Pittendrigh (1918-1996): In Fond Memory

The scientific study of biological rhythms (chronobiology) has really had a many faceted and colourful past in Europe and drew the attention of brilliant naturalists in the 18th, 19th and 20th centuries and is turning out to be one of the most interdisci­
nary branches of modern biology in the 21st century. The conceptual foundations of chronobiology in the 20th century were laid by Jürgen Aschoff, Erwin Bünning and Colin Pittendrigh. Their deep insight and contributions in the second half of that century account for the high degree of scientific elegance and experimental rigour of the subject. In fact, it was the symposium on Biological Clocks convened by Pittendrigh in the Cold Spring Harbor in New York in 1960, with Bunning as the chairperson and the seminal papers of Aschoff and Pittendrigh that ushered in an era of intensified experimental activity. Bünning’s address was a definitive version of the history of chronobiology.

By 1997, researchers began talking of a ‘party time’ for chronobiology since it marked the twenty-fifth anniversary of the discovery of the supra chiasmatic nucleus (SCN) in the brain of mammals, which is the pacemaker of circadian organization, and the identification and cloning of the first circadian clock gene in a mammal. The journal Science, in a December 1998 issue, ranked some of the findings in the field of biological clocks as the first runner-up breakthrough-of-the-year. By 2003 one of our fraternity could write: “The successes achieved by chronobiologists over the past decade have been the envy of the scientific community. Indeed it is not uncommon for scientists from a variety of disciplines to cite the advances in circadian rhythms as a proof of concept that they too will be able to unravel the mechanisms underlying a particular trait of interest”.

Colin Sanderson Pittendrigh was born in Whitley Bay, Northumberland, in the north of England. His ancestors were Scottish/Gaelic. He read The Origin of Species while in high school and later wrote “My high school interest in Darwinian evolution survived an undergraduate exposure to J W Heslop-Harrison’s Lamarckian convictions, flour­
ished during graduate school (Columbia) with Dobzhansky, and matured during several later years of friendship with G G Simpson” [1]. He was the undisputed doyen of biological rhythm research in the USA and founded a very influential school of chronobiology and his students are the leading lights in the field today. I have had
occasion to recall in print many of his scientific contributions, which served as the fountainhead for my own decade-long work on the *Drosophila* clock, and some of his personal traits, in a subjective account of biological rhythm researchers [2].

Pittendrigh wrote eminently engaging scientific papers that could be read and re-read for pleasure, in spite of the depth, scientific rigour and the gravity of the scientific contents. He never wrote a trivial paper and had scant regard for those who did. In 1954, Pittendrigh showed that the ‘gating’ (a term coined by him) of the eclosion rhythm in *D. pseudoobscura* was compensated for temperature changes. With this finding, one of the most important properties for circadian rhythms to serve in biochronometry, mooted earlier by E Büning, Karl von Frisch and Gustav Kramer, was firmly established.

Much before Konopka and Benzer reported in 1971 the isolation of *period* mutants in *Drosophila melanogaster* with drastically altered period length of the circadian clock regulating both pupal eclosion and adult locomotor activity, Pittendrigh and Bruce [3] had proposed an astonishing, original and explicitly formal coupled-oscillator model to account for the response features of the circadian rhythms of *D. pseudoobscura* to light and temperature perturbations. The principal merit of this model was that it ‘explained’ the phenomenon of transients in picturesque terms. The model predicted that 1) the basic, pace-maker oscillator will be shifted by light pulses *instantaneously* by magnitude that could be read off the standard light pulse phase response curve (PRC), and that 2) the *transients* do not represent ‘the time course and wave form’ of the basic oscillator. Thereafter it became standard practice to construct light pulse PRCs plotting *steady state* phase shifts, obtaining after the transient cycles had subsided, as a function of the perturbed phase. With this vivid and evocative description, he raised the PRC of *Drosophila* to the status of a powerful and precise tool, which was then used by subsequent workers (which includes, among others, E Büning, T Pavlidis, A T Winfree, W Engelmann, A Johnsson, D S Saunders, Sue Binkley, Serge Daan, M K Chandrashekaran and Vijay Kumar Sharma) in formulating *gedanken* and practical experiments and in constructing further predictive models to explain phenomena such as phase and period shifts, transients and entrainment.

The landmark publications of Pittendrigh are discussed by other contributors to this number, two of whom are also his direct students (see also V K Sharma’s article in this issue). The rest of this essay will be personal and anecdotal, and recall some of my
many meetings with Pittendrigh in Europe and in the USA. Rummaging through my papers on and by Pittendrigh I came upon his ‘Reflections of a Darwinian Clock-Watcher’ [1], inscribed with ballpoint ‘for Shekar with great respect & affection. Cheers! Pitt’. This profound memoir stirred in me much emotion when I received and read it in 1993. These anecdotes are recalled from memory, with feelings of reciprocal ‘respect and affection’ for Pitt. Yet, as Donald Kennedy is fond of reminding, memory is not history.

