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Govindjee's Photosynthesis Museum

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Presented below is a slightly modified article that I wrote about Govindjee, Professor Emeritus of Plant Biology, Biophysics and Biochemistry and Biophysics, at the University of Illinois at Urbana- Champaign (UIUC) twenty years after he had retired. It is based on my interview with him in July of 2019, in his office in Morrill Hall at UIUC. I thank Fred Zwicky for all the photographs used here. Also, see the prologue of this article by Arthur Nonomura.

CHAMPAIGN, Illinois – I am in Govindjee's office suite and I do not know where to look. Govindjee, a professor emeritus of plant biology who goes by the one name only, is a collector. There are layers of history here: artifacts and papers, books and photographs. There also are homemade scientific instruments that look like plumbing elbows, tiny satellites or props from vintage sci-fi movies.

Figure 1 shows Govindjee in his office with his "old" instruments, his books, and more.

Figure 2 shows some of the antique instruments Govindjee has kept, and he still cherishes them.

The above collection engulfs two tiny offices and a more expansive shared space that connects them. It spills into the hallway and around the corner, where a glass-faced "cabinet of curiosities" is loaded with items that have not been used for decades, but still retain an ageless, innovative luster.

Govindjee has each of these items catalogued in his memory, along with the names, dates and personalities of nearly every genius who ever tackled the puzzle of

Figure 1: Plant biology professor emeritus Govindjee, who has made key contributions to the scientific understanding of photosynthesis, is also an archivist and science historian. Photo by Fred Zwicky

Figure 2: A manometer, left; a telescope and a capillary tube, center; and a distillation column that were used in his early photosynthesis experiments. Photo by Fred Zwicky

photosynthesis. Photos of many of those geniuses are on the walls, with scribbled notes like: "*Andy Benson, co-discoverer of Carbon Fixation Cycle. September 24, 1917 – Feb. 6, 2015. A dear friend.*"

Figure 3 shows the unique instrument that one of his first Ph.D. students, Carl Nelson Cederstrand, built.

Figure 3: Govindjee's former graduate student Carl Cederstrand built this dodecahedron with 12 photocells. With this instrument, they demonstrated the physical presence of different spectral forms of chlorophyll *a*. Govindjee had earlier determined that the different spectral forms of chlorophyll *a* must contribute to different photochemical reactions in photosynthesis. [See Laura Cederstrand and G. Govindjee (2022) Carl Nelson Cederstrand (1927-2022): A biophysicist, an innovator, and a wonderful person. *International Journal of Life Sciences* 11(1): 21-27] Photo by Fred Zwicky

Govindjee guides me from one relic to another. He shows me Robert Emerson's 1928 Ph.D. dissertation, written in German. Emerson was Govindjee's mentor at the University of Illinois for two years – until an airplane crash took Emerson's life in early 1959. [See H. Lichtenthaler and L.O. Bjorn (2020) *Journal of Plant Science Research* 36(1): 5-24, for an English translation of this thesis, which is preceded by a Letter to the Editor by Govindjee; also, see Govindjee and R. Govindjee (2021) Personal reminiscences of Robert Emerson and Eugene Rabinowitch. *Journal of Plant Science Research* 37(1): 101-106.]

Figure 4: Govindjee still honors and remembers Professor Robert Emerson, his first mentor at Illinois. Photo by Fred Zwicky

Figure 4 shows a photograph of Robert Emerson on which, we have superimposed Govindjee's image.

Then, Govindjee showed me the microscopes through which he and his colleagues looked at algae in the 1950s and 1960s. Then there was a yellowing logbook that has the names of people – including a few Nobel laureates – who visited the photosynthesis lab over the years, with careful notations of what they were paid. [This is now located in the Archives of UIUC.] In a corner, there was a framed illustration of 18th-century scientists who contributed key findings to understanding photosynthesis. [This can be seen on page 8 (as Figure 1.1), in E. Rabinowitch and Govindjee (1969) *Photosynthesis*, John Wiley]

Govindjee's office suite contains a massive collection of documents, photos, reports and artifacts related to photosynthesis research. See Figure 5, for a sample.

Many people do not know it, but Illinois has been a leader in photosynthesis research for decades, a tradition that continues to this day. Govindjee is at the heart of a generation that made key discoveries about the complex and baffling process by which plants convert water, carbon dioxide and the discrete particles of light called photons into oxygen and the raw materials that make life possible on Earth. [See his own account of his

Figure 5: Some artifacts in Govindjee's office. Photo by Fred Zwicky

research: Govindjee (2019) A sixty-year tryst with photosynthesis and related processes: An informal perspective. *Photosynthesis Research* 139: 15-43.]

