Perspectives

Erwin Bünning (1906–1990): A centennial homage

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1. Historical backdrop

The study of biological rhythms, now called chronobiology, has had a hoary past in Europe and is replete with big names. It drew into its fold many brilliant scientists in the 18th, 19th and 20th centuries and continues to draw outstanding talent in the 21st century. The first record of a circadian rhythm was by the Greek philosopher Androsthenes describing the sleep movements of the leaves of the tamarind tree, when he joined Alexander of Macedon in his march on India in the fourth century BC. Carl von Linné (1707–1778) constructed a *floral clock* based on his knowledge of the opening of flowers at different hours of the day. The experimental demonstration of an endogenous component was first performed by the French astronomer de Mairan in 1729: he took potted *Mimosa pudica* plants into the perpetual darkness of a deep cave and reported that the nightly 'sleep' movements of the leaves persisted. Wilhelm Pfeffer (1845–1920) had built a laboratory for research on bean leaf movement rhythms at the University of Leipzig over a hundred years ago with temperature control and automatic switching of lights on and off for desired light: darkness cycles complete with built-in dawn and dusk simulations (Bünning and Chandrashekaran 1975). Jagadish Chandra Bose (1858–1937) wrote landmark papers on his findings on diurnal movements in plants. In the monograph *Life Movements in Plants* (in three volumes), written in 1918, 1919 and 1923, Bose had investigated with consummate care, all environmental factors that could modulate and interact with diurnal rhythms. Bose described the entrainment of plant movements to light: dark cycles and observed free-running periods in continuous light and continuous darkness as early as 1919 (Chandrashekaran and Subbaraj 1996). This work of Bose was cited by Bünning (1958) in his classic first monograph *The Physiological Clock*. In 1930 Bünning and Stern stressed that the periods of rhythms under constant conditions deviated from 24 h thus justifying the use of the expressive term *circadian* coined by Halberg in 1959. In 1932 Bünning did crossing experiments with bean plants having different periods and demonstrated that the F-1 generation had periods of intermediate durations clearly demonstrating the heritability of circadian rhythms. Bünning truly bridged the tradition of experimental chronobiology started by stalwarts like Pfeffer and Bose and the traditions of molecular and genetic studies of circadian rhythms.

2. Schools and teachers in Germany

The life and work of Erwin Bünning were shaped to a large extent by the forces, traditions, ideas and academic standards prevailing in the schools and universities of Germany. He has alluded to this in a few of his autobiographical essays (Bünning 1977). Erwin Bünning was born on 23 January 1906 in Hamburg as the son of the school teacher Hinrich Bünning and Hermine Bünning (born Winkler). His father was politically a social democrat and was firmly opposed to the Nazis. Hinrich Bünning taught German, English, mathematics and biology and was clearly the earliest academic influence of his son's life. Erwin Bünning often said that his father could identify all plants that grew in and around Hamburg. Erwin Bünning studied in school in Hamburg from 1912–1925 and during the senior years had already read "books which normally will be found only in university libraries" (Bünning 1977).

Schools in Scandinavia, Holland, Germany, Switzerland and Austria were excellent in terms of the quality of teachers and the niveau of teaching. Bünning studied biology, chemistry, physics and philosophy in the universities of Berlin and Göttingen between the years 1925–1928. Berlin was the work place of the Nobel Prize winners Otto Warburg, Otto Meyerhof, and Hans Spemann. Here worked also one of the re-discoverers of Mendel's work, Carl Correns; the plant

anatomist Gottlieb Haberlandt and the zoologist Max Hartmann. To join Berlin University as a student of natural sciences one had to enroll in the faculty of philosophy, for most German universities still had four traditional faculties: theology, medicine, jurisprudence, and philosophy. The leading botanist Hugo von Mohl (1805–1872) founded the first Faculty of Natural Sciences and Mathematics in Germany in 1863 in Tübingen University. The creation of this faculty was several years behind the creation of corresponding faculties in other European countries. Hugo von Mohl and his colleagues renamed the degree of Doctor of Philosophy (Dr. Phil.) as Doctor of Natural Sciences (Dr. rer. Nat). This is the background of the Ph.D. degrees of Anglo-Saxon universities which had not switched over. Philosophy, however, continued to be an important compulsory subject in German universities. Bünning was also quite happy in the choice of his second university–Göttingen, then considered to be the most powerful academic institution in the world for the study of mathematics and physics. His contemporaries at Göttingen were the physicist James Frank, the chemist Adolph Windaus, the zoologist Alfred Kühn, the physicists Werner Heisenberg, Pascual Jordan, Otto Hahn and Max Delbrück, all of whom, with the exception of Kühn, got the Nobel Prize in later years. Bünning received the Dr. Phil. in May 1929.

