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HISTORY & BIOGRAPHY

Sixty years of research on photosynthesis: a personal scientific autobiography

T. OGAWA

Kamisaginomiya 3-17-11, Nakano-ku, Tokyo 165-0031, Japan

Abstract

The following scientific autobiography is presented here as a homage to Professor Kazuo Shibata, who is the one who led me to do research in photosynthesis. He had invited me to Riken (The Institute of Physical and Chemical Research), and had launched the Japan–US Collaboration Project on "*The Solar Energy Conversion by Means of Photosynthesis*" and had invited many international scientists to Riken. My research, under Shibata, started on using a sensitive method for the determination of chlorophyll *b*, and of SDS-PAGE for the pigment protein complexes of the two photosystems. After Shibata had passed away at the age of 66, I found post-illumination CO_2 burst from cyanobacterial cell suspensions. This finding led me to study the CO_2-concentrating mechanism (CCM) and the function and structure of NADP(H) dehydrogenase complexes (NDH-I) in cyanobacteria, which were developed after I had moved to Nagoya University, and in several other laboratories in the world after I had retired from Nagoya University.

Keywords: CO_2-concentrating mechanism (CCM); cyanobacteria; Kazuo Shibata; NDH-I complexes; Riken (The Institute of Physical and Chemical Research); stomata.

Introduction

I started my research on photosynthesis under Kazuo Shibata at the Tokyo Institute of Technology on SDS-PAGE of pigment–protein complexes of the two photosystems. Leo P. Vernon invited me to the Kettering Research Laboratory, where I isolated the photosystem 1 (PSI) complex from *Anabaena variabilis.* Shibata moved to Riken in 1970 and invited me as a research staff. My research in Riken started with the finding of synergistic action of red and blue light on stomatal opening, followed by finding post-illumination CO_2 burst from cyanobacterial cell suspension and ABC-type transporters of bicarbonate and nitrate in the cytoplasmic membrane. Then, I isolated two mutants of *Synechocystis* PCC6803 defective in inorganic carbon (Ci) transport in *ndhB* and *ndhL*, respectively. In 1994, I was invited to Nagoya University, where we constructed many mutants, based on the whole genome sequence data crystalized at the Kazusa DNA Research Institute, which were used to discover the role of genes encoding (*1*) functionally distinct NADPH dehydrogenases, (*2*) an iron transporter, (*3*) a low-Mn sensing mechanism, (*4*) two types of CO_2-uptake systems, and (*5*) genes encoding sodium dependent-bicarbonate transporter. After retiring from Nagoya University, I had three research bases at the laboratories of Ikeuchi, Mi, and Pakrasi, and in addition, I visited Aro's lab (June–August 2003) and Rögner's lab (October–December 2007). Genetic and proteomic studies on the mutants done with the researchers in these laboratories advanced the understanding of the NDH-I complexes and the CCM.

Personal and academic life

I was born on 6 February 1940, as a son of Juzo (a lacquer worker) and Fumiko in Kainan (Wakayama province,

Highlights

- Key research contributions have been on the pigment–protein complexes of the two photosystems of photosynthesis
- Later research has focused on the molecular genetics of the carbon-concentrating mechanism (CCM) and on NDH-I complexes of cyanobacteria
- The world-famous Kazuo Shibata was Teruo Ogawa's mentor

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e-mail: og2600@gmail.com

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Japan). After 1958, I studied petrochemistry at Waseda University in Tokyo. I was most interested in quantum chemistry and statistical mechanics, which was taught by Professor Kazuo Shibata (1917–1983; Fig. 1). He is the one who made me curious and enthusiastic about research not only in biology but also in physics. After finishing my bachelor's degree in 1962, I did my master's degree at the Tokyo Institute of Technology, then joined Shibata's laboratory to do research in photosynthesis, and I have enjoyed it for 60 years. Now, a bit about Professor Shibata.

