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TRIBUTE

Satish Chandra Maheshwari (1933–2019)—a brilliant, passionate and an outstanding shining light for all of plant biology

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Abstract We present here a tribute to Satish Chandra Maheshwari (known to many as SCM, or simply Satish), one of the greatest plant biologists of our time. He was born on October 4, 1933, in Agra, Uttar Pradesh, India, and passed away in Jaipur, Rajasthan, India, on June 12, 2019. He is survived by two of his younger sisters (Sushila Narsimhan and Saubhagya Agrawal), a large number of friends and students from around the world. He has not only been the discoverer of pollen haploids in plants but has also contributed immensely to the field of duckweed research and gene regulation. In addition, he has made discoveries in the area of phytochrome research. The scientific community will always remember him as an extremely dedicated teacher and a passionate researcher; and for his wonderful contributions in the field of Plant Biology. See Sopory and Maheshwari (2001) for a perspective on the beginnings of Plant Molecular Biology in India; and see Raghuram (2002a, b) for the growth and contributions of this field in India.

Keywords Haploids · Duckweed · Gene regulation · Phytochrome · Plant molecular biology

Since 2019 the legal name of Govindjee is 'Govindjee Govindjee'; this manuscript was written while he was at JNU[1], New Delhi, India.

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Introduction

During the last few years, to the last days of his life, Satish Chandra Maheshwari (hereafter SCM; see Fig. 1 for portraits) served not only as an honorary professor at the University of Rajasthan, Jaipur, but also as an honorary scientist of the Indian National Science Academy (INSA), New Delhi. To the very end, he was actively involved in touring across the globe with the aid of internet, gathering all the recent advances in plant biology and disseminating the knowledge through several keynote lectures at various conferences. As a tribute to this passionate plant biologist, SCM, we provide a brief account of his early life and present a summary of his research contributions, particularly in the fields of duckweed research; haploidy and tissue culture; gene regulation; and the phytochrome. The story of phytochrome, particularly SCM's contributions, and his views are included in his own words in three separate boxes. This is followed by a wonderful reminiscence by his sister Sushila Narsimhan (SN), one of the authors.

Fig. 1 Two portraits of Satish C. Maheshwari, one from early days (left) and the other from recent days (right). *Source*: Archives of SN

Early life and education

SCM and his five siblings—two brothers (Girish, 1935–1996, and Ramesh, 1940–2019; see Chaudhuri et al. 2019), and three sisters (Kamla 1939–2020, Sushila and Saubhagya) grew up, under the loving care of their wonderful mother Shanti Maheshwari (1910–1983) and their father Panchanan Maheshwari (1904–1966), an internationally acclaimed plant biologist of the century (see https://en.wikipedia.org/wiki/Panchanan_Maheshwari; Steward 1967). The family relocated several times: from Agra to Jaipur (in 1937); from Jaipur to Allahabad (in 1938); from Allahabad to Dacca (Dhaka, now in Bangladesh) in 1939. In the mid-1945, Shanti Maheshwari moved, with the children, from Dhaka to Jaipur due to the aftereffects of World War (WW) II, returning back to Dhaka when the War was over. Finally, the entire family moved to Delhi in early 1949. Figure 2 shows two photographs of his early life with his family.

Initially, SCM studied in a Missionary School in Jaipur; and then, during 1939–1945, in St. Gregory High School (located on Subhas Bose Avenue of Luxmibazar, in Dhaka, Bangladesh), and after two stints in Dhaka and Jaipur, he received his matriculation (High School) certificate in 1948 from East Punjab University, Solan. He did his undergraduate studies, B.Sc. (Hons.) Botany, during 1949–1952 from St. Stephens College, a constituent College of the University of Delhi following which he obtained his masters (M.Sc. Botany) in 1954, also from the University of Delhi. Thereafter, he enrolled for his doctoral research on "*The Lemnaceae: A contribution to their biology, morphology and systematics*" under Professor Brij Mohan Johri and, for this research, he was awarded a Ph.D. (in Botany) in 1958 from the University of Delhi. It was there that he met his future wife (Nirmala), who received her Ph.D. in 1959. Figure 3 shows SCM with Nirmala and other family members including one of the authors (SN).