3. Earlier epochs in German universities

Bünning complained that there was too much philosophy and speculation instead of experiments in German universities in earlier epochs. The movement called "*romantische Naturphilosophie*" held sway over German biology for far too long. In France and Great Britain experimental work in the nineteenth century very nearly replaced pure speculation in astronomy, physics and biology. In Germany, the influence of certain philosophers remained very strong. This holds for Schelling (1775–1854), Hegel (1770–1831), and Oken (1779–1851). Only a *proper world of ideas* was considered to lead to any progress in learning about the world. Schelling called Bacon, Newton and Boyle destroyers of astronomy and physics. The great Goethe (whose influence may still be felt in the publications of certain present day botanists, especially morphologists) characterized Newton's optics as being plain nonsense. The dominant influence of speculation not only prevented experimental work being carried out but also prevented good experimental work from becoming known. Mendel had indeed communicated his findings to the famous botanist Carl Wilhelm Nägeli (1817–1891) who, indoctrinated by Oken and Hegel, wrote back "your results are only empirical data; nothing in them is rational". In the prevailing atmosphere some biologists like Hans Driesch (1867–1941) gave up laboratory research and took to philosophy (Bünning 1977).

4. Working in German universities in nineteen-thirties

Since jobs were scarce Bünning was happy when he was offered in 1930 an assistantship (wissenschaftlicher Assistent) in Jena, which had one of the larger botanical institutes in Germany. The botany tradition of Jena goes back to Goethe (1749–1832). Later on famous pioneers in several fields of botany, such as Schleiden, Pringsheim and Strassburger, worked in Jena. There was one full professor (*ordentlicher Professor*), the geneticist Otto Renner, one associate professor (*ausserordentlicher Professor*) responsible for teaching botany to pharmacy students and two assistants, Leo Brauner and Bünning. There was in addition a house keeper. There were no technicians or secretaries. The assistants worked 8 h days, five days a week supervising the studies of students. The monthly salary was about 65 US dollars, much lower than the salary of an elementary school teacher. Bünning (1977) writes:"But we found this to be fair. After all we had the chance to receive – in case of further successful research work – the title of (an unpaid) professor at the age of 35 years, and even the chance for a paid professorship between the ages 40 and 45. Many waited in vain for the realization of this dream and remained assistants for their entire lifetime. In those years, according to public opinion in Germany, being Herr Professor meant more than to own a Rolls Royce or a Mercedes". Professors also worked from 8 in the morning till late in the evening including all of Saturday and half of Sunday.

5. Jena during the Third Reich

The majority of students supported the Nazis. Most Professors were by tradition liberal, but with no sense of political involvement. But some of them unfortunately began making compromises. In May 1933, Prof. Otto Renner made a very strong public attack against the Nazis. In a seminar Renner described the great role Jewish scientists played in German intellectual life. He openly defended Leo Brauner, a Jew who was later forbidden by Nazi authorities to enter the institute and was forced to emigrate via England to Turkey. Bünning himself was considered to be some kind of sympathizer of communism which was then a dangerous stand to take. The students made life for Bünning difficult in Jena; this made him accept a lectureship far away in the University of Königsberg (Eastern Prussia, later Soviet Union).

6. The war years

Bünning went away to Indonesia 1938–39 for a year which was some respite for him from the Nazi atrocities. Frau Eleanore Bünning, however, would later recall that year with bitterness for she had stayed back with two small

children. Once back, he was conscripted into the army as a soldier in 1939. He wrote "My interest in this profession becomes clear from the fact that I never reached the rank of an officer" but a soldier he had to remain until the end of the war. The authorities found sufficient merit in Bünning to offer him a position of associate professor at the University of Strasbourg (now in France). This enabled his hapless family to leave Königsberg before the terrible end of that part of Germany falling into the hands of the Russians to be renamed Kaliningrad. He escaped becoming a prisoner of war in 1945 by hiking long distances through the Black Forests. Only after the end of the war did Bünning become a full professor in 1945 at the University of Cologne and later in Tübingen in 1946.