Kazuo Shibata

Kazuo Shibata (1917–1983) was born as a son of Seiho Takeuchi, one of the greatest painters of Japanese arts, and Kiho Mutobe who was a disciple of Seiho and a famous painter. He returned to Japan in 1957 after spending several years in the laboratories of Melvin Calvin (1911–1997) and Andrew A. Benson (1918–2015) at the University of California at Berkeley (for Calvin, *see* Govindjee *et al*. 2020; for Benson, *see* Nonomura *et al*. 2017) and C. Stacy French (1907–1995) at the Carnegie Institution of Washington, Stanford, California (for French, *see* Govindjee and Fork 2006). Shibata had specialized in spectroscopy and invented "an opal glass method" to measure spectra of translucent samples such as cell suspensions. Using this method, he measured spectral changes of protochlorophyllide in etiolated leaf and found a shift of absorption in the dark (later named Shibata Shift) after rapid conversion to chlorophyllide by light. He also had a position at the Tokugawa Institute of Biological Research, where Hiroshi Tamiya (1903–1984) was a director.

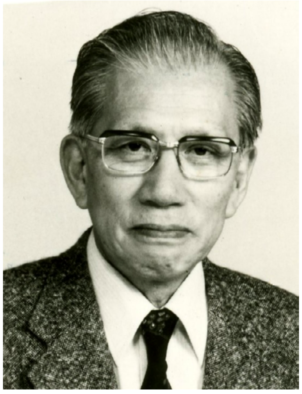

Fig. 1. A photograph of Professor Kazuo Shibata (1917–1983). Date of photo: unknown. Source: author's personal archives.

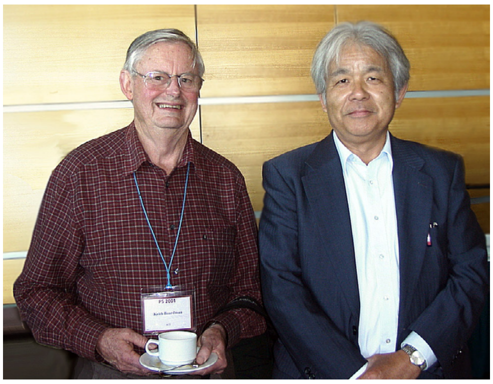

Fig. 2. A 2001 photograph of Keith Boardman (*on the left*) and the author (Teruo Ogawa) in Canberra, Australia. Source: personal archive.

My student days

I did research in the photosynthesis group of Shibata from 1962 to 1967. The instruments we used were *Cary 14* spectrophotometer and a Coulter counter. As I worked on the chromatographic separation of photosynthetic pigments, I found that chlorophyll (Chl) *b* reacts with hydroxylamine and its red band shifted to 663 nm closer to the peak of Chl *a*, which was at 666 nm. This led us to establish a sensitive method for determining Chl *b* in plant extracts (Ogawa and Shibata 1965). At that time, M. Itoh and S. Izawa, also in Shibata's lab, measured the size distribution of chloroplasts using a Coulter counter and found that chloroplasts shrink under low light. Soon after this finding, Izawa moved to the USA to work with Norman E. Good (1917–1992; *see* Hangarter and Ort 1992). An idea to separate the two photosystems by electrophoresis had emerged from the report by Boardman and Anderson (1964), who had fractionated digitonin-treated spinach chloroplasts by differential centrifugation and found that the heaviest fraction had PSII activity while the light fraction PSI activity [*see* Fig. 2 for a 2001 photo of Keith Boardman with me, as well as an article by Boardman (2023) on his own life's work]. I had learned that "cyanogum", a new carrier for electrophoresis, now known as acrylamide, was commercially available, and, thus, I used it for the separation of the two photosystems using our hand-made apparatus. After experimenting with many detergents, we found that sodium dodecyl sulfate (SDS) gave two pigment–protein bands with their Chl *a*/*b* ratio of 7.0 and 1.9, originating from the PSI and PSII complexes, respectively (Ogawa *et al*. 1966, *cf.* Ogawa 2003). Further, we used the same technique to successfully separate pigment–protein complexes of the two photosystems from *Anabaena*, *Porphyra*, and *Phaeodactylum* (Ogawa *et al*. 1968); we presented these new results at the 1967 Japan–US binational workshop on "Comparative Biochemistry and Biophysics of Photosynthesis" organized by Kazuo Shibata, Atsushi Takamiya, André Jagendorf, and Clint Fuller, held in Hakone, a famous resort area near Tokyo. Leo P. Vernon (1925–2010), who was also a participant in the above workshop, and then Director of the Charles F. Kettering Research Laboratory (*see* Vernon 2003), invited me as a postdoctoral fellow to his laboratory in Yellow Springs, Ohio.

