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Contributions of Rajni Govindjee in the Life Sciences: Celebrating her 88th Birthday#

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ABSTRACT

Here, we honour Rajni Govindjee, a leading photobiologist of our time, as she turns 88 in 2022. This follows the tribute given earlier by Thomas Ebrey on the occasion of her 80th birthday. After a brief introduction, we summarise her research accomplishments—carried out in a highly cooperative spirit with a large number of scientists. We conclude with recent greetings from some of Rajni's many collaborators. Since the previous tribute to Rajni was done so wonderfully well, we reproduce a good portion of it in Appendix 1 (also see Appendix 2).

Keywords: Robert Emerson, Eugene Rabinowitch, Emerson enhancement effect, Bacteriorhodopsin, photocycle

INTRODUCTION

Rajni Varma, after receiving her MSc in Botany (first division) in 1955 from the University of Allahabad, worked for 2 years in Plant Physiology under the mentorship of Shri Ranjan (1899–1969; Laloraya, 1970). In 1957, she joined the University of Illinois at Urbana-Champaign (UIUC) on a fellowship to work with Robert Emerson (1901–1959; Govindjee and Govindjee, 2021), a pioneer in the 'Light Reactions in Photosynthesis'. On 24 October 1957, Rajni married Govindjee (see https://www.life.illinois.edu/govindjee/) and changed her formal name to Rajni Govindjee. After the untimely death of Emerson on 4 February 1959, Rajni began her research under the mentorship of Eugene Rabinowitch (1898–1973) and completed her PhD in 1961 (for information on Rabinowitch, see Govindjee *et al.*, 2019; see Govindjee, 1961 for her PhD thesis). Thereupon, Rajni initiated a distinguished career at UIUC, investigating a number of scientific problems in basic photobiology. In a personal tribute on the occasion of Rajni's 80th birthday, Rajni's long-time colleague Thomas (Tom) Ebrey fittingly described her as 'Brighter than the Sun' (Ebrey, 2015). Figure 1 shows two portraits of Rajni

#Authors are highly thankful to the Chief Editor Professor Ashwani Kumar for inviting S. Balashov and co-authors to celebrate Rajni Govindjee's key research contributions in Life Sciences

Figure 1: Two portraits of Rajni Govindjee from two different times of her life; on the Left she is at home in Urbana, Illinois, and on the Right is when she was traveling in India.
Source: Family archives

Govindjee from two different times of her life. We present here a brief summary of her contributions in chronological order, basically to present in a single context most of her research work. We also wanted to emphasise that one of Rajni's many talents was to engage in successful team efforts to get to the bottom of her research questions. She first conducted these efforts to probe questions in photosynthesis in the laboratory of Eugene Rabinowitch, followed briefly by work in the laboratory of Christiaan Sybesma (Vredenberg and Govindjee, 2020). Most of her subsequent work was carried out in the laboratory of Thomas G. Ebrey which focused on how the retinal protein bacteriorhodopsin (bR) functions in the archaebacterium *Halobacterium salinarum* (formerly *H. halobium*). For additional information on Rajni, see Appendix 1 and Appendix 2.

FROM ALLAHABAD TO URBANA: FROM SHRI RANJAN TO ROBERT EMERSON AND EUGENE I. RABINOWITCH: 1950s–1960s

Rajni's first research paper (Laloraya *et al.*, 1956) described work that she carried out in the laboratory of Shri Ranjan at the University of Allahabad; she probed the effects of Carica curl virus infection on the amino acids in papaya leaves, in studies carried out with others including Tadimeti Rajarao (for Rajarao, see Govindjee *et al.*, 2022). Rajni and co-investigators showed that viral infection increased the formation, in particular, of asparagine. Fundamentally, these experiments and the resulting publication represented a nice entry into the use of paper chromatography and other biochemical tools.

