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TRIBUTE

A tribute to Hemming Virgin (1918–2005), a Swedish pioneer in plant photobiology

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Abstract We present here a tribute to Hemming Ivar Virgin (October 19, 1918–October 19, 2005), a pioneer in Swedish plant photobiology, developer of a University, and an outstanding educator.

Stockholm, Lund and Carnegie: viscosity, turgor, and chlorophyll synthesis

Hemming Virgin (pronounced as Virrgeen, with the stress on the last syllable) was born in Stockholm, where he graduated from high school in 1937 and obtained his doctoral degree in 1951 at Stockholm University under the guidance of Gottfrid Stålfelt. His early scientific work was concerned with an effect of light on what was at that time (when cytoplasm was considered a liquid without much structure) referred to as the *viscosity of protoplasm*. This was one of several blue-light effects in plants for most of which the photoreceptor molecules are now known. Hemming's plant material for this study was leaves of the water plant *Elodea* (*Helodea*), and he evaluated the change in ''viscosity'' of the cytoplasm by noting the movement of chloroplasts during centrifugation. This light effect was the first of many for which he came to determine the action spectra. Hemming's publications were not meant to be ''quick fixes''; his main paper about the light effect on protoplasmic viscosity consists of 103 pages (Virgin 1951).

After finishing his Ph.D. Hemming became a ''*docent*'' at Lund University, in southern Sweden. In 1952, while he was a docent, he went, for 2 years, to the Department of Plant Biology of the Carnegie Institution of Washington on the campus of Stanford University. There Robert Emerson had studied the minimum quantum requirement for photosynthesis and arrived at results that did not agree with those of the famous German biochemist Otto Warburg (see Govindjee and Krogmann 2006, for the time line of oxygenic photosynthesis). Hemming was given a working place in the basement of the Carnegie building, precisely where Emerson had worked earlier in the 1940s (see Govindjee 2004); Hemming claimed that Emerson's spirit and Warburg apparatus were still around.

Another topic under study at the Carnegie Institution was the light-dependent conversion of protochlorophyllide (Pchlide) to chlorophyllide *a*. James H. C. Smith had come to the conclusion that the photoconvertible Pchlide was not free, but attached to a protein in the plant, and he called the complex protochlorophyll holochrome. This protein is now called NADPH: Pchlide-oxidoreductase. At Carnegie, Hemming worked in this area of research and pursued it during the rest of his life; it was continued by one of his students and successor (CS, one of the authors of this paper). For his study, Hemming used absorption and fluorescence spectrophotometry, rapidly developing techniques at that time. At Carnegie he also continued his studies on the blue-light effect on cytoplasmic properties of cells.

Another outcome of Hemming's stay at Carnegie is a method for the determination of *turgor* and *elasticity* of plant organs (Virgin 1955). The idea for this method came originally from Vannevar Bush, then President of

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Carnegie; it was perfected by Hemming after his return to Lund, with input from Hellmuth Hertz (after whose grandfather the frequency unit was named), and Stig Falk, who later came to spend a long time with Hemming in Göteborg (Falk et al. 1958). This method was based on the determination of a resonance frequency when the specimen was made to vibrate. It later came to be used by many in Lund and elsewhere, and Virgin (1955) is still being cited for it.

Back in Lund, Hemming continued his studies on chlorophyll formation and discovered the light effect on Pchlide formation. When one of the present authors (LOB) took up advanced plant physiology studies in 1957, he came in contact with Hemming, who during half a spring semester introduced him to photobiology (Björn and Virgin 1958). When LOB returned to Lund in late 1958, Hemming had moved on to a post as *laborator* (now equivalent to *professor*) at the Agricultural University in Ultuna, near Uppsala. Despite the brevity of the tutor-apprentice relation, LOB and Hemming maintained a life-long friendship.

Agricultural University at Ultuna: cooperation with geneticists

At Ultuna, Hemming worked together with Diter von Wettstein and Albert Kahn on action spectra of submicroscopic changes in the etioplast when dark-grown plants are exposed to light. Virgin et al. (1963) showed that Pchlide was the photoreceptor, which triggered the morphological changes of the etioplast and started the dispersal of prolamellar bodies into thylakoids.