Teaching and research

For over 40 years (1954–1996), SCM served the Department of Botany at the University of Delhi starting with being a Lecturer and eventually becoming a full Professor in 1967. He was a dedicated teacher and a passionate researcher. During his tenure, he taught the then advanced courses, such as Plant Physiology, Biochemistry and Molecular Biology. Already in 1970, he had introduced and taught a course on Plant Molecular Biology, perhaps the first of its kind in India. Both in teaching as well as in research, SCM was interested in disseminating the historical aspects of science (Sree and Maheshwari 2019; Sree et al. 2019) as much as the scientific part of it.

His long visits and research abroad at Yale University, California Institute of Technology (Caltech), University of Oxford, and Harvard University had a great impact on his research outlook in India. In fact, he played a pivotal role in the establishment of the Department of Plant Molecular Biology at the University of Delhi South Campus. In recognition of his excellence in research, he was awarded several honors and distinctions, to name just a few: The Shanti Swarup Bhatnagar Prize in 1975, the Birbal Sahni Gold Medal in 1981, the J. J. Chinoy Memorial Gold Medal in 1983, and many more. Below, we present a

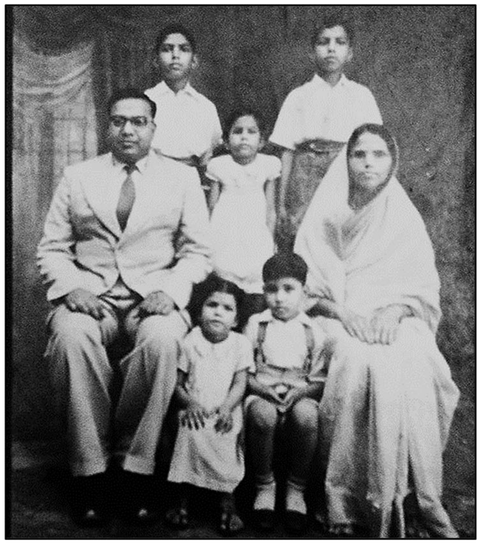
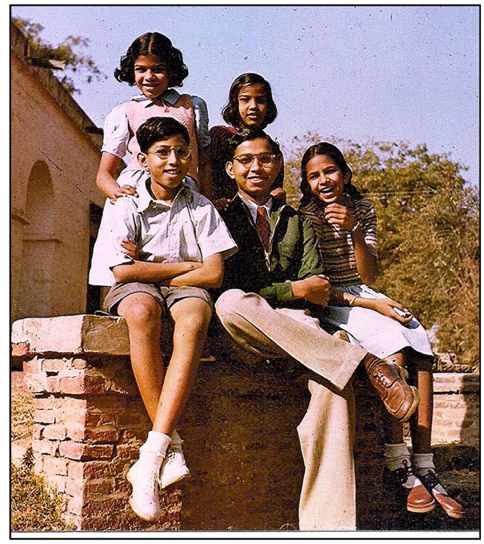

Fig. 2 Left: Photo of SCM with his family taken in Dacca (Dhaka) in 1948. Back row: Left (L) to right (R): Satish, Kamla, and Girish; middle row: Panchanan (father) and Shanti (mother); bottom row: L to R: Sushila and Ramesh. Right: Photo of SCM siblings taken in Delhi, 1952: Back row (standing): L to R: Sushila and Saubhagya; front row (sitting): L to R: Ramesh, Girish and Kamla. Source: Archives of SN

Fig. 3 A photograph of SCM's family taken in Delhi in 1986. L to R: Nirmala Maheshwari, Anjali Garg (Satish's niece), SCM, Kamla Garg, Rajendra Garg (Kamla's husband), and Saubhagya. Sitting: Manjuli (Ramesh's wife) and Sushila. Photo taken by R.S. Narsimhan (husband of Sushila). Source: Archives of SN

summary of his selected research contributions under four categories: (1) Duckweed (Lemnaceae) research, (2) Haploidy & plant tissue culture, (3) Gene regulation, and (4) Phytochromes.