Soon thereafter, Rajni's research focus transitioned to understanding the key steps in oxygenic photosynthesis. She began research with Robert (Bob) Emerson at the University of Illinois, Urbana-Champaign, but this period was cut short by Emerson's tragic death in an aviation accident on 4 February 1959. Rajni continued her research in the laboratory of Emerson's colleague at UIUC, Eugene Rabinowitch. In addition to other accomplishments, she proved that the Emerson Enhancement Effect in oxygen exchange, as measured by Robert Emerson, was in photosynthesis, not in respiration, as was suggested by Lawrence (Larry) Blinks (1959) from his measurements on transients in oxygen exchange. Rajni showed that the Emerson effect was observed in benzoquinone-mediated Hill reaction in whole cells; since respiration was completely inhibited by benzoquinone, the Emerson Enhancement Effect was clearly in photosynthesis and not in respiration (Govindjee *et al.*, 1960 and Govindjee and Rabinowitch, 1961). Further, to confront sceptics, Govindjee *et al.* (1962, 1964) did crucial experiments on chloroplasts showing the existence of the Emerson Enhancement Effect in NADP Hill reaction. There was thus no doubt that Emerson's two-light effect indicated the existence of two photosystems and two light reactions.

Rajni further determined that the short-wave photosystem had chlorophyll *a*, which was also shown by Govindjee and Rabinowitch (1960) in whole-cell photosynthesis. In combination, these studies clinched the discovery of two light reactions and two photosystems in oxygenic photosynthesis. Further, Govindjee and Govindjee (1965a, 1965b) showed new kinetic manifestations of the two-light effect through absorption changes in the 480–520 nm range. The 1931 Nobel laureate Otto Heinrich Warburg claimed that only four photons were required to produce oxygen and that 10% CO_2 and blue catalytic light were required (unlike the experimental conditions used by Emerson); Warburg then concluded that the Emerson Enhancement Effect was incorrect. Govindjee *et al.* (1968) instead demonstrated, under the conditions specified by Warburg, a minimum quantum requirement of 8–10 per oxygen and the presence of Emerson Enhancement, settling remaining doubts about the correctness of the effect.

WITH CHRISTIAAN (CHRIS) SYBESMA AND THEN WITH THOMAS (TOM) EBREY: 1970S

Rajni's research on oxygenic photosynthesis continued in the 1970s, but she expanded her work to anoxygenic photosynthesis with Chris Sybesma. In 1975, she began to investigate the photocycle of the microbial retinal protein bR (with Tom Ebrey).

Photosynthesis

Rajni exploited the use of lyophilised thylakoid membranes, investigating the effects of wet and dry heptane extraction on such membranes in the laboratory of Jean Lavorel in France (Govindjee *et al.*, 1970b). This method was highly useful in proving that absorption changes in Photosystem II (PS II) reaction centre 'P680' were not due to an artefact of fluorescence changes (Govindjee *et al.*, 1970a). Previously, Rajni had shown that NADP reduction in oxygenic photosynthesis requires two photosystems and two light reactions (see above). She thus carried out experiments, in collaboration with Chris Sybesma, on NAD reduction in anoxygenic photosynthetic bacteria relating it to the overall electron transport system there; for details, see Govindjee and Sybesma (1970, 1972). These studies were followed by examining the interaction of this system with viologen dyes, supporting the 'one light reaction-one photosystem' concept for anoxygenic photosynthetic bacteria (Govindjee *et al.*, 1974). Crucial to this discovery, Rajni collaborated on experiments to uncover the site of the unique role of bicarbonate on the electron acceptor side of PSII (see Govindjee *et al.*, 1976). Around this time, Rajni and G. Govindjee wrote an excellent article on the primary events in photosynthesis, published in Scientific American (Govindjee and Govindjee, 1974) with a view towards educating the general public about fundamental advancements in the field.