At the Kettering Research Laboratory in Yellow Springs, Ohio

It was my first trip abroad and my wife (Kazuko) and I arrived at Dayton, Ohio, Airport at midnight of

31 December 1967, and took a taxi to the home of Anthony (Tony) San Pietro who was then vice president of the Kettering laboratory and waiting for us with his wife, Arice. We were very excited to see a dreamy view of the village of Yellow Springs covered by snow and decorated with Christmas trees. Twenty-seven months of stay at the Kettering Institute was one of the most important periods that has influenced my life. At the Kettering lab, I was impressed to see many ultracentrifuges, which could be easily used by us. My first experiment in the laboratory was to separate the two photosystems of the cyanobacterium, *Anabaena variabilis*, using the detergent *Triton X-100*. We could isolate photochemically active PSI particles with a P_{700}/Chl *a* ratio of 100 (Ogawa *et al.* 1969). Subsequently, subparticles of PSI, named HP700 particles, were isolated from spinach, bean, *Anabaena*, *Scenedesmus*, and *Euglena* (Ogawa and Vernon 1969, Vernon *et al*. 1969). During my stay at the Kettering laboratory, I became acquainted with many scientists, such as Bacon Ke, Richard Dilley, Charles Arnzen, Berger Mayne, and Elwood Shaw in addition to Anthony San Pietro and Leo Vernon, mentioned above (for Ke, *see* Govindjee *et al*. 2022). In 1968, Professor Harry Y. Yamamoto (1936–2019) from Hawaii University joined us (*see* Yamamoto *et al*. 1962, for his contributions to the xanthophyll cycle, in his own words). Tetsuo Hiyama, also from Japan, visited Bacon Ke and discovered P_{430}, using PSI particles from *Anabaena* (Hiyama and Ke 1971). I recall that Kazuo Shibata had invited me to apply to join Riken (Rikagaku Kenkyusho, the Institute of Physical and Chemical Research). My wife and I left Yellow Springs (Ohio) at the end of March 1970 with our 6-month-old daughter (Chie) – keeping good memories of people in the Kettering laboratory and the neighborhood.

Beginning of research at Riken

After an interview, I was employed as a research member of Shibata's laboratory. It was a new laboratory, where Yorinao Inoue and myself focused on the process of photosynthetic oxygen evolution and stomata, respectively (*see* Fig. 3 for our photograph). Inoue constructed a system to measure thermoluminescence from chloroplasts and made significant contributions on the analysis of water-splitting system (Inoue 1976, Inoue *et al*. 1977); this was in collaboration with international scientists invited by Shibata, which included Govindjee and David Kyle (from USA), Itzhak Ohad (from Israel), William Rutherford (from UK), and Gernot Renger (from Germany). As one example of research from that time, published later, *see* Rutherford *et al*. (1984). Further, in 1973, Yoshichika Kobayashi was employed after finishing PhD under Mitsuo Nishimura at Kyushu University and he worked with Ulrich Heber, who had been invited from Düsseldorf University, in Germany. During this period, Graham Farquhar (from Australia) was visiting me; in addition, at the same time, Ichiro Terashima, a student of Tokyo University, also visited our laboratory and analyzed the light environment within mesophyll cells. Later, Terashima went to Farquhar's laboratory at the Australian National University, where he spent several years. This is how research connections are established!

