

## M K Chandrashekar (1937–2009)\*

*Vidyanand Nanjundiah*

**Maroli Krishnayya Chandrashekar, Editor of *Journal of Biosciences* (from 1991 to 1997) and *Resonance* (from 2003 to 2005), was a biologist who stood out from his peers as much on account of the quality of his contributions as because of his style. He made major contributions to our understanding of the interplay between time and the living world (which also became the title of a book he wrote). This article aims to bring together aspects of his life and work.**

### Introduction

Among Indian zoologists of his generation, Shekhar, or MKC, as he was also known, was among the few who choose to work on animal behaviour, all the more so on chronobiology. His special area of study was the periodicities associated with endogenous, near-24 hour (nearly exact, whence *circadian*) rhythms that are seen in creatures ranging from blue-green algae to humans. Innate movements in living organisms, especially plants, had intrigued Charles Darwin, Wilhelm Pfeffer and J C Bose. The field of circadian rhythm biology came up in the background of their work and Shekhar, his mentors and colleagues brought it to a noteworthy level of sophistication. In the Indian context, Shekhar provided a counterexample to his own assertion that “Bose’s tradition of going back to nature to understand living processes has practically vanished from India” (Chandrashekar and Subbaraj 1996). He hit upon an important problem early in his career and stuck to it, not paying heed to the traditional zoologist’s approach of concentrating on one well-defined group. At different times he worked on marine crabs, fruit flies, mice, millipedes, humans and ants. He carried out observations and delicate experiments that sought to uncover features of the ‘biological clock’ at a time when nothing was known of underlying mechanisms. He was a systems biologist long before the term came into vogue, with the difference that in his



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### Keywords

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case the system was the whole organism in the context of its natural environment. His work, along with that of many others, set the stage for the enterprise that is under way today, of integrating behavioural observations and the workings of ‘clock’ genes and gene products into one conceptual whole.

Two conjectures dominated the field of circadian rhythms. One, the ‘Bünning hypothesis’, held that organisms use circadian periodicity for photoperiodism: namely, as a yardstick to measure the changing duration of daylight in order to exhibit seasonal adaptations. The other, ‘Aschoff’s rule’ stated that an increase in the intensity of constant light caused a lengthening of the endogenous period for a night-active organism and a shortening for a day-active organism. Even though Shekhar worked long and closely with Bünning, his work contributed more to clarifying issues related to Aschoff’s rule, not Bünning’s hypothesis. Among the many awards and fellowships of learned academies that Shekhar picked up during his career, it pleased him most that he was chosen as the first recipient of (a literally meant) ‘Aschoff’s Rule’ by Aschoff himself (*Figure 1*). Interest in both hypotheses has waned in parallel with the entry of molecular biology and mathematical modelling into the field; concomitantly ecological and evolutionary thinking regarding circadian rhythms has decreased.

**Early days:** Shekhar was born on January 4, 1937 in Salem, Tamil Nadu, as the eldest child of Maroli Krishnaya and Rukmini; two brothers and two sisters were to follow. His father was a Traveling Ticket Examiner on the South Indian Railway Company and was frequently transferred from place to place. He went to school in Podanur and then Erode, where the family had moved in succession from Salem. Two strong memories that he carried from Erode were of a close brush with death and of the beginning of what was to be a life-long love for the Tamil and English languages. After his matriculation in 1953 he was sent off to Mangalore, his family’s ‘home town’, to study in St. Aloysius’ College. There he was fussed over by doting aunts and became something of a hero in college for his acquaintance with literature and willingness to stand up to teachers. The upshot was that he

**Figure 1.** MK Chandrashekar with ‘Aschoff’s Rule’ in front (Madurai, 1991). Instituted by the International Society for Chrono-biology for distinguished work in the field, the actual award is a 30cm ruler used by Aschoff in his work. The recipient of one year’s award chooses the next one.

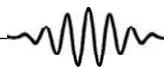


became slack in his studies and got a second class, not the expected first, in his Intermediate examination. That put paid to the possibility of getting a seat in Madras Medical College; thoughts of a medical career had to be shelved.