Photochemistry of bR

In 1975, Rajni's research interest turned to understanding a system that was quite different from 'photosynthesis'. The microbial retinal protein bR is a light-driven transmembrane protein pump and serves as a model membrane protein for studies of the photobiophysics of retinal proteins and light-driven ion pumps. Rajni joined Tom Ebrey's research group and her first studies on this new system ('purple membrane protein') were published in rapid succession over the next few years: (i) Ebrey *et al.* (1975) provided new results on the properties of several sterically modified retinal analogues and their 'photosensitive pigments'; (ii) Nakanishi *et al.* (1976) provided new information on 'allenic retinals and their visual pigment analogues'; (iii) Alfano *et al.* (1976) uncovered the picosecond kinetics of the fluorescence from the retinal chromophore of the purple membrane protein; (iv) Tokunaga *et al.* (1977) made new physico-chemical measurements on synthetic pigment analogues of the purple membrane protein; and (v) Govindjee *et al.* (1978) published detailed key information on various fluorescence parameters of the retinal chromophore of the purple membrane protein.

FURTHER RESEARCH WITH TOM EBREY: 1980S

In the 1980s, Rajni measured, in single turnover flashes, not only the high-quantum yield of proton release in purple membranes (~0.7), but also the similarly high ratio of protons to the M412 spectral photointermediate of bR (also 0.7); for details, see Govindjee *et al.* (1980). In 1981, Rajni collaborated with Rosalie Crouch (Medical University of South Carolina) and others to investigate (i) a special bR analogue (Crouch *et al.*, 1981); and (ii) photochemical properties of bRs formed from new retinals (Mao *et al.*, 1981). These studies were followed in 1982 and 1983 by in-depth investigations into the molecular mechanism of light-induced changes in proton movement (a) by removing the COOH region of bR (Govindjee *et al.*, 1982); and (b) by using blue, instead of white, light (Ohno *et al.*, 1983). With M. Tsuda, Rajni studied the effects of pressure and temperature on the M412 photointermediate, mentioned above (see

Tsuda *et al.*, 1983). In 1984, Rajni and co-workers made the important finding that neither the retinal ring nor the ring double bond is required for proton pumping by bR (Crouch *et al.*, 1984). Furthermore, and significantly, Li *et al.* (1984) found a long-sought correlation between proton pumping and the bR photocycle.

The year 1985 was a year of many discoveries on many fronts on the photochemistry of bR, which included collaboration with many scientists: (i) Tsuda *et al.* (1985) characterised the chromophore of a third rhodopsin-like pigment from *H. salinarum;* (ii) Chang *et al.* (1985a) provided mechanistic details of cation binding on bR; (iii) Chang *et al.* (1985b) showed that trans-to-13-cis isomerisation is essential for both the bR photocycle and proton pumping; (iv) Crouch *et al.* (1985) presented an abstract at a conference concluding that neither the retinal ring nor the double bond there is required for proton pumping in bR; and (v) Schiffler *et al.* (1985) provided detailed measurements on resonance Raman spectra on many bR analogues.

Rajni continued research in bR at a very high level in 1986: (i) Chang *et al.* (1986) provided a detailed mechanistic picture of divalent cation binding to bR; (ii) Crouch *et al.* (1986) published details of the physico-chemical properties of many synthetic bRs, which were very useful in understanding the overall process of how bR functions *in vivo*; (iii) importantly, Dancshazy *et al.* (1986) discovered a new intermediate in the bR photocycle; (iv) Govindjee and Ebrey (1986) provided a grand overview on all the information till then on light emission characteristics and properties of bR and rhodopsin—highly useful for beginning graduate students in Biophysics and Biophysical Chemistry; (v) Li *et al.* (1986) described a proton release site on the C-terminal side of bR; (vi) Marque *et al.* (1986) described how physico-chemical environment modulates the dynamic structure of the C-terminus site of bR; and (viii) Zingoni *et al.* (1986) dug deeper to find how the length of retinal polyene side chain affects the bR function.

The years 1987–1989 were equally productive years, during which a number of important discoveries were made: (i) Chang *et al.* (1988) described how blue and purple membranes can be regenerated from deionised bleached membranes of *H. halobium*; (ii) Dancshazy *et al.* (1988) described independent photocycles of spectrally distinct forms of bR in an article in the *Proceedings of the National Academy of Sciences of USA*; (iii) Govindjee *et al.* (1988a) and Govindjee *et al.* (1988b) described the key photochemical reactions and properties of methylated rhodopsins; and (iv) Govindjee *et al.* (1989) presented results on the different absorption spectra of the last of the intermediates of the bR photocycle. In addition to the productive collaborations in the Ebrey laboratory, the camaraderie extended to memorable gatherings at the homes of the Govindjee and Ebrey families (Figures 2 and 3, respectively).