Research contributions of SCM

Duckweed (Lemnaceae) research

SCM did his Ph.D. on the embryology of duckweeds (members of the family Lemnaceae) under the supervision of Brij Mohan Johri, a student and close associate of his father, Panchanan Maheshwari, who was Head of the Department of Botany at the University of Delhi (during 1949–1966). His first paper was on the embryology of *Wolffia*, one of the smallest angiosperms (Maheshwari 1954), which was published in 'Phytomorphology'. The most seminal work from SCM's Ph.D. thesis was published as two research articles in *Nature*. He studied the endosperm and the seed of *Wolffia* (Maheshwari 1956). Based on the embryological observations on *Spirodela polyrhiza*, SCM showed that the family Lemnaceae was closely related to Araceae, and that *Spirodela* was the link between Aroids and duckweeds (Maheshwari 1958). Some of SCM's work of his Ph.D. days, which involved new observations on the morphology and embryology of *Lemna paucicostata* (renamed recently as *Lemna aequinoctialis*) was put together by Ravinder Nath Kapil, and published jointly with him (Maheshwari and Kapil 1963a, b). After his Ph.D., SCM had the opportunity to work both at Yale and at Caltech (1959–1961), and on return to Delhi, he continued his work on Lemnaceae for a while, but soon shifted his focus to study the regulation of flowering. In an interesting paper, also published in *Nature*, SCM, together with O.S. Chauhan, showed that *Wolffia microscopica* is a short-day plant, and requires long nights for flowering (Maheshwari and Chauhan 1963).

The above mentioned work was followed by a series of papers in the 1960s demonstrating the role of cytokinins, newly discovered plant hormones (Miller et al. 1956; Letham 1963), and of a chelating agent EDDHA [ethylenediamine di (o-hydroxyphenylacetic acid], in inducing flowering even under non-inductive long day conditions in these duckweeds, which included several species of *Wolffia* and *Lemna* (Maheshwari and Seth 1966a, b; Maheshwari and Venkataraman 1966; Maheshwari and Gupta 1967; Maheshwari et al. 1967; Gupta and Maheshwari 1969, 1970a, b; Seth et al. 1970; Venkataraman et al. 1970). Subsequently, one of us, JPK, worked with him on flowering in *Lemna paucicostata* (now *Lemna aequinoctialis*), *Spirodela polyrrhiza* (now *Spirodela polyrhiza*), *Wolffia microscopica*, and *Wolffiella hyalina*, and showed that besides various chelating agents and plant hormones that could induce flowering in these duckweeds, salicylic acid is the most potent compound that induces flowering in most of these species, whether they are long-day, short-day or day-length insensitive plants (Khurana and Maheshwari 1978, 1980, 1983a, b, c, 1984, 1986a, b, c; Khurana et al. 1986, 1987, 1988a, b, c; Tamot et al. 1987). There is some evidence now that salicylic acid may work as a signal in inducing defense reactions in plants that may also trigger flowering (L. Pasricha, A.K. Tyagi and J.P. Khurana, unpublished).

In addition to studies on embryology, morphology and flowering in duckweeds, interesting work was also done in SCM's laboratory in the late 1970s on the characterization of nitrate reductase in both *Lemna* and *Wolffia*, which showed circadian/diurnal rhythm in its enzymatic activity (Bakshi et al. 1978; Devi and Maheshwari 1979). In the 1990s, the presence of cyclic AMP and cAMP phosphodiesterase in *L. paucicostata* was also demonstrated by SCM and co-workers (Gangwani et al. 1991, 1994, 1996). Gangwani et al. (1996) showed that cAMP can modulate changes in phosphorylation of the chloroplast proteins of *L. paucicostata*. However, despite the biochemical evidence for the presence and the role of cAMP in *Lemna*, the presence of genes associated with this signaling pathway in higher plant genomes, particularly *Spirodela polyrhiza* and *Lemna minor* (whose genome sequences are now available) needs careful examination. One of the recent publications where SCM contributed (Sree et al. 2015), "The duckweed *Wolffia microscopica*: a unique aquatic monocot", includes wonderful scanning microscopic photographs unravelling some very intricate cellular details, which were impossible to observe with the technology available earlier in the 1950s.