7. Later years

Cologne city was 85% destroyed. All the greenhouses were in ruins and 115 bombs made the landscape desolate. But there was some kind of a garden and there were cellars. The cellars were full of coal and vast amounts of these were bartered for a horse. This horse helped Bünning and his colleagues to collect parts and materials from old military barracks to build a botanical institute. The spirit of cooperation was excellent at that time. Teaching and research could be resumed on a modest scale just four months after the armistice. Bünning moved to Tübingen (his last move) in the course of 1946.

The botany institute in Tübingen was one of the very few in Germany which were not destroyed. The institute was built in 1846 under the direction of Hugo von Mohl. Part of the equipment was still from Wilhelm Pfeffer's Tübingen time (1878–1887). Bünning found in Tübingen a challenging tradition in botany. It was not only connected with Hugo von Mohl and Pfeffer but also with several other famous botanists. Here in 1694 Cammerarius discovered sexuality in plants and Carl Erich Correns rediscovered Mendel's Laws in 1900. Vöchting made his experiments on polarity and other aspects of developmental physiology. The ingenious Wilhelm Hofmeister (1824–1877) worked here in the years 1872–1877; he was a bookseller before he became a professor at the age of 39. One of the important postwar aspects of the university were the high degree of diligence and cooperation of students, most of whom were war invalids. Very early Bünning along with Adolf Butenandt, Georg Melchers and Anton Lang began to attend the brilliant lectures of the zoologist Alfred Kühn.

8. Working in Bünning's laboratory in the sixties

When I first arrived in Tübingen on 1 November 1964 it was Winter Semester. The Botanisches Institut on Wilhelmstrasse 5 looked much as it might have looked in Hofmeister's days. The biggest botany department of Europe had a small car-parking place close to one of the entrances to the botanical garden. There was one old Mercedes Benz car and seven Volkswagen beetles. I had wrongly concluded that the big car belonged to Bünning. It belonged to the sergeant (Haus Meister) Mr Schlauch, a hard-working Swabian.

Bünning's secretary, Frau Rätze, was a lady of many parts: sharp-witted, fast-talking and extremely efficient, she spoke "Hochdeutsch". She had played the role of Juliet in the stage play *Romeo and Juliet* in Berlin. The technical assistant was Ruth Kautt with a ruddy, friendly face. She gushed without inhibition that she once belonged to the Bundes Deutsche Mädchen brigade of Hitler and how she had madly hailed Hitler at Stuttgart. There was no secretariat, no more secretaries nor technicians. The professors then in the Institut were Walter Zimmermann (The Telom-Theory), Karl Mägdefrau, Helmut Metzner and Bauer. The docents were Kurt Richter and Wilhelm Nultsch. Nultsch was the author of a best selling botany text book which he wrote with a woman botanist (a rarity), Frau Dr Grahle. The research scholars impressed me as being a purposeful lot, moving around attending to various things and assisting the faculty in teaching and the practicals. Bünning's own office, with his private laboratory complex (a latter-day addition to Hofmeister's building), was referred to as the Führer-Bunker. I had a sitting place in these exalted quarters. All eight chronocubicles (1 × 1.5 m each) called 'Klimakammer' were in a cellar under the Führer-Bunker. I had access to two of them, both of which I used day and night between 1965 and 1967. After many unsuccessful beginnings to record the tidal and circadian rhythms in the Mediterranean green crab *Carcinus maenas,* I started my *Drosophila* eclosion rhythms experiments. It was Bünning's suggestion that I work with *Drosophila* and he persuaded Engelmann to teach me how to raise the flies in the laboratory. Bünning did not then reveal to me that there were two conflicting models to explain the entrainment and steady state phase shifts of circadian rhythms by light, the coupled oscillator model of Pittendrigh and Bruce and the single oscillator model of Bünning and Zimmer. Our first meeting in 1965, to discuss what kind of experiments on *Drosophila* may be of interest and significance, lasted some ten minutes. In that sense he was a genuine scientist who gave his students and co-workers total freedom. But later when the first two light pulse experiments yielded exciting data Bünning would amble in at 7.30 a.m. literally every day, to enquire what my day and night's labour had brought in terms of data. I had convincing experimental support for the coupled oscillator model which I described in my first paper on *Drosophila* and Bünning communicated to the journal (Chandrashekaran 1967). He seemed to have

grasped immediately that this was an important paper, which I had myself not quite known until several years later. These were the best post-doctoral research years, 1964–1967, I had spent anywhere, in terms of sheer adventure, creativity and excitement.