Fig. 3. A 1973 photograph at Riken. *Left to right*: Yorinao Inoue, Teruo Ogawa, Kazuo Shibata, and Yoshichika Kobayashi. Source: personal archives of the author.

My research on the function of stomata

I constructed a porometer to record stomatal movement (Ogawa and Shibata 1973). Subsequently, I constructed a new open gas-analysis system equipped with a gas mixer to record CO_2 exchange and evaporation by a single leaf under various CO_2 and O_2 concentrations and, interestingly, observed oscillations of CO_2 uptake and two steps of (in) gas exchange (*see*: Ogawa 1975, 1982). Although I did not analyze these phenomena further, I found that the papers published 50 years ago on these observations are still used by others in this field. In addition to the above, I learned that the uptake of K^+ and the malate formation in the guard cells cause stomatal opening. Further, our attempts to isolate the guard cells by sonicating the peeled epidermis of *Vicia faba* were indeed successful, which was done by breaking the epidermal and the mesophyll cells – leaving the guard cells intact! Using the sonicated epidermis, I found that malate is formed in the guard cells when dim blue light is added to cells under strong red light. We measured the action spectra for malate formation (Ogawa *et al*. 1978) and presented our data at the "International Conference on Blue Light Syndrome" organized by Horst Senger in Marburg in 1978. One of the participants, Eduardo Zeiger, became interested in my work and invited me to his laboratory at Stanford University, where I spent one month in 1984 to analyze the blue light effect on stomata (Iino *et al*. 1985, Zeiger *et al.* 1987). Since Ken-Ichiro Shimazaki, of the National Institute for Environmental Studies in Tsukuba, had already succeeded in isolating protoplasts of guard cells and became interested in my observations, mentioned above, I recommended him to visit Zeiger's laboratory, where he spent one year and became a leading scientist in the area of stomatal physiology.

Japan–US collaboration project on "Solar Energy Conversion by Means of Photosynthesis"

When Takeo Fukuda was elected as the Prime Minister of Japan, in 1976, and visited the US President Jimmy Carter, he requested Riken to provide information on possible projects between the two countries. Shibata proposed a project on "Solar Energy Conversion by Means of Photosynthesis", which was accepted. To start the project, a committee of seven young researchers from various research fields including Y. Inoue and myself (called seven samurai) was organized in Riken. Although Shibata retired in 1977, he stayed in Riken as an adviser to take care of the above project. A Solar Energy Research Group was formed, with Inoue as the Director, and Ogawa as the Associate Director, and the members were: Takaaki Ono, Masahiko Ikeuchi, and Hiroyuki Koike. The facility for growing algae was called "Algatron". One of the strains I harvested from Yunomine hot spring (above 85°C) in my home province (Wakayama) was a thermophilic cyanobacterium, *Thermosynechococcus vulcanus.* Further, Jian-Ren Shen isolated and crystalized a stable complex of PSII reaction center from this strain, which enabled him to determine the structure of the Mn-containing complex, which is essential for the water-splitting reaction (Shen and Kamiya 2000, Umena *et al.* 2011).

Finding post-illumination CO_2 burst from *Anabaena* cells

To focus and concentrate my research on algal photosynthesis, I modified the open gas-analysis system to measure CO_2 exchange from algal cell suspensions. This led to the finding of a post-illumination CO_2 burst from *Anabaena* cells originating from inorganic carbon (Ci) accumulated in the cells in the light (Ogawa and Inoue 1983). I learned that cyanobacteria and green algae possess a CO_2-concentrating mechanism (CCM) (Kaplan *et al.* 1980) and that Joseph Berry at the Carnegie Institution of Washington is organizing the 1st CCM meeting in Asilomar, California, in 1984. Berry invited me to the CCM meeting, where I presented the action spectrum for Ci uptake showing it to be driven by PSI (Ogawa and Inoue 1983). I met first Aaron Kaplan (Fig. 4) at the above-mentioned meeting in Asilomar; since then our collaboration on CCM started and has continued until now.

