



HISTORY & BIOGRAPHY

Tribute to late Prof. Sakae Katoh (1932–2025): discovery of plastocyanin and his research in photosynthesis

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Sakae Katoh, born in 1932, passed away on 21 May 2025, at the age of 92. He is renowned for the discovery of plastocyanin. In his early years, he had isolated and characterized *c*-type cytochromes from the red alga *Porphyra tenera*. He published his first four papers between 1959 and 1960, including one of the early papers in *Nature* (Katoh 1960a). During his efforts to purify cytochromes from the green alga *Chlorella ellipsoidea*, he discovered a blue copper protein in the place of cytochrome *c₆*, which was also published in *Nature* (Katoh 1960b).

The physiological role of plastocyanin became a subject of considerable debate. Nevertheless, Sakae Katoh ultimately discovered that plastocyanin accepts electrons from the cytochrome *b₆f* complex and subsequently donates them to P700 (Kimimura and Katoh 1972). For a comprehensive overview of his early career and the details of the studies exploring the role of plastocyanin, see his personal perspective (Katoh 1995) and a historical review (Katoh 2003); the former one contains a portrait. Here, I show his more recent (2014) portrait (Fig. 1).

I would like to emphasize that the photosynthetic electron transport through the two photosystems, using two reaction centers I and II, was a major working hypothesis at that time (see e.g., a perspective by Govindjee 2023). However, there were also other hypotheses, such as “three light reactions of photosynthesis”, which persisted even into the late 1960s (see Knaff and Arnon 1969). Sakae Katoh's seminal discovery of plastocyanin as an electron donor to P700 (Kimimura and Katoh 1972) provided the foundational evidence for the current model of photosynthetic electron transport. Even in later years, plastocyanin continued to be a main subject for him, or at least those around him in the lab believed it so, and a molecular model of plastocyanin was given to him at the “first” retirement party from the University of Tokyo in 1993 (Fig. 2).

With the outstanding achievements mentioned above, Sakae Katoh obtained his PhD in 1960. I recall that he once said that he simply bundled up several reprints of his papers, including the one published in *Nature*, put a cover on them, and submitted them as a doctoral dissertation by



Fig. 1. Prof. Sakae Katoh (photo taken on 20 September 2014).

his “youthful indiscretion”, according to his words. I have always wanted to check out the real thesis someday but never had the chance.

In 1973, Sakae Katoh established his laboratory on the Komaba campus of the University of Tokyo and broadened the area of his research, although it was still related to photosynthesis. Among his numerous achievements, I introduce here only the use of thermophilic cyanobacteria in photosynthesis research. In the late 1970s, he isolated a thermophilic cyanobacterium (called blue-green algae at that time) that shows maximal growth at 58°C, obtained from Beppu Hot Spring, and he began, with his coworkers, biochemical and physiological analyses of this organism (see Yamaoka *et al.* 1978). The proteins of this thermophilic cyanobacterium are so stable that it was possible to isolate chlorophyll–protein complexes by simple SDS-PAGE (Takahashi and Katoh 1982), and many biochemical and physiological studies were subsequently carried out using these samples. Some of the earliest works

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Acknowledgment: I thank Teruo Ogawa for providing the photograph for Fig. 3 for this Tribute. Sakae Katoh wrote in his personal perspective (Katoh 1995): “I thank Govindjee for carefully editing this”, and I would like to repeat his words after 30 years!

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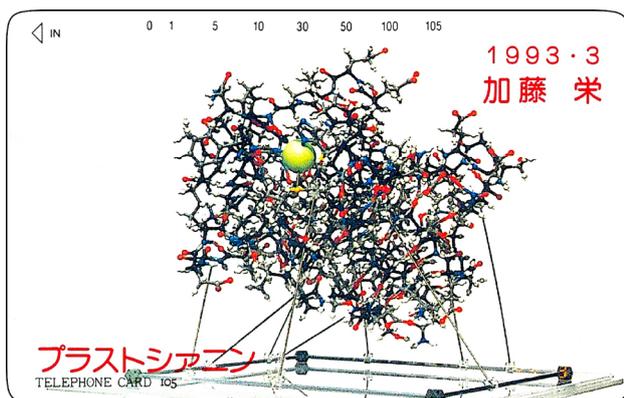


Fig. 2. A prepaid card for telephone calls distributed to the participants of the retirement party of Sakae Katoh at the University of Tokyo in 1993. The photograph of this card shows the molecular model of plastocyanin, which was “built up” by the collaboration of Sakae Katoh’s current and former students and presented at his retirement party.

were published in the early 1980s, on PSI (Takahashi and Katoh 1982), on PSII (Yamagishi and Katoh 1983), and on ferredoxin and FNR (Koike and Katoh 1980).