9. Tübingen revisited

I returned to Tübingen in September 1970 and joined as research associate of Wolfgang Engelmann, and stayed on until 1975. In 1967 I returned to India to work as a Council of Scientific and Industrial Research (CSIR) scientist in the National Institute of Oceanography in Goa. I had spent a year in India without much enthusiasm and accepted an offer to go to Berkeley as a Miller Invitation Fellow from 1968 to 1970. The social turbulence and student unrest of those years in Berkeley made me yearn for the peace and tranquility of the ancient town and university of Tübingen. I soon realized that it was mistake to have gone back to a place which was so cherished in memory. The times had changed, so too had Tübingen. The old student friends of my postdoc years were all gone and I was now married. Now the Botanisches Institut was called Institut für Biologie I and was housed in a brand new building in the lovely hill-top Morgenstelle. Bünning himself was to retire on his 65th birthday on 23rd January 1971 and the search was on to find a worthy successor, which was not easy. In Germany the ordinarius professors could continue in their job until they were 68 but the earliest opportunity to retire with all the pensionary benefits was 65. The ordinarius became automatically *Professor Emeritus* and got his full basic salary as pension. Soon after Bünning's retirement I noticed that even the idealistic German university system flounders when a big man like Bünning takes the bow and the institution suffers until his successor is firmly in place. Berthold Schwemmle, himself a student of Bünning, held the fort in the uneasy years 1971 to 1974 until Achim Hager became Bünning's successor.

At the end of March 1971 I attended an international meeting on *Circadian Rhythmicity* with Bünning and others from his group in Wageningen, The Netherlands A.D Lees of the 'hour-glass' model for circadian rhythms in aphids fame, was there too with D S Saunders. Bünning was chairman. He semed to take his retirement in his stride and had apparently prepared himself for the staid pace of life. He still came to the laboratory at 8 am and read the *Frankfurter Allgemeine* daily in the fore-noon. Afternoons he went for long walks with his wife. He continued to go to the University Library Tuesday mornings and worked on the 3rd English edition of *The Physiological Clock*. I had the privilege of helping him with the English. By then I got to like Bünning's company and spent long hours with him chatting. He really seemed to feel sorry to see me leave Tübingen in 1975 with my wife and daughter, to join the Madurai Kamaraj University. I would later return to Germany several times with financial assistance from the University Grants Commission (UGC) and the DAAD for periods of six weeks. During such visits I often stayed with the Bünnings.

During a visit to Tübingen in 1989 I noticed with much sadness the first symptoms of Alzheimer in Bünning. He kept repeating himself about a visit to Norway by ship with his wife and spoke of the beauty of the "northern light" *aurora borealis*. He also showed me a fan letter from an East German professor called Werner Plesse, who would later write a biography of Bünning. It is a very sad experience to see an intellectual slide slowly into Alzheimer's. In 1990 when I arrived in Tübingen he had been hospitalized. His last student Hans-Willi Honegger and I looked him up. He appeared to be confused and asked who was the friend I had brought along. On 4th October 1990 Bünning passed away. His wife told me in 1991 that the end was peaceful.