Program to exchange researchers between Riken and the University of Illinois at Urbana-Champaign (UIUC)

There were (and still are) many scientists leading the photosynthesis research at the University of Illinois at Urbana-Champaign (UIUC). To facilitate the activity of the Solar Energy Research Group, in Riken, we proposed a program to exchange researchers between Riken and UIUC, which, of course, was agreed by both sides. Thus, I visited scientists in several laboratories at the UIUC, which included those of Govindjee, William Ogren, John Boyer, and Charles Arntzen (Fig. 5) and I developed my research on stomata and CCM (Ogawa *et al*. 1982, Ogawa and Ogren 1985).

The shift of research from stomata to CO_2-concentrating mechanism

After returning from the University of Illinois at Urbana-Champaign and Stanford University, I completely shifted my research from the stomata to the CCMs. We recruited Tatsuo Omata, who had obtained his PhD under Norio

Fig. 4. A 1984 photograph of Teruo Ogawa (*on the left*), and Aaron Kaplan relaxing at a break during the first CCM meeting in Asilomar, California. Source: personal archives of the author.

Murata, at the Tokyo University, to develop the technique to isolate cytoplasmic membranes from *Anacystis nidulans*, to join the CCM research. Soon, protein analysis of the cytoplasmic membranes from *Anacystis* cells revealed that a 42-kDa protein was strongly induced when the cyanobacterial cells were adapted to low CO_2 (LC) conditions. For this research, Omata visited John Pierce at du Pont Co. in Delaware, USA, with an antibody raised against the specific 42-kDa protein, and then cloned the gene encoding this protein, which is a substrate-binding protein (named CmpA) of ABC-type HCO_3^- transporter (Omata and Ogawa 1986, Omata *et al.* 1999). The above-mentioned antibody was shown to cross-react with a 45-kD protein in the cytoplasmic membrane, which was found to be a substrate-binding protein (NrtA) of ABC-type nitrate transporter (Omata *et al.* 1989). It was around that time, I had invited Aaron Kaplan and, together, we analyzed the physiological properties of a high CO_2-requiring (HC) mutant of *Anacystis*, E_1, isolated in his laboratory; this was accomplished as I had visited him in 1986 and 1989, for three months each, in the Hebrew University in Jerusalem, Israel. We note that many scientists, including myself, have been working on CCM, using isolated HC mutants from *Synechocystis* PCC6803 and *Synechococcus* PCC7942 (*Anacystis nidulans* R2). However, these mutants still possessed Ci-transport activity and had impaired carboxysome containing Rubisco. After returning from Jerusalem, I measured the Ci-transport activity of more than a hundred HC mutants of *Synechocystis* and succeeded in finding two mutants that lacked the transport activity (Ogawa 1990). Complementation experiments on these mutants revealed that they had mutations in *ndhB*, as well as they had a new component named *ndhL* (Ogawa 1991, 1992). I, then, constructed mutants by inserting kanamycin-resistant cassettes into the respective genes and named the mutants M55 and M9. I sent these mutants to several scientists, at their request, including Koji Asada and his PhD student, Hualing Mi, who was then at Kyoto University. Using the mutants, mentioned above, Asada and Mi demonstrated that PSI cyclic electron flow was dependent on NAD(P)H (Mi *et al*. 1992, 1994). Tatsuo Omata left Riken in 1992

Fig. 5. Photographs taken at the University of Illinois at Urbana-Champaign in early 1980s. *Clockwise* (*from the top left*): with John and Jean Boyer; Charles Arntzen; G. Govindjee; and William and Carolyn Ogren.

for Nagoya University and there, he continued research on Ntr and Cmp transporters. To my pleasure, I was invited, in 1994, to become a Professor at the Bioscience Center, newly instituted at Nagoya University.