**Madras (1955–1964):** Nevertheless the family shifted to Madras (now Chennai) in 1955. It was too late to join any other college, and he recalled his first year there as the most depressing of his life. However, not having anything else to do, he could indulge in all the reading he wanted to in the Madras University Library and other public reading rooms. Even then his interests were eclectic. Adi Shankaracharya, C G Jung and Christoph von Fürer-Haimendorf were among the writers he read. Salvation came a year later when he joined Presidency College to do zoology and went on to earn Bachelor's and Master's degrees. The college was famous for its intellectual traditions; C V Raman and S Chandrasekhar had studied physics there. In spite of a domestic atmosphere of genteel poverty, generally uninspiring teaching and dull fellow students, college life exposed him to a new and exhilarating world. Once again books made the difference. Now there was an entirely new set of authors that included P B Medawar, Julian Huxley, Gavin de Beer and J T Bonner. They helped shape a scientific world view centred on evolution that lasted all his life. His favourite teacher, P K Menon, was a committed evolutionist – and also (until then) a confirmed bachelor. Menon inclined him towards Schopenhauer, whose misogynist tract *Über die Weiber* Shekhar came back to read many years later in the original. He was inspired in turn to expand on the theme of women as 'one of Nature's agreeable blunders'. The essay won him a prestigious literary prize. Already proficient in Tamil (which was not his mother tongue), Shekhar developed a feeling for the English language while at college. A Master's by examination followed an uneventful BSc; the eloquently dull one-line syllabus was 'Phyla as patterns of organisation'. After becoming a teacher himself in Madurai, Shekhar was to say that syllabi were academic straitjackets, used by teachers to see what they did not have to teach and by students to find out what they did not have to learn.

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He was set on joining the soft-spoken S Krishnaswamy (with whom a life-long friendship had begun) to do a PhD in the University of Madras. The decision had to be approved by Professor C P Gnanamuthu, Head of Department and Director, Zoological Research Laboratory, who was known to be at the same time both excessively modest (about his own considerable contributions to the biology of parasitic copepods) and short-tempered. But Gnanamuthu had other ideas. One day he summoned Shekhar and matter-of-factly informed him that he would be his research student. The topic for research was dictated forthwith: "Studies on the basal...no, standard...no, no, basal metabolism of a few tropical poikilotherms". As Shekhar recalled wryly, "This meant all animals save birds and mammals. But insiders knew that the animals would be isopods, copepods, crabs or any other marine invertebrate". The topic – which could not be changed – depressed Shekhar: August Krogh's pioneering studies on respiration had led to the general belief among physiologists that while one could speak of a 'standard' metabolism in invertebrates, they did not have a 'basal' metabolism.

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He began measuring oxygen consumption in the intertidal crab *Emerita asiatica* and was soon convinced that he was stuck with a lacklustre problem. As it happened, the course of his future scientific life was about to be set: entirely by accident, he discovered something unexpected. It turned out that even when the crabs were maintained in the laboratory under constant environmental conditions, their movement and respiratory activity varied periodically. The rhythms had a diurnal component and were also in tune with the lunar cycle. It was almost as if the crabs were anticipating the rise and fall of the tides as they did in their natural habitat on the seashore (Chandrashekar 1965). His sense of wonder on making the discovery is described in an account that he wrote for *Resonance* (Chandrashekar 1996). J Enright had found swimming rhythms in crabs of the same genus by 1960, but Shekhar did not learn of it until after his own independent discovery.

Interpreting the discovery was a different matter. At that time the field of circadian rhythm research was split. There were those