Pittendrigh had two levels of social intimacy and was addressed as ‘Colin’ by those who were very close to him like Erwin Bunning, Jürgen Aschoff, his family and his inner circle. To others, like me, he was Pitt. I first saw him in the spring of 1966 when Aschoff had invited him to give a talk in the Max-Planck-Institute for Behavioural Physiology at Seewiesen. Aschoff introduced him and Konrad Lorenz presided over the meeting, a measure of the esteem in which they held their guest. It was a memorable talk and Pitt was at his inspiring best. Lorenz interrupted him a couple of times and Pitt politely answered the questions, but the third time he said “Konrad we'll discuss these matters over beer at Andechs” referring to the famous Andechser Monastery where the world famous Bavarian beer is brewed.

After the talk we drove down to the Andechs Kloster. I was literally tongue-tied in the presence of all these impressive men Lorenz, Pittendrigh and Aschoff. The otherwise talkative Prussian, Hoffmann, also listened in silence to Pittendrigh. Pitt was taking to task a poor colleague of Aschoff for daring to question the need for a ‘coupled-oscillator model’.

The next time I heard Pitt was in Stanford University early in 1969 when I was a Miller Invitation Fellow in Berkeley. Hans-Willi Honegger, the last among Bunning’s students, was a postdoc with Jim Enright at the Scripps Institution of Oceanography at La Jolla, California. Willi drove all the way to Berkeley to pick me up and we drove on to Palo Alto to Pitt’s lecture. There were rumours that, persuaded by the charismatic Donald Kennedy, then Dean of graduate students at Stanford, Pitt was likely to leave Princeton for Stanford University. Introducing Pitt to the audience Kennedy said that Pitt was a most unusual person “a Dean who does research, a Scot who drinks bourbon and a trout fisherman who not only ties flies but raises them”. Once again the talk was superb with Pitt taking out his handkerchief and mopping his face and reminding the audience that “a horrendous amount of work and data” had gone into
the figures he was showing. Later in that year Pitt spoke in Berkeley introduced by Paul Licht. After the talk, past sunset, Pitt drove me up Euclid Avenue in the Berkeley hills and pulled up at a place from where there was a breathtaking view of the San Francisco Bay, the Bay Bridge and the city itself, beautifully lit up. By this time I had picked up enough courage to make conversation with him. It was mostly about Bünning and how much he too admired him.

After the hectic Berkeley years (1968-1970), I yearned for the peace of a European university and returned to Tübingen. Bünning was around but would retire in 1971 on turning 65. In the autumn of 1973 we heard that Pitt was giving a series of seminars at the MPIV of Aschoff. I persuaded Bünning to accompany me to listen to Pitt. By then Pitt had told me that ‘Erwin’ was not warming up to him anymore. Bünning asked me if I thought ‘Colin’ would much value his presence and I said “most certainly”. Aschoff and Pitt were indeed happy to see Bünning. That was the only time I saw the ‘trinity’ together. Pitt gave two power-packed seminars, which were well received.

The next and the last time I spent a leisurely period with Pitt and Mikey was in July 1987 in Holland. I had attended a Gordon Conference in Plymouth, New Hampshire, and after the conference, before crossing the Atlantic, stayed for two nights in the cozy Harvard Linnean Street home of Hanna and Woody Hastings. W J Rietveld had organized the Conference of the International Society for Chronobiology at Leiden, NL, which was well attended. Pitt, Mikey, Aschoff, the Fleissners, Franz Halberg, Lawrence Scheving, Dora Hayes, Charles Czeisler, Gene Block, Terry Page. Michael Young, Bronėk Cymborowski, Serge and Ruth Daan were all there. I was not sure if I could join the exalted company of Pittendrighs, Aschoff and Daans, who largely kept to themselves. Pitt, sensing my hesitation, said warmly “Shekar we’d love to have your company”. Serge and Ruth invited me to go to their home in Paterswolde near Groningen, at the close of the conference, in the company of Pitt and Mikey. Serge drove us with our baggages and we all arrived around 5 p.m. Mikey and Pitt were on their way to Andechs for a three month stay with the Aschoffs at the invitation of Alexander von Humboldt Foundation. So they had a lot of things to carry. We all stayed very happily together for six lovely, sun-drenched warm days with Serge and his family. Serge Daan’s family was full of medical doctors. Ruth and her sister Eva (both from Germany) and their parents were doctors, their brother and sister-in-law were also doctors and the family Hohe knew the Aschoffs very well; both Serge’s
mother and father were doctors too. Aschoff was a medical doctor and so was his father Ludwig Aschoff.

Pitt regaled us with stories and quotes from Alfred North Whitehead, T S Eliot and Walter de la Mare. In fact Pitt had used the memorable line – *Why this absurd concern with clocks, my friend?* – of Walter de la Mare as a motto for one of his papers. Pitt and I gave seminars in the Department of Zoology at the University of Groningen. I found it a bit daunting to give a formal talk with Pitt sitting in the audience but he seemed to be very interested in the work I had started at the Madurai Kamaraj University on the circadian clocks of bats and mice.

We loafed happily through the streets of Amsterdam and Groningen and went to the Van Gogh Kroeller-Moeller museum and now and then Pitt, Serge and I lapsed into shop talk. Pitt would have been 68 that year and was in robust health and spirits. On July 24, 1987 Pitt, Mikey and I were on our way to Germany taking an Inter-city train at Groningen via Zwolle and Arnheim. There we parted company because they were going to Munich and I to Tübingen to see the Bünning. I was glad that I could help Pitt and Mikey with their heavy baggage while changing trains at Zwolle and Arnheim, a kind of *guru seva* (service to the teacher).

**Suggested Reading**


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