Hemming also initiated phytochrome research in Sweden and investigated the role of phytochrome in plastid development during irradiation of dark-grown plants (see e.g., Virgin 1961, 1978). With phytochrome activation, the lag-phase in chlorophyll formation could be abolished and the formation of carotenoids could be stimulated.

The first difficult years in a new place: the Carnegie Institution of Göteborg

In 1962, Hemming, as the first regular full professor of botany, accepted the new chair of plant physiology at Göteborg University. There had been no botany department before, and the only building that was offered was the old Carnegie sugar plant (named after David Carnegie, of Scottish origin, not Andrew Carnegie), which soon was nicknamed ‘‘Carnegie Institution of Göteborg’’. Its location and facilities were not ideal for scientific experimentation. When it rained, water came through the roof: fungi grew on the walls, and lectures and microscopy had to be housed in nearby, also very primitive, buildings.

Hemming told us a story: The Carnegie sugar plant was located in the harbour area close to the old gallows-lea. Murders had occurred in the neighbourhood of the department. To reach the department, one had to pass a long and even in daytime scary alley. Hemming had hired a young and alert lady as secretary. She was much appreciated, liked her job, and everything seemed to be OK. But one day she asked for a private conversation with the professor. She seemed embarrassed and said that she had to quit her job. Hemming asked if anything unpleasant had happened in his department. Oh, no, she said, ‘‘but yesterday evening I came here with my fiancé and showed him where I was working. But when he saw the neighbourhood, he said that he would not allow me to continue my work’’.

A new institute building in the Botanical Garden

The 1960–1970s period was the time of rapid expansion of the Swedish university system, but as evident from the above description, the government’s priorities were not on creating good working environment for teaching and research. Hemming laboured hard to get better conditions for his rapidly growing staff. In 1969, a new ‘house’ was built in the Botanical Garden. Hemming was rightly proud of his new department. In addition to plant physiology, other departments and divisions with their own professors joined in the new building: microbiology, systematic botany & plant ecology, chemical ecology, marine botany, plant molecular biology and marine ecology. There was also new and upgraded equipment.

Hemming served as full professor in Göteborg for 21 years and then continued to work daily as an emeritus professor for an additional 20-year period (Fig. 1 shows a photograph of Hemming Virgin in the 1980s). His interest in chlorophyll formation and other light-dependent processes in plants set the agenda for the plant physiology research at his department in Göteborg. Chloroplasts

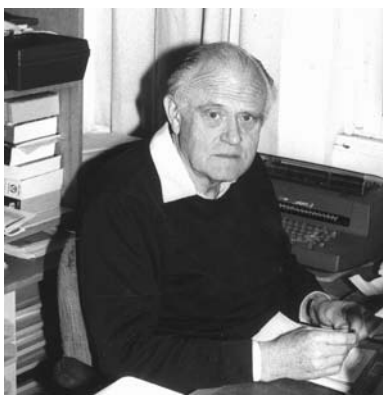

Fig. 1 Hemming Virgin at his desk, in the 1980s

remained one of the main research topics also under Hemming's successor (CS). Hemming's last publication (Virgin 1996) dealt with chlorophyll biosynthesis; this paper appeared almost half a century after his first publication (Virgin 1948). It is striking that Virgin is often the sole author of his papers. This is a reflection of his principle that he should not appear as a co-author on his students' publications just because he was the supervisor.

Phytochrome, plastid differentiation, photosynthesis and pollutants

The phytochrome effect on chlorophyll formation was also a part of Hemming's early studies in Göteborg, but much of the work was published with students as sole authors**:** Lars Arvidsson showed that the phytochrome effect on the lag-phase was a local phenomenon limited to the irradiated cells, and Conny Liljenberg that the stimulation of chlorophyllide esterification was a phytochrome-regulated process. Other phytochrome-regulated processes studied in Hemming's laboratory were the unrolling of wheat leaves (Wagné 1964, 1965, Virgin 1990) and germination of lettuce seeds (Widell et al. 1981, 1985).