(e.g. E Bünning) who believed that the rhythms were endogenous, that is, innate, and those (e.g. F A Brown) who had held on to the view that they were driven by subtle environmental cues. It was clear to Shekhar that he had made an interesting observation and that it was linked to something significant. By then he had come across the contributions of Bünning<sup>1</sup>, Aschoff and Pittendrigh<sup>2</sup>, besides Brown. He made up his mind to join, after his PhD, a research group where he could talk to the experts in the field and the facilities were better than in Madras. Unlike what was then considered the standard option for Indian students in comparable situations, he chose Germany, not the USA or UK. The reasons were many. Erwin Bünning, the person who had first shown that circadian rhythms had a genetic basis and were therefore likely to be adaptive, was in Tübingen. Another reason was that he had been gripped by Richard Goldschmidt's book *Portraits from memory*, a first-person account of the rich tradition of zoology in German universities. (The book never left its hold on him. He enjoyed recalling parts of it and conversing about Boveri, Driesch and Spemann). Carl Correns, one of the re-discoverers of Mendel's laws, had worked in Tübingen. A role may also have been played by the friendship that was developing with a visitor, Gerhard Neuweiler. Himself from Tübingen, Neuweiler had taken the even more unusual step of coming to Madras on a post-doctoral fellowship, in his case to work on giant fruit-eating bats (flying foxes). A letter to Bünning elicited an enthusiastic response and soon Shekhar was off to Germany on a German Academic Exchange (DAAD) fellowship, to be converted after one year into a more prestigious and better-paying fellowship from the Alexander von Humboldt Foundation.

**Tübingen (1964–1967):** Shekhar's personality and scientific temperament made him a hit with his hosts, especially with Bünning. Here he was to carry out the phase-response experiments for which he became famous. The conceptual underpinning had been provided earlier by Pittendrigh. Colin Pittendrigh of Princeton, one of the triumvirate of circadian rhythm research whom Shekhar held in particular regard – Jürgen Aschoff and

<sup>1</sup> See *Resonance*, Vol.1, No.7, 1996.

<sup>2</sup> See *Resonance*, Vol.11, No.5, 2006.

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Bünning being the other two -, had brought into the field a level of elegance and quantitative rigour. Unlike most other workers Pittendrigh targeted his approach at the clock itself and only secondarily at its behavioural consequences (among other things it led to his developing the concept of ‘teleonomy’; unfortunately it did not catch on).

Pittendrigh argued that even though the mechanism behind circadian oscillations might remain unknown, insight into its nature might be obtained by considering it in the abstract, as a purely dynamical entity. He advocated probing the oscillator by perturbing it with external stimuli that were known to act as entraining agents (*Zeitgebers*, literally ‘time givers’) and observing the consequent phase shifts. In a brave conjecture he asserted that the topology of the resulting *phase response curve* reflected that of the underlying oscillator. The approach is formally analogous to something that physicists do, namely guessing the shape of a potential energy function by carrying out scattering experiments. Shekhar exploited it to the full. Today fashion has shifted in the direction of ‘clock genes’ and the manner in which their expression is regulated; the wealth of information accumulated by way of phase response curves awaits a full understanding.

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In the beginning, a longish period was spent in looking for tidal rhythms in the green crab *Carinus maenas*. The rhythms remained weak, whether in Tübingen, where the crabs were brought, or closer to where they were found, in Helgoland. At Bünning’s urging Wolfgang Engelmann initiated Shekhar into the study of the eclosion rhythm in *Drosophila pseudoobscura*. The phenomenon was extraordinary: in synchronized populations maintained in a constant environment (e.g., in darkness), adult flies emerged from pupae every 24.5 hours in bursts. It was as if pupae had a reasonably accurate sense of the natural day-night cycle. Those that could not make it slightly before subjective dawn on one day – that being the optimal time for the wings to dry out slowly and become fully functional – needed to wait a full (near) day to try again. Earlier workers had shown that light could phase-shift the eclosion rhythm. But the work had been plagued by the occurrence



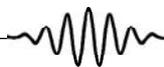
of transients before the rhythm was restored. Because of this it was impossible to say whether the final phase was reached instantaneously or gradually. According to Pittendrigh and Bruce's model, behavioural observations merely reflected the 'hands', not the inner workings, of the clock. Zeitgebers such as light were postulated to effect the inner machinery instantaneously. But how could one test the hypothesis? Shekhar had the insight to come up with the technique of using *two* light pulses in rapid succession. Thereby he was able to make the case for the existence of an 'inner clock' whose phase was shifted by light essentially instantaneously (Chandrashekar 1967).