FROM 1990 UNTIL RETIREMENT IN 1999–STILL WITH TOM EBREY

During this period, Sergei Balashov and Ella Imasheva (from Moscow State University, Russia) were two of Rajni's major collaborators. We first summarise here the work that Rajni carried out in collaboration with Sergei and Ella. Figure 4 shows a 2014 photograph of Rajni Govindjee with Ella Imasheva and Sergei Balashov when Rajni visited the couple in California.

Govindjee *et al.* (1990) provided the most comprehensive and thorough measurement of the quantum efficiency of the bR photocycle. In addition, laser-induced irreversible damage of bR was observed and two photoproducts were described. Balashov *et al.* (1991a) showed that at high pH, there is a red shift in the absorption band of bR, coincident with deprotonation of several tyrosines—offering a chemical clue to this phenomenon. Balashov *et al.* (1991b) provided detailed information on the quantum yields of the forward and the back (light) reactions of bR at liquid nitrogen temperatures. Significantly, Balashov *et al.* (1992) and Balashov *et al.* (1993) showed that mutation of Arg82 to Ala in bR causes (i) a drastic increase in the pK_a of the retinal counterion residue Asp85 and the rate of the Schiff base deprotonation, but a decrease in the rate of proton release in the system; and (ii) changes in dark

Figure 2: A 1984 group photograph at Rajni's residence. Among others are Yiannis Koutalus (red shirt, in the front row); Jiang-Guo Chen (in black, third from the left); and (from left to right in the back row) Govindjee, Rajni, Cheng-Ho Chang, Suyi Liu, Tadashi Nakamura and Burr Nelson. *Source:* Suyi Liu

Figure 3: A 1984 photograph of Tom Ebrey cooking dinner outdoors with Rajni (extreme left) watching. *Source:* Suyi Liu

Figure 4: A 2014 photograph in California. Left to right: G. Govindjee, Ella Imasheva, Rajni Govindjee and Sergei Balashov. *Source:* Sergei Balashov

adaptation, providing additional clues to the overall mechanism of the bR photocycle, specifically on the mechanism of thermal isomerisation of the retinal chromophore. The authors showed that thermal isomerisation is catalysed by the protonation of Asp85, the pKa of which is controlled by Arg82. Next, Govindjee *et al.* (1992) showed that mutation of Tyr57 to Asn inactivates the bR photocycle—providing a molecular-level understanding of the overall process; moreover, Govindjee *et al.* (1994) showed that in this inactive mutant, lowering the intrinsic pKa of bR's Schiff's base can restore its light-induced deprotonation steps.

Research with Sergei and Ella continued, but many other co-workers were also involved. Among these were Prof. Rosalie Crouch (mentioned earlier) and Prof. Don Menick from Medical University of South Carolina (MUSC), who developed the expression of mutant bRs in native *H. salinarum* cells. These mutants provided powerful tools to study the roles of individual residues in intramolecular proton transfer and the proton pumping mechanism. Balashov *et al.* (1995) studied the consequences of changing Arg82 to Lys on the bR photocycle, which resulted in the discovery of coupling between the Schiff base counterion and the proton release group, the site of protein release into the extracellular medium. Govindjee *et al.* (1995) studied the effects of changing Tyr57 to Asn or Phe, and Balashov *et al.*

(1996a) showed the difference the change of all trans to 13cis in bR makes to the pK(a) of Asp85 in the system. Subsequently, Balashov *et al.* (1996b) carried out a detailed examination of the function of Asp85 in the bR photocycle including the associated proton release events, and Govindjee *et al.* (1996) further examined the function of Arg82 (cf. above) in relation to the pKa of the proton release group; in addition, Govindjee *et al.* (1997) showed the effect of mutating Lys129 on proton release. Das *et al.* (1999) examined the effect of pyrylretinal analogues of bR. To cap it all, Balashov *et al.* (1999) examined the role of the proton release group of bR and its key components, Glu134 and Glu204, in the control of the rate of the final step of its photocycle at low pH. In addition, the roles of Thr205 and Ser193 in proton conductance and release were also examined (see Lu *et al.*, 2000).