The above-described contributions of SCM in the field of Lemnaceae have attracted worldwide attention in recent years, due to the resurgence of research on duckweeds (see footnote[1]). This is evident from the fact that five international conferences have been organized in the past decade on duckweed research, the latest, 5th in the series, was held in September 2019 in Israel. We note that the 4th International Conference on Duckweed Research and Applications, held in Kasaragod, Kerala (Sree and Khurana 2018), and, organized by the Central University of Kerala, was dedicated to SCM for his "Lifetime contributions in the field of duckweed research" (Sopory et al. 2019). His participation in this conference, delivery of a keynote lecture, and enthusiastic interactions with participants from across the world, was a major highlight of this event, and will surely be remembered for years to come.

Haploidy and plant tissue culture

One of the interests of SCM's lab was to study the process of anther development. His research team cultured anthers of *Datura innoxia* to follow the pollen development in anthers; however, they, instead, found embryo like structures arising out of the cultured anthers (Guha and Maheshwari 1964). On further analysis, they confirmed that the embryos and plantlets had their origin in pollen grains and were in fact haploid in nature (Guha and Maheshwari 1966, 1967); two of these articles published in 1964 and 1966 appeared in *Nature*. According to Maheshwari (1982), it was a most unexpected and unbelievable spectacle when one day Sipra Guha brought cultures in cytokinin containing media, showing anthers of *Datura innoxia*, full of embryos. This discovery had an international impact and many other groups (in China, France, Japan and UK) started working on using anther culture as a tool for raising haploid and homozygous diploid lines in many different plant species. This was possible since, in the meantime, SCM's lab had carried out detailed studies on the role of physical (high/low temperature and light) and chemical (including hormones) factors

[1] Raghubir (Raj) Prasad, of the Forestry Department of Canada, who had worked, for his D.Phil, on *Lemna minor* (a member of Lemnaceae) during 1958–1961, with G.E. Blackman of Oxford, UK (see e.g., Prasad and Blackman 1965a, b), recently wrote to one of us (GG): "I remember both Satish and Nirmala as very enthusiastic, knowledgeable, dedicated and hardworking plant biologists of our time. I marvel SCM's thorough work on the Lemnaceae." Prasad, further, praised the two for their friendly interactions with all the Indian graduate students, postdoctoral fellows, and established scientists they met abroad.

in inducing haploid pollen to enter into the phase of embryogenesis (Sopory and Maheshwari 1976a, b; Tyagi et al. 1979, 1980, 1981b). The details and implications of this important landmark discovery were reviewed by Maheshwari et al. (1980, 1982). This phenomenon was repeated, in the laboratory, on several other plants: *Petunia*, *Albizzia*, *Cassia* and wheat (Sopory and Maheshwari 1973; Gharyal et al. 1983a, b; Rajyalakshmi et al. 1995). Further, pollen-derived haploids were also used to develop salt and streptomycin resistant cell lines (Tyagi et al. 1981a, 1984).

Besides anther culture, tissue culture of other explants and plant material was also successfully achieved, as in *Arabidopsis*, *Brassica*, tobacco, legumes, cereals, which SCM thought would turn out to be important model systems from the Indian agricultural perspective (Maheshwari et al. 1965; Anand and Maheshwari 1966; Gupta et al. 1966; Gharyal and Maheshwari 1980, 1981, 1983, 1990; Rajyalakshmi et al. 1988, 1991; Parihar et al. 1995).

SCM's interest was also to move towards genetic engineering and hence work was initiated on protoplast cultures of *Nicotiana sp*, *Solanum melongena*, *Capsicum* and rice (Gill et al. 1978, 1979; Malhotra and Maheshwari 1980; Saxena et al. 1981a, b; Chaudhury et al. 1993, 1994). When in the 1990s, the new Department of Plant Molecular Biology (at South Campus of the University of Delhi) was established, and new faculty had joined, the ways and means of gene delivery were explored. An electroporator was constructed from local supplies and used to deliver gene constructs into rice protoplasts, cell suspensions and even in germinating seedlings (Chaudhury et al. 1993, 1994, 1995). Similarly, cellular permeabilization was also used for gene delivery in *Brassica* (Parihar et al. 1994). These investigations laid the foundation for raising transgenics in the coming years and a comprehensive review on rice transformation was compiled and published (Tyagi et al. 1999).