While in Tübingen Shekhar revelled in the opportunity to meet and sometimes befriend biologists whom he had admired at a distance. Aschoff and Pittendrigh were among them. Then there was the formidable Konrad Lorenz, who headed a Max-Planck-Institut in Seewiesen. It gave Shekhar a special feeling to recall that Lorenz had been at Königsberg and shared a Professorship there that had been held at one time by Immanuel Kant. Lorenz's posthumously published 'Russian manuscript', which was written in a prisoner of war camp and in which he first spelt out how Kantian epistemology could be understood on an evolutionary basis, was a favourite of Shekhar's. Lorenz wanted to know why all zoologists in India were working on DNA, a question that with slight rewording might equally well be asked today.

**Goa and Berkeley (1968–1970):** Leaving Tübingen after the completion of his stay as Humboldt Fellow was a wrench. What transpired after coming back to India soon persuaded him that he had made a mistake. After some forgettable days spent doing nothing in Delhi while waiting to be posted, he joined the National Institute of Oceanography in Panaji (Goa) as a CSIR Pool Scientist. He enjoyed the Goan way of life thoroughly but scientifically the stay was sterile, the conditions of work awful and adjusting to the demands of the CSIR bureaucracy difficult. An anguished newspaper article on the hapless situation of scientists in India and the impossible demands made on them by politicians brought a gentle rebuke from the Director, Dr. N K Panikkar.

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Before long he made up his mind to get away at the earliest. He had communicated his despair to Werner Loher, a zoologist whom he had come to know in Tübingen and who had since moved to the USA. He applied for and obtained a Miller Fellowship at the University of California in Berkeley to work with Loher. The two of them reported finding a circadian rhythmicity of oviposition in a grasshopper (Loher and Chandrashekar 1970). But because the title of the paper omitted to mention the crucial fact that they had discovered extracephalic entrainment to light, the significance of the work remained unappreciated. There were two other papers co-authored with Loher on the effect of light intensity on phase-shifting the *Drosophila pseudoobscura* eclosion rhythm. It was during his stay in Berkeley that an event occurred that opened up a qualitatively different approach to circadian rhythms, namely the discovery of the first clock gene (in *Drosophila melanogaster*) by R Konopka in Seymour Benzer's laboratory in Caltech.

**Figure 2.** At a party during the meeting of the International Society for Chronobiology in Nordwijk, the Netherlands, in the 1970s. Shekhar with Klaus Brinkmann and Gottfried Wiedenmann to his right; Wolfgang Engelmann with the lantern and Martin Schrempf at lower left.



**Return to Tübingen (1970–1975):** Having just then married, his wife Shashikala had accompanied him to Berkeley, and the stay there was personally enjoyable. However, culturally and intellectually it was a let-down after Tübingen. He made up his mind to return and was welcomed back with the prospect of a regular university position to work with Bünning's former student, his old friend Wolfgang Engelmann. But neither then nor later would he be able to recapture the sense of exhilaration that he experienced during his first stay. Time had moved on, there were new faces; the laboratory had shifted from its famous and aesthetically

pleasing building close to the historic old town to a steel and glass monstrosity on the hill that looked like any US lab. Furthermore, Bünning was due to retire shortly. Given the German university system the consequences were fraught with uncertainty for the rest of the group, which made for a tense atmosphere.

In contrast, in terms of science the five years spent in Tübingen from 1970 to 1975 were a success (Figure 2). With Engelmann's help



Shekhar plunged into experimentation immediately after arrival, this time with a new automatic recording device that made the tedious manual counting of flies unnecessary. During this period he carried out experiments that demonstrated a functional separation between the 'on' (or 'dawn') and 'off' (or 'dusk') components of a phase-resetting light pulse (Chandrashekar *et al* 1973). Pleasingly, flies responded to the dusk component, corresponding to sunset, in the first half of the subjective night and to the dawn component, which simulated sunrise, in the second half. By then Theodosios Pavlidis had predicted from topological arguments that under certain conditions the phase response curve must contain a 'singularity' at which the phase shift exhibits a jump discontinuity and the phase itself remains undefined. Arthur Winfree had defined the critical intensity and duration of the light pulse required to shift the oscillator to the singular point. By making use of radiant energy as the relevant perturbing stimulus – and not the intensity or duration separately – Chandrashekar and Engelmann (1973) demonstrated that the phase-response curve exhibited a strong non-linearity close to the putative singular point. They followed this up by showing that it was indeed the product of stimulus strength and duration that was crucial (Chandrashekar and Engelmann 1976). The singular point itself was unstable: reaching it was a hit-or-miss affair, achievable in only 10% of the trials. At this time Shekhar also managed to clear up conflicting claims in the literature on the effects of temperature on the eclosion rhythm (Chandrashekar 1974). He showed that the problem had been caused partly by the fact that (unlike light) a temperature pulse appeared to act continuously. In anticipation of a similar observation that was to be made later in the case of light pulses, he found that the phase response curves for low- and high-temperature pulses were approximate mirror-images of each other.