Research on the molecular genetics of cyanobacteria at Nagoya University

When I moved to Nagoya University, the project to sequence the whole genomic DNA from *Synechocystis* PCC6803 was nearly completed at the Kazusa DNA Research Institute, which had been directed by Satoshi Tabata. Based on their sequence data, we constructed many mutants by inserting cassettes giving resistance to various antibiotics and then analyzed their phenotype(s). The Bioscience Center, at Nagoya, provided us possibility to invite international scientists and I was requested to take care of it. Thus, during the nine years of my stay at Nagoya University, I had the pleasure of inviting Himadri Pakrasi, Arthur Grossman, Martin Spalding, and Andre Jagendorf from the United States, Aaron Kaplan from Israel, and Martin Hageman from Germany for six months or one year each, and that along with their families. We note that the whole genome sequence data, that had crystallized, had left a tremendous impact on cyanobacterial research, and many workshops were organized inside and outside of Japan (Fig. 6). In November of 1996, the US–Japan workshop on the "Molecular Biology of Cyanobacteria" was held in Grand Canyon, with Wim Vermaas and myself as the US and Japan organizers, respectively (Fig. 7). A proposal on the molecular genetics of cyanobacteria applied to "Human Frontier Science" by Wim Vermaas as a leader, and,

Fig. 6. A photograph taken at a European cyanobacterial workshop held in Vienna, Austria, in 1996. *From left to right*: Himadri Pakrasi, Donald Bryant, Teruo Ogawa, Aaron Kaplan, and Hans Matthijs.

Fig. 7. A group photograph of the participants of the US–Japan binational workshop held at Grand Canyon, USA, in November 1996.

Fig. 8. A photograph of the members of the "Human Frontier Science Project" in Nagoya, Japan. *Left to right*: George Schmetterer, Donald Bryant, Matthias Rögner, Willem Vermaas, Teruo Ogawa, and Masahiko Ikeuchi.

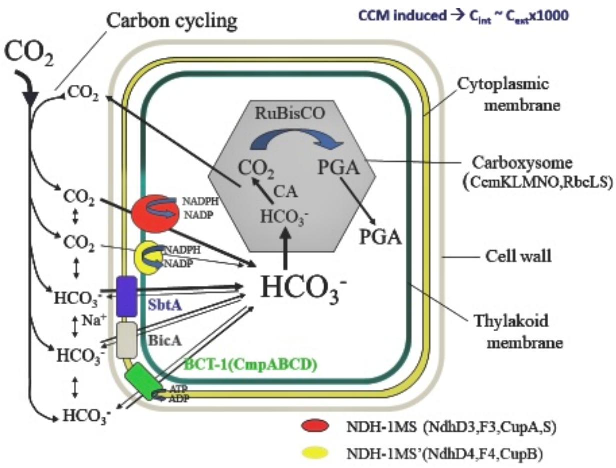

Fig. 9. A schematic model for the CCM in *Synechocystis* PCC 6803 cell. Two CO_2 uptake systems on the thylakoid membrane and two HCO_3^- transporters (SbtA and CmpA) on the cytoplasmic membrane were identified by us (*cf.* Kaplan *et al.* 2008).

Fig. 10. (*Left*) A 2004 photograph with Professor Yun-Kang Shen and Hualing Mi taken in Shanghai. (*Right*) A 2006 photograph with Eva-Mari Aro taken in Jangzhou, China.

Fig. 11. *Top left*: Teruo Ogawa with Itzhak Ohad (~2016); *top right*: with Gernot Renger (~2013); *bottom left*: with Harry (~2019) and Millie Yamamoto; *bottom right*: with Ulrich Heber (~2016).