Gene regulation

Control of gene activity was a topic of great interest in the SCM lab. With the advent of recombinant DNA era, the SCM group collaborated with one of us (AKT) to understand the regulation of photosynthesis-related gene expression. Chloroplast genomes of *Vigna aconitifolia* and *Oryza sativa* were cloned to localize photosynthesis-related genes. In *Vigna*, development-dependent regulation of steady-state transcript levels by light was observed for chloroplast-encoded photosynthesis-related genes, namely, *psaA*, *psaB*, *psbA*, *psbC*, *psbD*, *psbE* and *rbcL* (Kelkar et al. 1993). In rice also, light exposure of dark grown seedlings led to accumulation of more mRNA for *psaA*, *psbA*, *psbD* and *rbcL* in comparison to age-dependent increase in their transcripts. Combinatorial effect of development and light resulted in an enhancement of the expression of these genes by 26 to 62-fold (Kapoor et al. 1994). Certain rice genes (*psaA*, *psbA*, *rbcL*) were also shown to undergo diurnal fluctuations in their mRNA levels (Grover et al. 1996). To further understand signal transduction components involved, seedlings were exposed to monochromatic red/-far-red light, calcium ionophore (A23187) and chelators (EGTA, BAPTA), inhibitors of protein phosphatases (okadaic acid and NaF) and kinases (staurosporine). From these studies, regulation of gene expression was found to involve phytochrome, calcium and protein phosphorylation (Grover et al. 1999a). Furthermore, SCM's team observed that more transcripts accumulated in the shoots than in the roots of rice seedlings (Kapoor et al. 1993). By deploying agonists and antagonists of calcium and protein phosphatases/kinases, their role in spatial control of gene expression was also observed (Grover et al. 1998).

Among the nuclear-encoded photosynthesis-related genes, *psbQ*, encoding 16-kDa polypeptide of oxygen-evolving complex of *Arabidopsis*, was cloned and found to be light-regulated (Grover et al. 1999b). Further, promoters of *psaF* and *petH* from spinach were examined in protoplasts from leaves and roots of rice; their results showed higher activity in leaf than in root protoplasts. In addition, transgenic rice showed *petH* promoter activity in the green leaves and in the young anthers, reflecting on the conservation of function of a dicot promoter in a monocot (Mohanty et al. 2000).

The phytochrome story

This story has a history; what follows here was written by SCM at the invitation of one of us, Vineet Soni (VS), for publication in the Proceedings of the International Conference on Photobiology, Phytochemistry and Plant Biotechnology (it was submitted on May 1, 2019, for the conference held on May 8–9, 2019, in Udaipur, India; see

Fig. 4 A 2019 photograph of SCM with Vineet Soni, taken by. Neha Verma. *Source*: Archives of VS

Fig. 4 for a photograph of SCM with VS). Instead of condensing the story given by SCM, we decided to present below, essentially, verbatim, his text, in three Boxes, for the sake of honoring his personal perspective on the "History of phytochrome research" and its background.

Box 1 has the prelude to the story of phytochrome; Box 2 has the story at Yale about SCM's work with Bruce Bonner; and Box 3 has SCM's interesting story on the encounter with Yale police. Text in square brackets is by GG.

We end this entire tribute with a personal account by SCM's sister (SN), and three photographs: a 1980 photograph showing two of us (JK & AT) and two 2007 photographs showing Nirmala & two of us (SS and GG) in the supplementary material.