10. The 'Biological Oscillations' workshop of 1978 at Madurai

In 1975 when I was packing up to return to India for a second time Bünning asked me if I knew that I was doing the right thing this time. I told him I did not know, it was a shot in the dark, and added "I would know in five years from now". Five years was a short time anywhere in India of the mid-1970s to get worthwhile science going in a state university. S Krishnaswamy who, as reader in the Zoological Research Laboratory, had taught me marine biology and animal physiology when I was in the last year M.Sc. at the University of Madras in 1959–1960, was now the head and coordinator of the School of Biological Sciences (SBS) at the Madurai Kamaraj University when I joined there as reader in June 1975. For close to two and a half decades the SBS would be ranked among the best schools teaching integrated biology in universities. SK was a very unusual boss. He got most of his colleagues appointed as readers by 'invitation' and not by routine newspaper advertisements and gave them full freedom to teach and do research as they pleased. I rented a house close to the Krishnaswamy's in a small residential colony in south Madurai. My wife and daughter, then only three, stayed in Bangalore for the next year and a half, for it was very hot in Madurai (9°58' N lat., 78º10' E long.). In later years, after leaving the place, I recalled that it was always 39°C in Madurai. For the first year, not having to bother about family, and without a proper laboratory to fall back on, I could do a lot of field work in the open at night and in the caves with R Subbaraj and G Marimuthu. Settling down in India after an absence of seven years in the West was difficult but the process in my case was surprisingly short.