Matthias Rögner, George Schmetterer, Masahiko Ikeuchi, and myself as members, was approved and we had a group seminar every year, once in Nagoya (Fig. 8). The research at Nagoya University, using the mutants, identified and functionally characterized the role of genes encoding (*1*) functionally distinct NADPH dehydrogenases (Ohkawa *et al*. 2000), (*2*) an iron transporter (Katoh *et al.* 2000), (*3*) a low-Mn sensing mechanism (Pakrasi *et al.* 2001, Ogawa *et al.* 2002), (*4*) two types of CO_2-uptake systems (Shibata *et al*. 2001), and (*5*) genes encoding sodium dependent-bicarbonate transporter (Shibata *et al.* 2002). Among these genes, I was most interested in the *ndh* genes involved in two CO_2 transport systems, which included *cupA* and *cupB* essential to the transport. I retired from my Professorship at Nagoya University in 2003 but decided to continue research in Hualing Mi's laboratory at the Shanghai Institute for Biological Sciences, in Shanghai, China.

Research after retirement from Nagoya University

There had been significant progress on the subunit structure of the NADPH dehydrogenase in Professor Eva-Mari Aro's lab at the University of Turku, in Finland, where I spent three months (June–August 2003) working on a joint project on *ndh* mutants. Professor Himadri Pakrasi (of Washington University in St. Louis) had invited me to join a newly launched project. And, I decided to have three research bases for this: at Ikeuchi's lab in Tokyo, Mi's lab in Shanghai, and Pakrasi's lab in St. Louis. In addition, I spent three months (October–December 2007) in Rögner's lab at the Ruhr University. Genetic and

Fig. 12. A photograph of a Chinese artwork painted by Zhang da Zhuang.

Fig. 13. A 2024 photograph with Kazuko, my wife, taken in Liege, Belgium.

proteomic studies on the mutants of *Synechocystis* sp. PCC 6803 and *Thermosynechococcus elongatus* were done with the researchers in these laboratories (Zhang *et al*. 2004, Battchikova *et al*. 2005). Indeed, the above studies advanced the understanding of the NDH-I complexes and the CCM. We published more than eighteen peer-reviewed papers, book chapters, and reviews during this period. To get a glimpse of this area and time of research, the readers may consult the following five: Zhang *et al*. (2004), Arteni *et al*. (2006), Xu *et al*. (2008), Folea *et al*. (2008), and Bernát *et al*. (2011), together with a schematic model for the CCM in a *Synechocystis* PCC 6803 cell (Fig. 9).

After returning to Japan from Rögner's lab, in Germany, I stopped doing bench work myself, but continued to discuss research projects and publish papers with the groups of Drs. Mi and Weimin Ma, the latter had opened a new laboratory at the Shanghai Normal University after receiving PhD under Mi. A paper by Mi's group was published last year in the Journal of Biological Chemistry (Liu *et al*. 2024). Fig. 10 shows a photograph with H. Mi and Y.K. Shen as well as Eva-Mari Aro (mentioned earlier). I sent the above-mentioned paper to my Japanese friends with a comment "*This is the last paper in my life. Bravo!! I am now free from publishing papers*".

Concluding remarks

It was a "butterfly effect" that I met Professor Kazuo Shibata as an 18-year-old rustic student. If I did not meet him, my life would have been completely different. He had many friends abroad and invited them to Riken. I am really happy to be able to have taken his friendship. Although many of my friends have already passed away, they always live in my mind (Fig. 11). Shibata was a good artist (a painter). Although I don't have such a talent, I have enjoyed visiting museums and art galleries and

Fig. 14. *Left to right*: Ichiro Terashima, Masao Kitajima, Teruo Ogawa, Yorinao Inoue, Masahiko Ikeuchi, and Takaaki Ono; this photo was taken in 2017, in a park near my previous residence in Tokorozawa.

have acquired many engravings in Nagoya as well as an artwork from Shanghai drawn by Zhang da Zhuang, who was a nephew of the famous Zhang Binlin (Fig. 12). In the congratulatory speech at our wedding, Shibata mentioned only about the thorny path waiting for me. However, my wife, Kazuko, has always been with me. I sincerely thank her for her support – always with me (Fig. 13). I close this autobiography by showing a photograph of people who had worked in the same research group, as I did, in Riken (Fig. 14).

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