In addition to Rajni's research with Sergei and Ella described above, she also collaborated with many other investigators and also expanded her studies to retinal proteins other than bR. Liu *et al.* (1990) measured light-induced (bulk) electrical signals from uniformly oriented bR samples; Tierno *et al.* (1990) looked at the effects of fluorinated compounds; Beishel *et al.* (1991) studied unusual bR analogue pigments; Hazard *et al.* (1992) examined the incorporation of fluorotyrosine in bR. Further, Beischel *et al.* (1994) examined the azido tetraflurophenyl retinal analogue and its function, while Misra *et al.* (1997) showed, using E204Q mutant that the proton uptake and its release are indeed rate-limiting steps in bR photocycle! Combined, these many studies provided an in-depth and comprehensive understanding of how the bR cycle functions *in vivo*. In studies on retinal proteins other than bR, Lukashev *et al.* (1994) examined the pH dependence of the photochemistry and photobiology of archaerhodopsins, and Liang *et al.* (1993) studied the metarhodopsin intermediates of the Gecko eye (visual) cone pigment P521, a 'true' animal opsin protein.

Figure 5 shows a photograph of Suyi Liu when he once visited Rajni at her home in Urbana, IL, long after her retirement. Figure 6 shows a photograph of Rajni with Burr Nelson and Sergei Balashov in the graduate students' office in Tom Ebrey's lab, and Figure 7 shows Rajni having lunch with Masahiro Kono and Yiannis Koutalos, while at a conference.

Figure 5: A 2005 photograph at 2401 Boudreau Drive, in Urbana, Illinois. Left to right: Rajni Govindjee, G. Govindjee, Wei Sun and Suyi Liu. *Source:* Liu's archives

Figure 6: A 1994 photograph of Sergei Balashov, Rajni Govindjee and Burr Nelson in the graduate students' office at UIUC. *Source:* Masahiro Kono

In addition to working on the bR photocycle and finding its mechanism, Rajni also continued to work on photosynthesis, the area in which she had made major discoveries in the 1960s (see above). In Norio Murata' Lab in Japan, and together with George Papageorgiou, visiting from Greece, Rajni showed light-induced and osmotically induced changes in chlorophyll *a* fluorescence in two strains of cyanobacteria that differ in membrane lipid unsaturation (Papageorgiou *et al.*, 1999). This research topic continues to be pursued in several laboratories today.

Figure 7: Left to right: Masahiro Kono, Yiannis Koutalos and Rajni Govindjee enjoying a meal together at a 1990s meeting of the Biophysical Society of America. *Source:* Masahiro Kono

POST-RETIREMENT

After retirement in September 1999, Rajni's very last scientific paper was on the pH dependence of the photocycle of visual pigment rhodopsin (see Kuwata *et al.*, 2001), continuing work on which she collaborated in the prior decade. However, Rajni increasingly shifted her focus to reading and enjoying biographies of political leaders around the world. In addition, she has been contributing to reminiscences of her influential PhD professors, Robert Emerson and Eugene Rabinowitch; see, for example, Govindjee and Govindjee (2021) and Govindjee *et al.* (2019). She also participated in writing a tribute to Maarib Bazzaz, a former PhD student in G. Govindjee's laboratory (Govindjee *et al.*, 2020). At present, Rajni is now engaged in fully enjoying nature and following global politics.

Messages from Rajni's Colleagues and Friends, Including Co-authors

Sergei and Ella Balashov

Working with Rajni and Tom was great pleasure! Rajni is such a bright and kind person. Please say hello to her!—Rajni is an accomplished biophysicist. She has very high standards in science and research conduct. As a colleague she sets example and gives inspiration.