"The most exciting thing for me was … I want to show you a picture," Govindjee says, jumping up and stumbling over a chair on the way out of his tiny office. He leads me to a giant, hand-painted poster – a diagram of photosynthesis – hanging on a door just outside the office. He made this chart in the early 1960s, and it still hangs in a place of prominence in this photosynthesis "museum." It is as big as he is (see Figure 6).

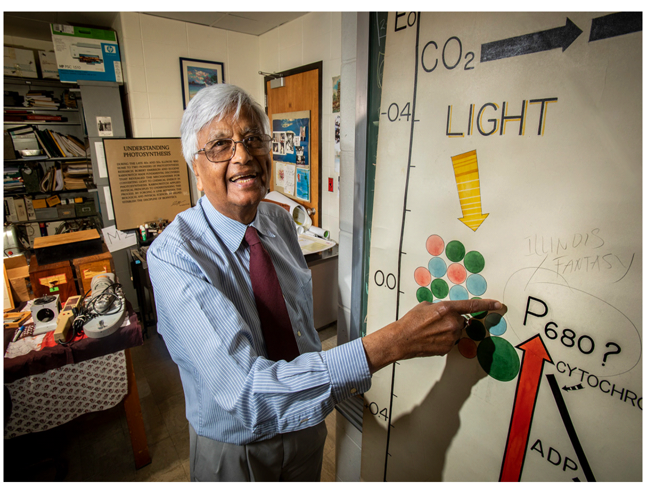

Figure 6: At a conference in the early 1960s, another researcher defaced a poster of Govindjee's proposed photosynthesis pathway as an "Illinois Fantasy," but Govindjee's hypothesis [for the existence of reaction center of Photosystem II, P 680] was later proved correct. Photo by Fred Zwicky

"This is where my work is," he says, pointing to one region on the chart. "We showed that bicarbonate is needed for electron and proton flow from one molecule to another. If you remove bicarbonate, then everything stops," he said. [For a review of the Z-Scheme that is exhibited in the poster, see Govindjee, Shevela D., and Björn L.O. (2017) Evolution of the Z-Scheme of photosynthesis. *Photosynthesis Research* 133:5-15]

Bicarbonate is only one of the many molecular players in the complicated photochemical dance that makes photosynthesis possible. In the beginning, of course, none of these chemicals or mechanisms were known. [For a review of the unique role of bicarbonate discovered by Govindjee and others, see: Shevela, D., Eaton-Rye, J.J., Shen, J-R. and Govindjee (2012) Photosystem II and unique role of bicarbonate: A historical perspective. *Biochimica et Biophysica Acta* 1817:1134-1151.]

A few steps away from the poster are three dusty wooden boxes. Govindjee opens one to reveal a series of colored glass filters. In their early efforts to understand how photosynthetic organisms interact with light, he and other scientists exposed algae to different colors of filtered light and watched to see which wavelengths the

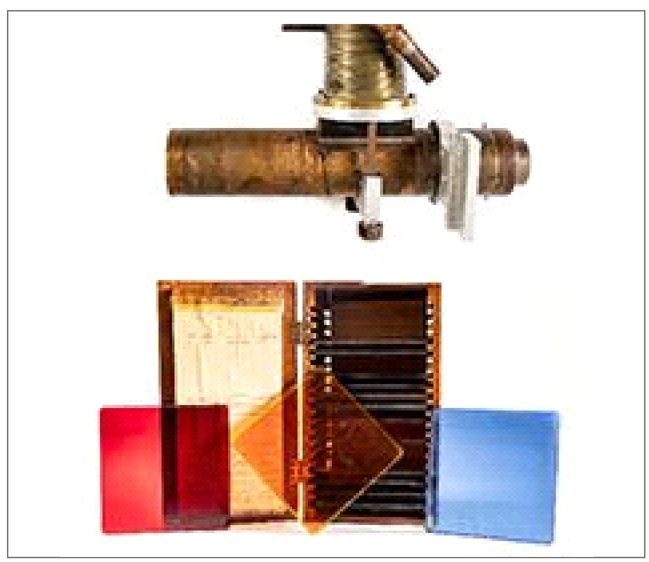

Figure 7: Top, an instrument that led to the discovery of two light reactions and two pigment systems in photosynthesis. Bottom, colored filters allowed researchers to measure photosynthesis under different wavelengths of light. Photo by Fred Zwicky

Figure 8: From left, a syringe for transferring precise quantities of algal cells, feathers used to dust glass vessels, an electrometer to measure low light intensities, and a hand-held spectroscope for checking the spectral distribution of light in photosynthesis experiments. Photo by Fred Zwicky

algae absorbed and which they used for photosynthesis (see Figure 7). Figure 8 shows other pieces of equipment used in the early days — a feather to clean the manometer vessels, a hand spectroscope to check the transmission of glass filters, and more.