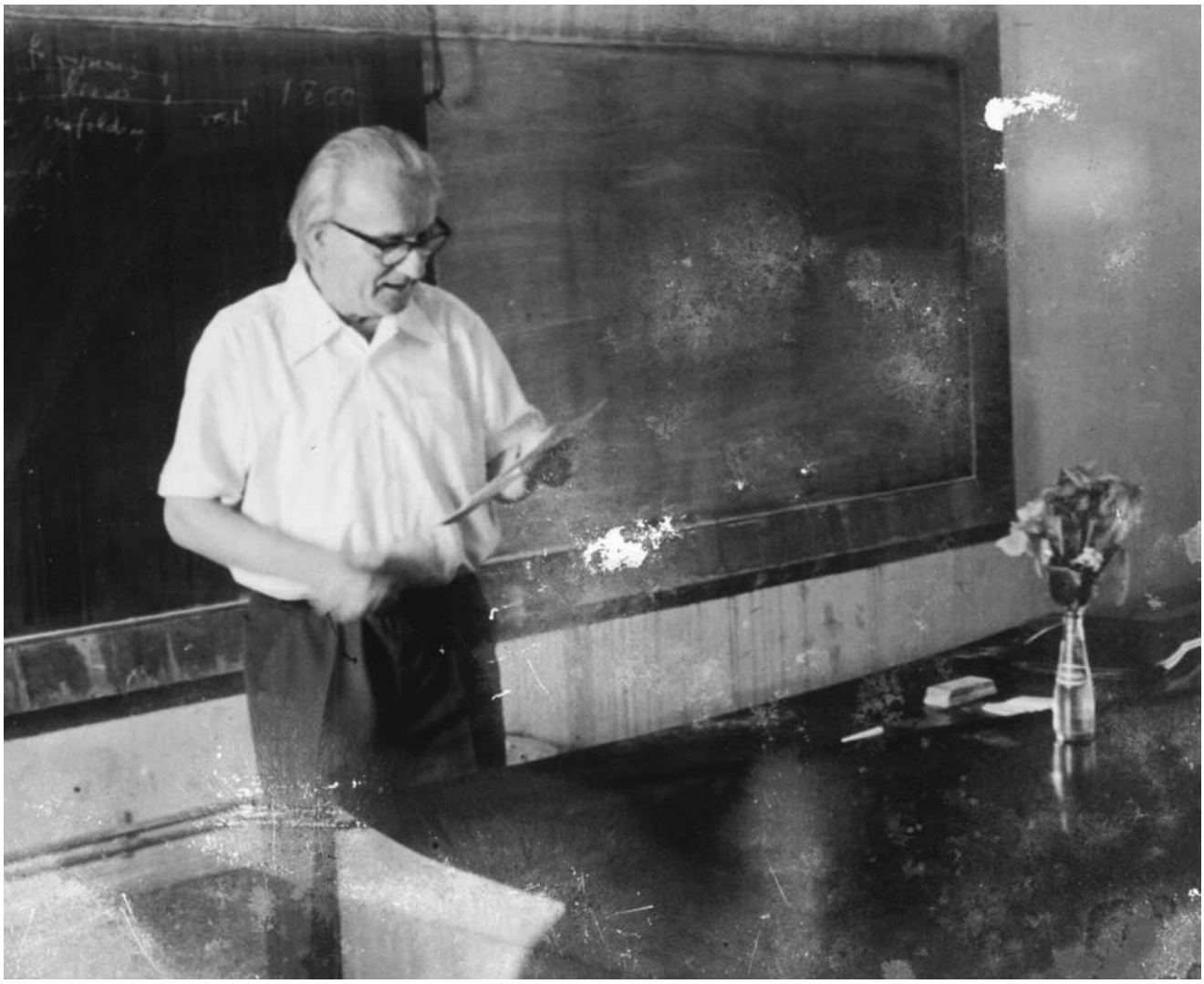

Figure 1. Bünning addressing the participants in the 'Biological Oscillations' workshop at the Madurai Kamaraj University in 1978.

By the beginning of 1978 equipment for neurophysiology and chronobiology had arrived from Germany and the lab became functional. We, my students and I, had picked up sufficient confidence by then to organize a workshop on *Biological Oscillations*, the first of its kind, from 16th to 24th December 1978. E Bünning, W Engelmann, David Saunders (Edinburgh) and Klaus Brinkmann (Bonn) all readily agreed to be teacher participants meeting their own travel expenses. Vidyanand Nanjundiah, then at the Centre for Theoretical Studies, Indian Institute of Science, L R Ganesan of Madura College and I were teachers on the Indian side. Nanjundiah, at thirty one, was the youngest teacher participant. The student participants were hand-picked, and among them was Madhav Gadgil. The workshop had to be run on a shoe-string budget and accommodation and meals were difficult to manage. The guest rooms had been booked for the international participants in another conference, called *Biological Applications of Solar Energy* organized by a colleague. Yet the enthusiasm of the participants verged on euphoria. I was moved to see Engelmann struggle with heavy baggage on arrival at the airport in Bangalore. In a cardboard box he had a freshly potted *Desmodium* plant, raised for our workshop in the green house of the Botanisches Institut at Tübingen. His personal belongings amounted to a tube of toothpaste, tooth brush, and underclothes.

S Krishnaswamy inaugurated our workshop and Bünning spoke on *The History of Chronobiology*. We offered "hands on" experiments on sleep movements in *Desmodium gyrans* the Indian telegraph plant, made famous by J C Bose, circadian rhythms in the flight activity of bats,

Figure 2. Bünning and his wife Eleanore with M K Chandrashekaran in 1978.

wheel running activity of squirrels, cockroach etc. The workshop was run on the lines of the German university Grosspraktikum. I had gained some skills helping Engelmann conduct his biannual *Grosspraktika* between 1972 to 1975. Every morning one of the teachers spoke for an hour, mostly about their own work. The rest of the day was devoted to the experiments. Of the participants three turned later to full time circadian rhythm research, in the departments of zoology of the Banaras Hindu University, Meerut University and Raipur University. Looking back, that was reward enough for those of us who taught in the workshop. Today chronobiology has struck firm roots in India (Chandrashekaran 2005). The participants vastly enjoyed meeting in person David Saunders, already well known for his classic *Insect Clocks* and Bünning, whose book was the bible of chronobiologists. I got Bünning to inaugurate our first chronocubicle complex of three 8' × 8' rooms with ventilation but without windows. At the close, from Christmas day for a whole week I traveled with the Bünnings and Engelmann to Trivandrum, Kovalam and Thekkady. Some time during the week Bünning said "You did the right thing in returning to your country".

Figure 3. Some of the participants in the 'Biological Oscillations' workshop. At left Wolfgang Engelmann, L R Ganesan, David Saunders and Asha Chandola.

11. Character traits of Bünning

Erwin Bünning had varied interests and was much more than a chronobiologist. He published over 260 papers in various fields of plant physiology and general biology and a very popular text book on plant physiology. Bünning and Frey-Wissling at the University of Zürich were the two greatest botanists of Europe of the twentieth century. Only 50 or so of the papers and monographs he wrote deal directly with circadian rhythms and photoperiodism. Like Charles Darwin, he was also interested in the power of movements in plants and wrote a monograph on the subject. Bünning liked to be called a biologist and not a botanist and a travelogue he wrote in 1949 had the title: ("In the forests of Northern Sumatra: a biologists travel diary"). He had at one time or the other worked with prokaryotes, algae, fungi, mosses, ferns, higher plants, insects and hamsters.