Jianguo Chen

Hi Rajni: This is Jianguo Chen. Happy Birthday. Best wishes to you and your family.

Thomas Ebrey

Dear Rajni: Special congratulations on the occasion of your 88th birthday! I am sure it is a lucky number. Not only were you the glue that held the lab together, but you were also a constant joy with your intelligence, skills, and optimism about getting things done. A true treasure.

Elisabeth Gantt

Happy Birthday to Rajni.

Zarina Hock

I am in awe of Rajni's scientific achievements. To think she balanced all that with her family life, her friendships, her volunteer work, is truly outstanding.

Masahiro Kono

Please give Rajni my best and wish her the happiest of birthdays. Also, let her know that I wish I knew everyone's birthdays when I was in the lab. Yiannis Koutalos' birthday is on Saturday the 26th November, and mine was last week on the 19 November. We could have had a great excuse for group lunches or cakes in lab for all those years! Best wishes.

Yiannis Koutalus

Hi Govindjee, good to hear from you! Give my regards to Rajni, and my wishes for many happy returns!………

Osamu Kuwata

Thank you for the delightful information about Rajni, with whom I have fond memories, life and work at Prof. Tom Ebrey's lab at the University of Illinois at Urbana-Champaign. Please pass my hearty words for celebrating her 88th birthday, and sincere wishes!!

Jie Liang

Dear Rajni, I wish you a very happy 88th birthday! I cannot believe it has been so long, even since our last chance encounter in Shanghai, although it feels it was just a few months ago when I was in the Ebrey lab and we played badminton together.

I am very grateful for your friendship—there were so many valuable things you taught me during my academic formative years. I was a new student finding my ways around in science and in this country. You have been so kind in helping me and guiding me in many ways, not least the difficult dye and laser experiments.

I also remember the kind and generous parties where you and Govindjee had invited the whole Ebrey lab over—it made me feel so warm, and it was also where I had my first taste of brandy. Take good care and we will be celebrating your 98th and 108th birthdays! Yours, Jie.

Suyi Liu

Dear Rajni: Many thanks for your guidance and help while I was a student at University of Illinois at Urbana-Champaign. Happy Birthday!

Saurav Misra

Dear Rajni, I am delighted at the chance to wish a happy 88th birthday to my former mentor, (senior) colleague, fellow scientist and one of the loveliest, most all-around sterling people it has ever been my pleasure to know and to learn from. May the next few years bring you as much interest and joy as the last few, and I hope to meet you again in person soon!

Raghubir (Raj) Prasad

My heartfelt congratulations to Rajni Govindjee (neé Varma) on her 88th birthday that just passed. I had the good fortune to have known her since 1954 while we were in the Department of Botany, University of Allahabad, India, as graduate students in the Plant Physiology Lab of Prof. Sri Ranjan—both of us being first division students in our own areas in different years. After completing my MSc, in 1956, I worked on the role of auxins in sugarcane, whereas she was working on the changes in amino acids caused by virus- infection in plant leaves since 1955. In 1957, she went to USA to the University of Illinois at Urbana-Champaign (UIUC) to study under Prof. Robert Emerson, while I went to UK to study under Prof. G.E. Blackman of Oxford University, both on special fellowships. On the extra-curricular side, I must mention two exceptional things about Rajni (i) being selected to be the student representative in the very first Indian delegation to China; and (ii) being a topmost swimmer—having crossed the river Yamuna in a record time. I wish Rajni good health, happiness, and longevity in the years ahead.

Barbara Zilinskas

By reading this article, I learned so much about Rajni's many scientific contributions she has made throughout her professional career. It is very impressive, and I marvel how she accomplished so much while leading a double life as devoted mother, grandmother, and wife, as well as friend to many (including me) and gracious and kind host to so many visitors, grad students on Monday night lab meetings and countless dinners and parties, and so much more.

CONCLUDING REMARKS

We end this special toast to Rajni on her 88th birthday with three photographs. Figure 8 shows Rajni with her lifelong partner in science and life (Govindjee) when they were visiting Sergei Balashov and Ella Imasheva in California several years ago; Figure 9 shows Rajni with her friend Rita Khanna under the plaque honouring the research of Carl Woese of 'Archaea' fame; and Figure 10 shows her with Tom Ebrey, who she worked with for many years.