In the process, Govindjee and colleagues discovered that algae and plants use several types of chlorophyll *a*, each with its own unique light preferences. Chlorophylls are the molecules that give most plant leaves their characteristic green color and do the work of converting sunlight to chemical energy, a process that generates oxygen as a byproduct.

Over time, the researchers have pieced together much of the photosynthetic puzzle. Figure 9 shows Govindjee enjoying his retired life.

After Emerson's death, Govindjee reinvestigated a scientific debate that had simmered between Emerson and Nobel laureate Otto Warburg. Each scientist had reported the number of photons needed for algae to produce a single molecule of oxygen. But their results differed – by a lot. Warburg said only four photons were needed per oxygen molecule; Emerson said it was 12. With painstaking care, Govindjee and his wife, Rajni

Figure 9: Govindjee holding a flask with a copper sulfate solution that he used in experiments to filter out the heat from white light. Photo by Fred Zwicky

Govindjee, who earned her Ph.D. at UIUC and continued to work as a research scientist in photosynthesis, demonstrated that Emerson's calculations were correct (R. Govindjee, E. Rabinowitch, and Govindjee (1968) Maximum quantum yield and action spectra of photosynthesis and fluorescence in *Chlorella*. *Biochimica et Biophysica Acta* 162: 530-544).

The Govindjees also found that chlorophyll *a*, one of several chlorophylls employed in photosynthesis, contributed to two light reactions that together drive photosynthesis. Figure 10 shows some of the instruments they had used in their research (For Chl *a*, see Govindjee and E. Rabinowitch (1960) Two forms of chlorophyll *a in vivo* with distinct photochemical function. *Science* 132: 422; and R. Govindjee, J.B. Thomas and E. Rabinowitch (1960) Second Emerson effect in the Hill reaction of *Chlorella* cells with quinone as oxidant. *Science* 132: 421.)

Humor is a common feature of displays in Govindjee's office suite. In one, plant biology professors Donald Ort, Stephen Long and Govindjee have their faces superimposed on a "Star Trek" poster (see Figure 11).

Over the course of more than 60 years of research, Govindjee has known collegially, become friends with, or feuded — armed with Star Trek Phasers—over light reactions with many scientific giants, and his work

Figure 10: From left, a lens, an integrating sphere, and a mirror were used in early photosynthesis experiments. Photo by Fred Zwicky

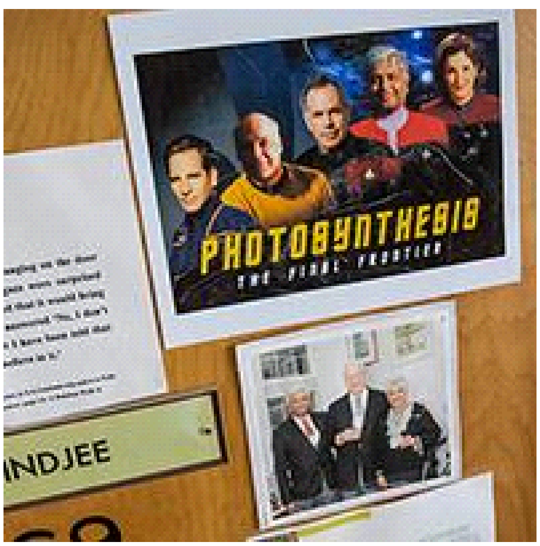

Figure 11: A photo of one of the doors leading to Govindjee's office. It not only shows Don Ort, Steve Long and Govindjee (top right), but, also, President Stanley Ikenberry with Govindjee and Rajni, when Govindjee had received an award. Photo by Fred Zwicky

Figure 12: Govindjee at work in his office. Photo by Fred Zwicky

today also involves recounting their personal reminisces in relation to the history of photosynthesis. He is the author or editor of dozens of books on photosynthesis. He also has written or contributed to multiple historical reports. See his web page: https://www.life.illinois.edu/govindjee/. His recent publications page provides evidence of his current high academic activity: https://www.life.illinois.edu/govindjee/recent_papers.html

At age 90, Govindjee still works at light speed as an educator, scientist, and historian (see Figure 12). He has traveled regularly around the world to lead educational sessions and speak at conferences; and even in the wake of the Covid-19 pandemic, is sharing his knowledge with other scientists *via* online video conferences, particularly with colleagues in China, Japan, Germany, The Netherlands, Sweden, and India. He remains engaged in promising research at home and overseas. He writes about pivotal events in photosynthesis research. And he collects: letters, documents, posters, arguments, and artifacts. They are all here somewhere in his office, in this tiny shrine.

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