When the above research was ongoing and progressing, I had joined Sakae Katoh’s lab in 1982, and my first published paper was about the isolation of PSI sub-particles from thermophilic cyanobacteria (Sonoike and Katoh 1986). After the Nobel Prize was awarded in 1988 (to Johann Deisenhofer, Hartmut Michel, and Robert Huber) for the crystallographic analysis of the reaction center of anoxygenic photosynthetic bacteria, the reaction center of oxygenic photosynthetic organisms became one of the focal points of crystallographic analysis, and many of the materials initially used in these studies were thermophilic cyanobacteria.

Concerning the research conducted in the mid-1980s, I would like to introduce some experiments in our laboratory that have never been published. At that time, the protein complex with chlorophyll-binding subunits PsbB and PsbC, together with the D1/D2/cytochrome b_{559} proteins (PsbA/psbD/psbE/psbF), was the smallest unit that showed PSII activity. Since most of the chlorophylls were thought to be bound to PsbB/PsbC, experiments were conducted to isolate the PsbB/PsbC complex with PSII activity. However, as the D1/D2/cytochrome b_{559} protein dissociated from chlorophyll-containing PsbB/PsbC, the activity decreased proportionally, and we could not isolate PsbB/PsbC with PSII activity. At the time, the laboratory members, including Sakae Katoh, believed that the experiments had failed. As readers may know, however, about two to three years later, a group led by Prof. Kimiyuki Satoh at Okayama University successfully isolated the D1/D2/cytochrome b_{559} protein complex with its PSII activity, clearly demonstrating that this complex is indeed the reaction center of PSII (Nanba and Satoh 1987). Sequence homology between the reaction center subunits of anoxygenic bacteria and those of the oxygenic photosynthetic organisms was known even at that time, but we did not pay much attention to it. The whole matter



Fig. 3. Photograph taken in 1985 during the stay of Bacon Ke in Japan after he had retired from the Charles F. Kettering lab. Standing (right to left): Sakae Katoh, Leo P. Vernon, Bacon Ke, Teruo Ogawa. Sitting (right to left): Furn Vernon, Keiko Ke, Kazuko Ogawa. Photo courtesy of Teruo Ogawa.

taught us the importance of molecular biology as well as that of looking at data without preconception.

In later years, Sakae Katoh shifted his study to stress physiology and ecophysiology. Except for his stay at the Charles F. Kettering Lab (Yellow Springs, Ohio, USA) working with Anthony (Tony) San Pietro from October 1964 to December 1966, all his research was carried out in Japan. He retired from the University of Tokyo in 1993 and moved to Toho University. Finally, he entirely retired from his academic position in 1998. During his service to the universities, he mentored many students as a supervisor. Some of them became professors at various universities, *e.g.*, Hiroyuki Koike (Chuo University), Akihiko Yamagishi (Tokyo University of Pharmacy and Life Sciences), Yuichiro Takahashi (Okayama University), Jian-Ren Shen (Okayama University), Yasuhiro Kashino (University of Hyogo), and myself (Waseda University). I must note, with gratitude, that I was a research associate in the laboratory when Sakae Katoh had retired from the University of Tokyo and inherited many laboratory equipment from him as a kind of ultimogeniture.

Finally, I would like to introduce Sakae Katoh’s two convictions. I remember that he told me several times that “Good work speaks for itself”. He disliked “advertising” his work, although many people may find it difficult to share his conviction now under current academic circumstances. His other conviction was the necessity of the service to others. He was always open to sharing resources and lab equipment with other researchers. Sakae Katoh had carried out most of his early work in “an ill-equipped underground laboratory” during the post-war period in Japan, but his activity was not restricted by such a condition. He considered that young scientists should have a strong belief in the future, even under unsatisfactory conditions, and the seniors around them should help them. I end this Tribute by showing a photograph of Sakae Katoh, with several others, when Bacon Ke was visiting him in Japan in 1985 (Fig. 3; for Bacon Ke, see Govindjee *et al.* 2022).

I believe that Sakae Katoh was a great scientist, both in his research and in his maturity of thought. Please join us in remembering Sakae Katoh and his many contributions to our community.

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