Box 1 Prelude to the story of phytochrome, essentially in SCM's words

"To my mind one of the greatest achievements in botanical science is the isolation of the red-far red absorbing pigment called phytochrome, back in 1959. It is a spellbinding story that began in the 1920s, perhaps even earlier – if besides the work in USA, we also consider some work done in Europe. In my personal view, the discovery of "phytochrome" was deserving of a Nobel Prize (https://www.nobelprize.org/). Nobel Prizes have been awarded to scientists working in photosynthesis, often in Chemistry, or Physics or Physiology or Medicine. However, since Alfred Nobel's 'Will' did not include botany and agriculture, many discoveries have not received the recognition they deserve. (There is, however, the Crafoord Prize, which includes Biosciences: https://www.crafoordprize.se/startsida.)

While the role of light in photosynthesis is well known [see e.g., Shevela et al. (2019)], light has also a very significant role in breaking dormancy in seeds and buds as well as in inducing flowering in plants – and these latter effects are controlled by very weak light [See Björn (2015) for a glimpse of the area of Photobiology]. Plants are now known to have several photoreceptors, but perhaps phytochrome is the most important and distributed in all parts of a plant. Recent work has unraveled the extraordinary mode of its action as a light-induced kinase. Further in its active, FR (far-red) absorbing, form it also enters the nucleus and allows light to turn on key genes. The story of the discovery and isolation of phytochrome is a long one but started with a critical finding by James Bonner, who in [the] 1930s taught Plant Biology at Caltech (California Institute of Technology, Pasadena, California) in USA. Nirmala, my wife, and I spent a year with him, discovering new things about [RNA and] RNA polymerases in plants [see e.g. Nirmala Maheshwari's paper: Huang et al. (1960)]. Bonner, after finishing his Ph.D. with Kenneth V. Thimann and Fritz Went, decided to work on the mechanism of photoperiodism. In the 1930s, he found (jointly with K.C. Hamner of Chicago) that a very brief exposure to red light in the middle of a long night (otherwise inductive of flowering) completely abolished flowering [See e.g., Hamner and Bonner (1938)].

Photoperiodism in plants was originally discovered at USDA (United States Department of Agriculture) in Beltsville, Maryland, just north of Washington, DC. Usually most fundamental discoveries have come from universities, but many discoveries in plant biology and agriculture have been made at USDA; here, active work was done and a discovery was made that FR (far red) light (given as flashes, but immediately after R (red) light) completely negated the effect of an earlier treatment. By the 1950s, two botanists M.W. Parker and H. Borthwick were leading plant research at USDA. But already around the middle of the 1940s, Borthwick had approached Hendricks, the first Ph.D. student of the great Caltech chemist Linus Pauling, then in USDA's Soils and Mineral Division [Hendricks was a pioneer in unraveling the X-ray structure of silicates and other soil and clay components]. Hendricks threw himself whole-heartedly into Borthwick's project. To get an idea of the photoreceptors involved, the two together set out to determine the action spectrum using live plants – often coming back to the lab at night, switching on the light and flashing monochromatic beams through a giant spectrograph that they had specially built, using two prisms (each nearly a foot long) and "throwing" spectrum [light of different wavelengths] that was 8 feet wide on the back of a large hall. Then, Borthwick and Hendricks deduced the existence of a proteinaceous pigment with a chromophore that had two isomeric forms and interconverted with R and FR light. Using a special custom-built difference spectrophotometer and live tissue, they had already demonstrated that pigment in the cells could be converted into a R or FR absorbing forms by beams penetrating such tissues. Everything pointed to the existence of a pigment; however, by the end of an International Botanical Congress, at that time, it still remained to be isolated in a tube or a cuvette! [To get a scientific picture at that time, see Borthwick et al. (1952)]"

Box 2 The story at Yale about SCM's work with Bruce Bonner, in his own words

"This is the point now to introduce work at Yale (in Connecticut, USA) and the encounter with the Yale Police (see Box 3). We had spent our first year in USA in the lab of Arthur Galston who had moved from Caltech as a full Professor and had Bruce Bonner as a senior Research Associate. Bruce had come from the San Francisco area (in California) but had a postdoctoral research experience on yeast at the Pasteur Institute in Paris, France (this is around the same time Jacques Monod and Francois Jacob were working on the *E. coli* β-galactosidase and the *lac* operon). My father (Panchanan Maheshwari) had known Borthwick and taught us a little about R and FR effects and Bruce found that I was familiar with the phytochrome literature. On the way to Montreal (Canada) around the middle of 1959 August, many plant biologists passed through Yale from New York. Hendricks was one such visitor. And standing in the seminar room in the Galston wing, Hendricks gave Bruce a brief account of the progress they had made in their research (luckily I was also present) and I remember Hendricks finally saying that the evidence for the existence of the pigment was absolutely compelling but now it was for biochemists to isolate the pigment