All the while Bünning kept suggesting to Shekhar that he should stay on and consider making Germany his home. But the absence of the circumstances and companionship of his first stay in Tübingen, combined with the birth of a daughter and the feeling that she should be exposed to Indian culture, made him think of returning to

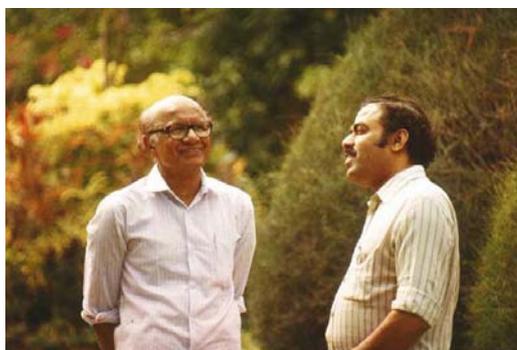
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India if he could find an independent position. At the invitation of S Krishnaswamy, his old friend from Madras days, he had visited the Department of Biological Sciences in the newly started Madurai University in 1973. He came back impressed by the quality of the people he met there and their sense of commitment to the place. Along with Neuweiler (then in Frankfurt), Krishnaswamy had been trying to put together an Indo-German collaborative programme in neurobiology and behaviour and urged Shekhar to come to Madurai. In December 1974 Shekhar cut the negotiations short by abruptly accepting the offer of a Reader's position in the Department of Biological Sciences. Both Neuweiler and Bünning were taken aback by the suddenness of the decision and tried to persuade him to delay the move. His close friend Kutubuddin, disappointed though he was personally, reassured him by saying "The weather there will always be good, the food tasty and the people friendly". And so it turned out to be, more or less, over the 20-odd years that Shekhar spent in Madurai. (The weather was rarely good. Years later, the first thing he tended to say – with a pleased smile – when we met on a cool morning at the bus stop on the way to work in Bangalore was "It was 37 degrees yesterday in Madurai".)

**Figure 3. S Krishnaswamy and Shekhar (Botanical Gardens, Madurai Kamaraj University, 1983/84).**



**Madurai (1975–1996):** He early realised that S Krishnaswamy – ‘a man of extreme diffidence and genuine humility, the most consistent agnostic I knew’ – had set his mind on building up from scratch a first-rate, modern school of biology in a State university. Today this would be an unrealistic expectation to say the least. It was beginning to seem so even then. But Krishnaswamy pulled it

off (Figure 3). Thanks to the calibre of its early recruits, the School of Biological Sciences in Madurai Kamaraj University became recognized as one of the best places in India for post-graduate teaching and research in biology. Both how it managed to attain the heights that it achieved and what accounts for the course it has taken subsequently, deserve careful study. Indicative of the importance of seemingly minor



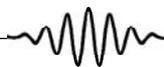
practices for shaping the sociology of a community, Shekhar and his colleagues invariably pointed to the daily lunch club as a hidden factor behind the effervescence of biology in Madurai. Even if they did not understand much of what transpired, occasional visitors who were privileged to participate could sense structure emerging from the apparent complexity. The whole thing sounded like a chaotic mix of raised voices, harsh words and Kumbakonam jokes, but what mattered seemed to get sorted out and the participants dispersed with smiles, having somehow finished eating in the meanwhile. Krishnaswamy used to say that along with the Meenakshi temple and mallige (jasmine) flower, it was the lunch club that made Madurai special.

