. However, I had only a limited knowledge of microbiology and so I was not sure if I could work on phages. After I decided to work on gp18 of phage T4, Prof. Engel introduced me to Prof. Edward Kellenberger, an electron microscopist and well-known biophysicist who had made early contributions on the observation of phage growth in infected bacterial cells. While working at the Biocenter, from time to time I would visit him with questions I needed answering, and every time he was very kind, thoughtful and patient, teaching me a lot while answering my questions. At this time Dr. Roel van Driel was a postdoc in Prof. Kellenberger's laboratory, and he had previously worked on hemocyanin in Groningen, the Netherlands. In fact, because we previously were working in the same field, we knew each other's name. When I asked him how much prior knowledge of microbiology or genetics was necessary to work on phages, he said that I should not worry about molecular genetics or molecular biology and that it was simple. Since another researcher who had previously worked on hemocyanin was also now working on phages, I thought that probably I could do so too. Roel taught me how to make large-scale cultures (usually 20 L) and how to isolate tails by large scale SDG (sucrose density gradient) centrifugation. Soon after I arrived in Basel, Jürg Tschopp returned from his military service to finish his Ph.D. work. He had found that the tail sheath protein can readily dissociate from the tail as a monomeric form, gp18, when dialyzed against low ionic strength buffer and that the monomeric gp18 can reassemble to form the extended sheath onto the tube-baseplate.

When I saw the negatively stained electron microscopy pictures of the reconstituted tails, I noticed that the sheath formation was quite highly cooperative in the sense that we can see either complete tails or naked tube-baseplates, but I was not sure if all the tube-baseplates in the picture were competent to bind gp18. I therefore added various amounts of monomeric sheath protein, gp18, to a constant concentration of tube-baseplates and looked at the length distribution. The results indicated that all of the tube-baseplates were indeed competent and that there was a critical concentration of monomeric gp18. The results were published in the *Journal of Molecular Biology* in 1979 (Arisaka et al. 1979) . One of the big events while I was at the Biocenter was that the Nobel prize was granted to Prof. Werner Arber in the Microbiology Department for his contributions which led to the discovery of restriction enzymes.

In the spring of 1979, Professor S-I. Ishii at Hokkaido University came to the Biocenter to deliver a talk on concanavalin A. I had a chance to see him and mentioned that I was looking for a job back in Japan. He promised me that he would let me know if he found a job opportunity for me. I did not hear from him for awhile, but towards the end of the year, he called me on the phone from Japan to say that an assistant professor position was available and would I be willing to come to his laboratory. I took it as a great personal opportunity and immediately answered yes.

In the beginning of April 1980, I flew to Sapporo to take my new post. My wife and our 1-year old son had returned to Japan some weeks earlier and waited for me in Sapporo. I had believed that once in Prof. Ishii's laboratory I would be working on the protease that was the focus of his laboratory. However, he mentioned that if I would like to continue my work on the tail of phage T4, then I may continue working on phage. I later learned that in 1963 he was the first person to discover that R-type pyocin, a bacteriocin from *Pseudomonas aeruginosa*, had the same shape as the contractile tail of phage T4. I was very happy to continue working with the tail of phage T4. In 1980, Kao and McClain at the University of Wisconsin reported that the experimental phenomenon "lysis from without" was caused by the lytic activity of gene product 5 or gp5 (Kao and McClain 1980). Then, Duda and Eiserling (1982) subsequently reported that guanidine hydrochloride treatment of the tube-baseplates resulted in detachment of the tube from the baseplate. Based on our observations of our experimental system in which we isolated the tube-baseplate, treated it with 2 M guanidine hydrochloride and then determined in which fraction the lytic activity resided, it turned out that the lytic activity was neither in the tube nor in the baseplate, but in the supernatant and that the molecular weight was 42 kDa, which was consistent with the molecular weight of gp5 as known at that time. Apparently, gp5 dissociated from the tube-baseplate. We had isolated the lytic enzyme and showed that it had *N*-acetyl muramidase activity, the same activity as the T4 lysozyme (also known as gpe). The results were published in the *Journal of Virology* in 1985 (Nakagawa et al. 1985).