We all proceeded to Montreal where my father was chairing the Embryology section and where both Nirmala and I were to talk on work we had done in India. ………………[we had] decided to take the second day off to spend at the Montreal Botanical Garden (where I had lunch with Hendricks and Borthwick, two great plant biologists of that time)"

Box 3 Experiments at night and encounter with Yale police, sometimes in 1959, in SCM's words

"On return from Montreal, Bruce Bonner decided to go straight for phytochrome isolation and although I was invited only in the late evening as I headed for our apartment, I decided to come back after dinner and join Bruce. Nirmala (my wife) had gone to bed early and since I did not know that Bruce was going to work non-stop, I did not wake her up. As for Bruce, he went through grinding of pea seedlings in liquid nitrogen, homogenizing live tissue, precipitating its proteins by ammonium sulphate and purifying them by dialysis and finally passing them through a vertical chromatography column. But early morning as sunrays penetrated our seminar room and where the deep freezer was kept, we could see bluish green phytochrome which had eluted in a few fractions. *I am thus the second person to see isolated phytochrome, but Nirmala Maheshwari and an officer of the Yale police* [see below] *were the other humans to see it*

As I mentioned above, I had left Nirmala home, but when she woke up at about 4 AM, she found that I was missing. Thus, she called the Yale Police to find her missing husband. The cold room at Yale had an inner supercool area and a separate entry section. Neither Nirmala nor the Yale Police had any idea that we would be in the inner cold room all night. So, they were really distraught as they had searched every lab in the building, and only then they arrived on the 6th floor seminar room, at the extreme end when a new day had broken. Bruce and I had just moved out of the cold room to move and store our precious fractions from the fraction collector to the deep freezer, kept in the seminar room! I do not think the Yale police had any idea of phytochrome! Nirmala was very upset and angry with me rather than bother about the phytochrome. But around the first week of September, phytochrome had been isolated. Bruce wisely decided not to publish his achievement and embarrass the scientists in USDA. He told me: "Satish there is no point in trying to outsmart the great people in USDA". But the USDA team also worked hard. By December, 1959, their paper (Butler et al. 1959) had been published, as communicated by Hendricks to the Proceedings of the National Academy of Sciences, USA [GG added: This was possible because of the imaginative work of Warren Butler: see Butler et al. (1959); Benson (1998) has described Butler's story and noted Lila Butler recalling Warren Butler's elation that evening, when he said to her, "Lila, *I think we've hit on something big."*]

Bruce Bonner later published the first paper on the existence of the pigment in *Mesotaenium* sp., a green alga, [GG added: "and in a liverwort *Sphaerocarpus* (Taylor and Bonner 1967)]. He retired later as Chairman of the Plant Biology Department of the University of California, Davis. Many years later the experience at Yale led me to initiate the first studies in India on the isolation of this pigment and also the mechanism of its action. Our research group at Delhi University as well as that of Sudhir Sopory found effects of the phytochrome conversion on the influx and efflux of calcium ions. There is now growing evidence that phytochrome may have more than one mode of action. (GG refers the readers to the continued interest of SCM in the phytochromes: see e.g., Malik et al. (1992), Mehta et al. (1993), Grover et al.(1999a); cf.: Campbell and Bonner (1986)]"

Personal reminiscences

By Sushila Narsimhan
(A full account is available by sending an e-mail to: sushila@narsimhan.com)

My brother Satish (hereafter SCM), the eldest of six siblings, had imbibed many personality traits of my father. He was a strict disciplinarian, a stickler for punctuality, a voracious reader, an academician with an unconditional scientific temper, commitment and a vision that crossed all borders. The Department of Plant Molecular Biology founded in 1988 was the labour of his love driven by his passion for the advancement of science in India. Further, he had set very high standards for himself and worked from dawn to dusk all 7 days in a week, at home or in the department.