Bünning has written a delightful biography of his role model, with whom he shares many characteristics, Wilhelm Pfeffer (Bünning 1975).

Bünning did have to a degree the classical traits of the quintessential German Ordinarius Professor of his times, of aloofness and the reputation of not being easily accessible. This image was further fortified by his being a man of few words, a quality he said that was common to people from Hamburg. He was intellectually precocious, obtaining his Dr. Phil. when he was 23, just seven semesters after matriculation, and the Dr. Habil at the age of 25. He had published four important papers by the time he was 20. Even though he became an Ordinarius Professor at 39 there are clear indications that he would achieved the distinction even earlier had it not been for the war. He held the Wilhelm Pfeffer Chair in Tübingen and turned out to be the true inheritor of Pfeffer's legacy.

Like all truly great men he was a humble person. In 1981 The National Academy of Sciences (USA) asked him about discoveries he considered most important. His answer is a model of genuine scientific modesty. He wrote: "Experiments from 1929–1935 proving that certain biological 24 hr rhythms in plants and animals are endogenous and inherited. Also proving that, under constant conditions, the periods of these rhythms are not exactly, but only about 24 hr (therefore now called circadian rhythms). I made during that time also the first cross-breeding experiments with strains of different periods. During these years and later on, I demonstrated that these rhythms have adaptive values, for example for measuring the length of days (photoperiodism)".In an unpublished hand-written piece (in my possession) he had written "I should state that my main basic experimental results and ideas were published between 1929 and 1937. Everything published later on was nothing but going into more details".

He often said that he detested class-room teaching, in which characteristic he was unlike Pfeffer. He did not lecture anymore after his formal retirement and did not offer to teach any courses, which German ordinarius professors could do by right. According to Bünning, Pfeffer, on the other hand, lectured on the very last day of his life. Early in Bünning's career he wished to have his own Max-Planck-Institut. The Max-Planck-Society showed no interest for they still looked on the study of biological rhythms as a form of metaphysics. Interestingly, Bünning never referred in lectures or in print to what is widely known as 'Bünning's hypothesis', which postulated that endogenous rhythms were much like yardsticks of seasonal time measurement (photoperiodism). This postulate was made in a paper he published in 1936 (Bünning 1977) which became a citation classic of *Current Contents* in 1982 and also turned out to be the most cited paper of the journal. He side-stepped all scientific controversies, including the "endogenous *versus* exogenous origin of rhythms" or the "hourglass *versus* oscillatory nature of biological rhythms". He always stated his standpoint without ambiguity and let his case rest.

He said often "what is worth telling can also be told in a few words". He gave his research students a lot of freedom and they needed to see him only if they had something new to show. If he found something being shown to him commonplace, he would say "fine, fine, just proceed". If what was being shown was novel or exciting then he would perk up and start "Komisch…" (strange) and spend more time looking it over. He had occasion to use the word more than once when I showed him the results of my early experiments with *Drosophila*. Even though he was not very effusive himself, he seemed to like the company of those who were talkative like his secretary and two men students, one of whom became a gardener after obtaining his Dr.re.Nat,, and the other who became the professor of botany in the university at Bonn. Since I was in awe of him in the beginning, it took me a long time to be familiar with him. Bünning had spent six months in Lahore University and six months in the laboratory of P Maheshwari in Delhi University in the late 1950s. Two students from India got their Dr. Phil with him, one being the grandson of Maharishi Karve. Bünning was well read about the 'real' India and was a friend of the famous Indologist Helmut von Glasenap. He used to quip that the great Glasenap knew everything about the religion, philosophy and ancient heritage of India but was at a loss if one asked him what Indians ate.

12. Honours

The universities of Glasgow, Freiburg/Br., Erlangen and Göttingen conferred honorary doctorates on him. He was a Member of the Deutsche Akademie der Wissenschaften, Berlin, Leopoldina, Halle, Heidelberger Akademie der Wissenschaften, Bayerische Akademie der Wissenschaften, National Academy of Sciences, USA, Washington, Foreign Member of the Royal Society of London and an Honorary Fellow of the Indian Academy of Sciences (1986).

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*e*Publication: 14 February 2006