In connection with plastid differentiation and chlorophyll formation, the topic of initiation of photosynthesis during greening of dark-grown plants was of great interest (Egnéus et al. 1972). Lennart Axelsson demonstrated an increased photosensitivity of the chlorophyllide during the so-called Shibata shift (named after K. Shibata of Japan), and Birgitta Klockare found that the phytochrome system influenced the composition of the spectral forms of Pchlide. In 1972 Hemming returned for a sabbatical to Carnegie Institution at Stanford and this time he brought home the technique of computer-assisted spectrophotometry and spectral deconvolution (Virgin and French 1973; cf. Govindjee and Fork 2006).

The electron micrographs (EMs) of the etioplast never ceased to fascinate Hemming. One of his students, Hans Ryberg, became the EM master and studied the prolamellar body and the development of the plastid (Ryberg et al. 1980). His wife, Margareta Ryberg, established the use of immuno-gold labelling and showed that NADPH: Pchlide oxidoreductase was localized in the prolamellar body (Dehesh and Ryberg 1985). Hemming's interest was broadened to include the composition of the membranes of the prolamellar bodies, the prothylakoids and the young thylakoids in the greening chloroplast, as investigated especially by Eva Selstam and Anna-Stina Sandelius (Selstam and Sandelius 1984).

As mentioned earlier, Hemming kept his interest in the Pchlide-to-chlorophyllide conversion. Many students, not mentioned here, were lucky to have worked with him. His last Ph.D. student Birgitta McEwen, whom he supervised long after his retirement, described the different forms of Pchlide in various tissues from dark-grown bean plants (McEwen et al. 1991; Virgin and McEwen 1995).

Hemming did not have as much time for his own experiments as he would have liked. However, he studied the effect of water deficit on chlorophyll formation, the effect of phytochrome on the plastid morphology of *Spirogyra*, as well as the effect of norflurazon (a herbicide that inhibits carotenoid synthesis) and dibutylphthalate (a plastic additive that is polluting the environment) on chlorophyll formation (Virgin et al. 1981). Hemming also continued his studies on chlorophyll *b* formation, for which he determined an action spectrum (he was convinced that chlorophyll *b* is formed from newly synthesized chlorophyll *a* molecules). Later he also became interested in the phenomenon of greening potatoes and during his last years he was fascinated by the development of the mesocotyl and the fact that this organ, which in maize can be more than 10 cm long in darkness, is hardly formed at all in light (Virgin 1996).

After his retirement, Hemming and one of us (CS) had the opportunity to travel to Japan. This was a great scientific as well as a cultural experience. A memorable incident occurred the last evening of his stay in Japan at the time of going to the airport by taxi. Hemming and CS had left the taxi and checked in for the flight to return to Europe. On his way to line up for the passport queue, Hemming looked very pale and said to CS: ''I have lost my wallet with my passport''. Just then the taxi driver came running shouting ''Mister, Mister you forgot your wallet!'' What a relief, and what an example of Japanese honesty! Upon return to Sweden, Hemming said with a sigh ''nothing is like returning home''.

In addition to scientific research, Hemming was active in science policy, for instance in the Natural Science Research Council and in the Royal Swedish Academy of Sciences. He also wrote articles about topics in plant physiology in the daily newspapers. He was very fond of music and had a large record collection. He had the gift to set text to music. Most students were felicitated by Hemming after their public examination (''disputation'') with suitable new-written texts to different well-known tunes. Each text was written by Hemming for the occasion and described the doctoral student's life. It was always presented in the evening at the PhD celebration, as a performance of the ''docent'' choir. No one was allowed to practice in advance (as an academic should always be well-prepared) and the result was therefore many times more amusing than enjoyable. A part of a docent choir at such a performance is shown in Fig. 2.

Hemming was single and lived alone throughout his adult life, although he kept in close touch with his relatives.

Fig. 2 After the public examination of doctoral students (''*disputation*''), it was the custom that Hemming would sing together with associate professors (here, Conny Liljenberg to the left in the picture and CS to the right). The melody would be a well-known tune, while the text, describing the student'life, was written by Hemming for the occasion

His graduate students were family for him. In 1986, he was awarded the Linnaeus Gold medal by the Royal Physiographical Society in Lund. He was found dead in his home when one of us (CS) came to congratulate him on his 87th birthday. We will always remember him with warmth; he was a gentle and a dedicated scientist.

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