At that time, crystallization and structure determination of phage proteins were beyond my wildest dreams. Many tail proteins were sticky when isolated and tended to make aggregates unless other tail proteins were present and able to bind to the protein. gp18, for example, spontaneously formed the so-called polysheath, the conformation of which resembles the contracted sheath. Believing that the atomic structure of the tail proteins would not be solved before I retired (which turned out to be wrong!), my colleagues and I carried out a couple of experiments in which we mapped the mutation sites of gene 5 and gene 18 mutants (which I had collected from the original authors) and differential chemical modifications of gp18 to identify the contact residues of the subunit. Gene 5 mutants included ts (temperature sensitive) and hs (readily inactivated by heat) as well as am (amber stop codon), mutants and gene 18 mutants included ts, cs (cold sensitive), hs and CBW (carbowax-resistant) mutants as well as am mutants. The determined mutation sites were later mapped onto the three-dimensional (3D) structure of gp5 and gp18 when the 3D structures were eventually elucidated and this helped us to understand the relationship between the phenotypes and the mutations (Takeda et al. 1998). Differential chemical modification of gp18, the sheath protein, was performed using monomeric gp18 and the tail to determine which residues were at the subunit–subunit or subunit–tail-tube interface (Takeda et al. 2004).

In 1990, when Professor Ishii retired, I moved from Hokkaido University to the Tokyo Institute of Technology (TIT) where I remained for the rest of my career, first as an Associate Professor and later as a full Professor. Around the time of moving from Hokkaido to Tokyo, I attended a couple of biennial phage meetings in the USA. One of these was the Phage Biology Meeting (originally called the T4 Meeting) that was successively organized at Evergreen State College by Elizabeth Kutter; the topics included not only assembly, but also replication, transcription and translation. The other meeting was the biennial Phage/Virus Assembly Meeting (originally Phage Assembly Meeting), the location of which depended on the organizers.

At that time, many phage researchers were leaving the field of bacteriophage and starting work on either animal or plant viruses. One of the leading scientists at that time in the assembly field was Prof. Johathan King at the Massachusetts Institute of Technology who emphasized that the target of the next era in our field would be that of supramolecules and that phage would be the ideal target. He also encouraged us, young researchers (at that time, I was still young) to collaborate with X-ray people and not wait until X-ray people became interested in your system; rather, he urged us to crystallize the protein or protein complex of interest ourself and bring it to the X-ray people. Then they would most certainly be interested, he emphasized. However, at that time the field of structural biology of phage appeared to me to be still too far away. It took me 10 more years until I seriously thought about a project inf structural biology.

In 1994 our laboratory at TIT acquired a modern type of analytical ultracentrifuge, the Beckman Coulter XL-A. It very quickly became an important tool for analyzing protein complexes in solution. Three years later, I encountered Dr. Allen Minton through the RASMB (Reversible Association in Structural and Molecular Biology) internet forum when I asked some question concerning solution interaction and he replied to my question. We soon started to communicate with each other which led to my inviting him as a visiting professor for 3 months in 2001 at TIT.

It was in 1996 at the FASEB meeting of the Phage/Virus Assembly Meeting in Saxtons River in Vermont that I met Prof. Michael Rossmann for the first time. After my talk on the study of tail proteins, he came to me and mentioned that my system was interesting and that if I wished, we could collaborate. I was very excited to hear such as proposal from such a great figure as Michael Rossmann in the structural biology field. It was a fateful encounter. At that time he had two Russian students, Petr Leiman and Victor Kostychenko, working in his laboratory who had also worked in Vadim Mesyanzhinov's laboratory in Moscow. Vadim and I knew

each other already and were good friends. We had once met at the Biocenter in Basel when he was visiting from Moscow. He had previously held a postdoc position in Prof. Kellenberger's laboratory and continued to visit the Biocenter from time to time after he had left. Soon after my encounter with Michael Rossmann, a student, Shuji Kanamaru, came from Prof. T. Imoto's laboratory at Kyushu University to start as a D.Sc. student in my laboratory on the topic of the gp5 protein. He obtained his Ph.D. in 1998 and went to work in Prof. Rossmann's laboratory as a postdoc. It was then that the real collaboration between our two laboratories started. By this time the nucleotide sequence of gene 5 had been reported by Gisela Mosig and collaborators, which indicated that gp5 has a lysozyme domain in the middle of the gene and that the C-terminal domain had a curious repeating sequence of VXGXXXXX. Originally, we thought that the curious repeats were not so important because this fragment was cleaved off anyway upon "maturation," but it turned out that the C-terminal domain is retained in the tail lysozyme complex (Kanamaru et al. 1999). The significance of the role of the C-terminal domain became evident when the 3D structure of the tail lysozyme complex was solved in 2002.