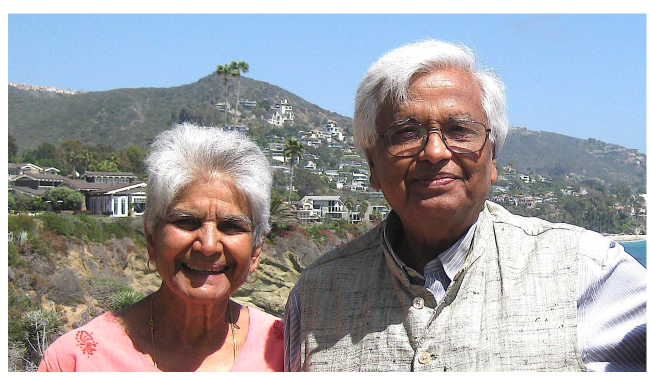

Figure 8: A 2014 photograph of Rajni Govindjee and Govindjee Govindjee while visiting California. *Source:* Sergei Balashov

Figure 9: Rajni Govindjee and Rita Khanna under the plaque for Archaea. Photo, taken in mid-2000s, by Govindjee Govindjee

Figure 10: Thomas (Tom) Ebrey and Rajni Govindjee studying a map trying to figure out where they were when at a Biophysical Society Conference. *Source:* Figure 2 in Ebrey (2015)

APPENDIX 1: ON RAJNI'S COLLABORATIVE SPIRIT

Celebrating distinguished photobiologist Rajni Govindjee for her pioneering research in photosynthesis and photobiology on the occasion of her 88th birthday, we cite Ebrey (2015); the following text has been reproduced with permission.

'Rajni was a master collaborator, working with dozens of people prominent among those like Koji Nakanishi's group on artificial rhodopsins to get experiments done and the first report on bR was with Tom and Fumio Tokunaga collaborating with Rosalie Crouch on the first artificial bR ever created substituting retinal1 with retinal 2 (the aldehyde of vitamin A2) and to explore its properties.

After that Rajni did not look back and was at the centre of subsequent work on many additional artificial retinal-substituted bRs with Rosalie Crouch, Don Menick, Koji Nakanishi, Valerie Balough-Nair, Laura Eisenstein, and Mudi Sheves in the 1980s. She was also one of the first to study the fluorescence of bR with me (Ebrey). She also pioneered studies on the quantum efficiency of bR photochemistry, which became a well-established photobiological subject at Illinois in the tradition of Robert Emerson. Together with Chung-ho Chang, Rajni initiated studies ranging from the effects of cation binding to the colour and photochemistry of bR. Working with Robert (Bob) Callender's group, Rajni provided samples and helped interpret Resonance Raman studies (see e.g., Schiffmiller *et al.*, 1985) of bR and worked with Laura Eisenstein's group on Fourier transform infrared spectroscopy (FTIR) studies of bR.

Another area pioneered by Rajni was the study of proton pumping by bR using flash photolysis methods. The effects of high pressure and temperature on the bR photocycle were studied by Rajni and Motoyuki Tsuda. One of Rajni's most successful collaborations was with Sergei Balashov [see the main text], Ella Imasheva, and Eugene Lukashev on bR mutants. Working closely with Rosalie Crouch and Don Menick and members of their groups, Rajni helped illuminate the role of Arg82 in controlling light-activated proton release in bR. Rajni also initiated studies using site-directed mutants to elucidate the role of Tyr 57 and Lys129 in bR function. Working with Saurav Misra and co-workers, Rajni helped elucidate the role of Glu204 of bR in the proton-pumping photocycle. Rajni was also active in working on the photochemistry of visual pigments with Jie Liang and others. In another study with Osamu Kuwata, Rajni used laser-induced photolysis to study the coupling of proton uptake with Metarhodopsin II formation upon photolysis of rhodopsin. Another successful collaboration was work with Robert (Bob) Rando's group on the photochemical properties of methylated rhodopsins.