SCM's life was based on '*simple living, high thinking.*' In his professional life, he had suffered many setbacks on account of paucity of funds which must have motivated him to lead a frugal life-style so that he could help the needy and divert a major part of his life-savings towards his cherished goal of scientific advancement. His wife Nirmala shared his passion for research which was vital for the accomplishment of their goals. He was stubborn in many ways and usually projected a stern look; but he was also kind-hearted and helped everybody, be it his siblings, or students, or assistants. He bonded very well with all his nieces and nephews and truly wished that some of them would pursue science and work under his guidance. His joy knew no bounds when my younger daughter (Ruchira) decided to study Plant Molecular Biology under him; and later moved to Indiana University- Purdue University, at Indianapolis (IUPUI) for PhD, and then to Stanford University California, for a postdoc position in Biochemistry under Patrick Brown.

SCM was also very concerned about the well-being of his personal assistants and generously supported them for the education of their children. Many of them lived in his house and took care of him, especially after the demise of his wife Nirmala on August 26 2009, and even after he moved away from Delhi and relocated himself in Jaipur (Rajasthan). There existed a special bond between him and his assistants. In fact, an evidence of this can be seen from the fact that, in early-June 2019, when he fell sick and was hospitalized, all his assistants (including his former Delhi-based assistants) rushed to Jaipur to pay their obeisance and pray for his speedy recovery. Their gesture profoundly shook the attending doctor (Dr. Anjum Khan) who telephoned me and said, "I am truly amazed, for I have never seen this kind of love and devotion from assistants towards their employer! This speaks volumes about your brother being such a good human being. Don't worry, we shall take good care of him." SCM recovered, and was soon discharged and taken home. But alas! The recovery turned out to be short-lived. Three days later, on 12th of June 2019, at midnight he fell unconscious, was rushed to the hospital, but succumbed to lung cancer detected rather late.

Fig. 5 SCM on the right giving his research presentation in a private session to Rajni Govindjee (L), Sneh Lata and GG. Photo taken by AP in 2017 in Delhi. *Source*: Archives of AP

Fig. 6 SCM with two of his former students Sneh Lata (on his right) and Ashwani Pareek (on his left). Photo taken by GG in 2017 in Delhi. *Source*: Archives of AP

My brother was a connoisseur of Western classical music and owned a nice collection of requiems and music compositions—Gregorian, Buxteheude, Handel, Bach, Mozart and Verdi. His favourite was Cristobal de Morales Missa pro defunctis. In fact, in one of his last emails to me, he expressed a wish that he would like this to be played in his memorial service. As per his wish, the Memorial Service, attended by his family members, students, colleagues and friends, began with Morales' soothing mass requiem *Missa pro defunctis*.

Concluding remarks

In addition to Satish Maheshwari, we have lost, in the recent past, Prasanna Mohanty, another top plant biologist of India, a PhD student of one of us, GG (see Prakash and Tiwari 2013; Tiwari et al. 2014; Naithani and Govindjee 2018). During his last few years, Satish was very active in scientific discussions with many others including two of the authors (AP and GG). Figure 5 shows a photograph from this period. SCM had been a visionary for advancement of plant biology in India. He followed his passion towards basic research by updating himself with the advanced technologies and knowledge from time to time in the world class research institutes across the globe, working with some of the top researchers in plant biology of that time. He further trained and established these advancements in India. Figure 6 shows two of his former students (Sneh Lata and Ashwani Pareek; see Grover et al. 1993). SCM's lectures and science-stories have inspired many young minds; he will remain as a role model for the future plant biologists. Neera Bhalla Sarin (of JNU) added: "I feel honored that I was close to SCM during the last years of his life. I feel fortunate to have been among one of the first students to whom he taught Plant Molecular Biology at the University of Delhi. He was one of the greatest teachers of all times!"

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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