In 2001, I had the opportunity to organize an international conference, the 7th Keihanna International Conference on Molecular Biophysics: New Approaches to Solution Interaction of Biological Molecules, to be held in July 27–29, Keihanna, Kyoto, Japan. Upon consultation with Allen Minton regarding whom I might invite to give a talk as an AUC (analytical ultracentrifugation) expert, he recommended Dr. Peter Schuck, also from the NIH. Peter Schuck accepted the invitation and was one of the invited speakers. I was very much impressed by his presentation at the meeting on the use of SEDFIT, an analysis suite developed by Peter. SEDFIT has changed the field of AUC to a great extent due to its ability to derive the sedimentation coefficient distribution [c(s)], and it has become a standard method of analyzing AUC data. Since then I have attended his workshop twice to learn how to use the software.

Shuji Kanamaru had brought with him the expression system of gene 5 to Prof. Rossmann's laboratory and was soon successful in crystallizing gp5. The structure was eventually solved and found to have a triple-stranded β-helix in the C-terminal repeat sequence region. Apparently, the C-terminal needle plays an essential role in making a hole in the outer membrane of the host cell by "digging" a hole so that the lysozyme domains are able to approach the peptidoglycan layer, thereby allowing the tail tube reach the inner membrane. The result was published in Nature (Kanamaru et al. 2002). In 2006, Rossmann, Arisaka and Mesyanzhinov were successful in obtaining a HFSP (Human Frontier Science Program) grant which lasted 3 years.

The bacterial Type 6 secretion system (T6SS) translocates protein toxins from the cytosol to a target cell by means of a syringe-like supramolecular complex resembling the contractile tail of T4 phage. VgrG proteins, which are the homologs of the phage gp27-gp5 cell-puncturing complex, are considered to be located at the tip of the bacterial T6SS apparatus. Kazuya Uchida, another Ph.D. student in our laboratory, overexpressed and purified VgrG1 of *Escherichia coli* O157 and found that it formed a trimer in solution and that it is rich in β-structure. We also solved the crystal structure of the trypsin-resistant C-terminal fragment of *E. coli* O157 VgrG1 (VgrG1C^{G561}) at 1.95 Å resolution. VgrG1C^{G561} forms a three-stranded antiparallel β-helix which is structurally similar to the β-helix domain of the central spike protein (gp138) of phi92 phage, indicating a possible evolutionary relationship (Uchida et al. 2014).

Between 2012 and 2017, Moh Lan Yap, a former student who obtained her Ph.D. in our laboratory, was a postdoc in Michael Rossman's laboratory. She reconstructed a baseplate structure from seven wedge proteins and crystallized and determined the atomic structure of the baseplate by both X-ray crystallography and cryo-electron microscopy. The molecular weight of the complex was 3.3 MDa. It was surprising and interesting that the resolution of the structure from cryo-electron microscopy exceeded the resolution determined by X-ray crystallography (Yap et al. 2016).

I retired from TIT in 2014, delivering my "Last Lecture" in March to a theater containing around 200 people, many of them my scientific colleagues and former students. From my current perspective, looking back at my 40 years of research, a couple of things are apparent. First, at each turning point in my career pathway, say, from my Masters course at the University of Tokyo to my Ph.D. at the Graduate School at Oregon State University to my Postdoc at the Biocenter of the University of Basel and so on, I always experienced invaluable encounters with other scientists that helped to determine my future direction. Secondly, collaborations have been extremely important and fruitful in my research, through which I was able to positively extend my research area. In many cases, collaborations turned into good friendships, for which I feel very fortunate. I cannot list all of the names here, but I am sure they know who they are. Last (but not least) I would like to acknowledge the collaboration with the hard working graduate students in my laboratory, which was the driving force for much of my research and for which I would like to express my deepest and sincerest gratitude.

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Compliance with ethical standards

Conflict of interest Fumio Arisaka declares that he has no conflicts of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by the author.

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