Besides, Rajni helped mentor many graduate students including Jim Hurley, Paul Kilbride, Jianguo Chen, Boryeu Mao, Gretchen Sassenrath, Roger Calhoon, Suyi Liu, Chung-ho Chang, Yiannis Koutolos, Dipa Apte, Roy Jonas, Ching, Pa Yuan, Masahiro Kono, Jie Liang, Saurav Misra and Miao Lu. In addition, Rajni welcomed many visitors to the lab, such as Fumio Tokunaga, Motoyuki Tsuda, Tchiya Rosenfeld, Brian Becher, Bridgette Barry, Tadashi Nakamura, Tatsuo Iwasa, Jeff Marque, Kim Bagley, Qingguo Li, Kazuhiko Kinoshita, Koki Ohno, Zsolt Dancshazy, Mudi Sheves, Osamu Kuwata and Akio Maeda as well as many undergraduate researchers.

While Rajni has been a life buoy to many, she has also, to mix nautical metaphors, been a wonderful home port to her two children Anita, an accomplished computer scientist, and Sanjay, an engineering professor at the University of California Berkeley, as well as to her husband Govindjee. In addition to her accomplishments in scientific research, Rajni brought her standards of excellence and collaboration to bear on her athletics. An avid swimmer and a badminton champion, she was a highly sought-after teammate in competitive badminton on the UIUC campus, where her athleticism, strategic execution in the game and competitive *joie de vivre* earned her the respect of an international group of enthusiasts. We know that she played badminton not only with those who were older than she, such as the late George Foster, a professor in Fine Arts who was in his late seventies, but also with students who were half her age. She also frequented several athletic facilities, where she was a regular fixture in fitness swimming. It is also known when she was only 10 years old, she swam across the Yamuna River in Allahabad [now Prayagraj]. Rajni was the ideal collaborator, welcoming new people into the lab, and training them on all sorts of techniques sharing with everyone her knowledge and ideas not only in her papers but also in her presentations and discussions at many scientific meetings.'

Paraphrasing Ebrey (2015): 'Rajni has made unique and important contributions to research and science education, through her love and dedication for the field of photosynthesis and photobiology—her dedication to service and education, as well as research, has enriched the photosynthesis and photobiology community—[all] will forever be in gratitude for [her] most outstanding contributions.'

APPENDIX 2: ON THE CONFLUENCE OF PHOTOSYNTHESIS AND PHOTOBIOLOGY

(Reproduced from <https://www.linkedin.com/pulse/govindjee-rajni-confluence-photosynthesis-dr-ravi-sharma/>with permission)

In writing about Rajni Govindjee, Ravi Sharma wrote that she, together with Govindjee: 'is truly the confluence of Photosynthesis and Photobiology on the sky of Plant Sciences.' He added: 'Rajni played a major role discovering that Emerson's two-light effect was indeed not due to respiration as Larry Blinks had been suggesting but due to photosynthesis. Further, in her work on the quinone Hill reaction, … a short-wavelength form of chlorophyll a (Chl *a* 670) was in the same pigment system as chlorophyll *b*. She followed this line of thinking by establishing that Emerson's two-light effect was seen in NADP photoreduction by chloroplasts. …. Rajni with Govindjee also demonstrated that the (maximum) photosynthetic quantum yield was consistent with a two-step model, even in synchronous young cultures of *Chlorella* and in the presence of 10% CO_2. Rajni's active involvement in photosynthesis ended in 1974 with her widely noticed overview article with Govindjee on the 'primary events in photosynthesis' published in Scientific American. After a short period of research on bacterial photosynthesis, Rajni moved on to work in photobiology… Further, the Department of Plant Biology of the University of Illinois administers an *Annual Govindjee and Rajni Govindjee Award for Excellence in Biological Sciences*—that is fitting to her interest in educating the young and the beginners (https://sib.illinois.edu/graduate/grants/Govindjee; and https://www.life.illinois.edu/govindjee/photooftheyear2022. html).'

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