Shekhar's work began to proceed smoothly once he figured out that Krishnaswamy was inherently incapable of turning down a request; therefore his responses had to be interpreted accordingly. 'No problem' meant that something was unlikely to get done and 'Absolutely no problem' meant that it was impossible. Krishnaswamy had already picked a young man with flair, R Subbaraj, to work with Shekhar. Subbaraj had qualified to do a PhD at two supposedly more prestigious places, the Indian Institute of Science in Bangalore and the Tata Institute of Fundamental Research, Bombay. But his heart was set on working with bats and working with Shekhar. D Uma, G Marimuthu and Sripathi Kandula joined Subbaraj in due course; apart from Uma, they were all to become colleagues. Shekhar took to the ancient town of Madurai with its rich cultural heritage and, crucially, spectacular 'bat caves'. But his sense of belonging never developed the intensity that it had in Tübingen.

The circadian rhythm work carried out in Madurai made his group known internationally. In roughly equal parts it involved the study of phenomena associated with rhythmicity in insectivorous bats, field mice and humans. With Marimuthu and Subbaraj, he reported that social cues from conspecifics could synchronize the flight activity rhythm in *Hipposideros speoris* (Marimuthu *et al.* 1978). Subbaraj and he generated the first dark-pulse phase response curve in chronobiology, on the tomb bat *Taphozous*

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*melanopogon*; it was the mirror image of the light pulse phase response curve for the same animal (Subbaraj and Chandrashekar 1981). Dilip Joshi (another student) and Shekhar showed that *H. speoris* was capable of responding to the dimmest intensity (5% of starlight) and shortest duration (0.0625 msec) of light found to entrain or phase-shift a circadian rhythm (Joshi and Chandrashekar 1982, 1984). Viswanathan and he discovered that the circadian clock of newborn pups in the field mouse *Mus booduga* was entrained by an unusual, but in hindsight perfectly understandable, social cue, namely the presence and absence of its mother (Viswanathan and Chandrashekar 1985). There was also an endogenous component to the pup's rhythm and the entrainment worked only within limits. As Shekhar liked to say, not forgetting to draw the implication for human newborns, 'too much mother' was as bad as 'too little mother' (Viswanathan and Chandrashekar 1988). Vijay Kumar Sharma, then a student and subsequently a colleague in Bangalore, found that light-induced phase shifts in *Mus booduga* were sensitive to the spectral composition of the light used (Sharma *et al.* 1998). The reasoning, based on a behavioural observation, had been used before in order to infer the existence of two classes of photoreceptors in *H. speoris* (Joshi and Chandrashekar 1985). While at Madurai, under the aegis of the Indo-German collaborative programme Shekhar oversaw regular workshops on electrophysiology and neurobiology. They were the only ones of their kind in India and attracted students from all over the country.

Investigations on human circadian rhythms could begin only after the arduous process involved in the construction of an 'isolation bunker' was gone through. The first experiments involved Marimuthu as the subject and L Geetha followed him; their findings were striking. Confirming an older observation of Aschoff's, the subjective estimation of short intervals of time (either 2 min or 2 h) was positively correlated with the period of wakefulness – as if the body knew at the time of waking when it would go to sleep that night (Chandrashekar *et al.* 1991a). The female menstrual cycle was not coupled to the cycle of sleep and wakefulness



(Chandrashekar *et al.* 1991b). Similarly, the rhythms of body temperature and sleep-wakefulness could get desynchronized. Curiously, and contrary to common belief, the length of sleep did not depend on how long one had remained awake before it (Chandrashekar *et al.* 1997). Occasionally a subject would remain awake for 32 h before going to sleep for 16 h, adding up to a *circadian* rhythm of 48 h. An interesting consequence was that the interval between meals got enormously lengthened.

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In 1991 Shekhar took up the editorship of *Journal of Biosciences* and carried on for seven years. This was a newborn journal created by the amalgamation of three others. One was of the same name; the others were *Proceedings (Plant Sciences)* and *Proceedings (Animal Sciences)*. Shekhar had always been a votary of biology as a unified science and had fought against narrow compartmentalization whenever he could – both in Tübingen and in Madurai, though with little success. As with everything he did, he carried out his editorial duties with the lightest of touches. But the editorship did not begin smoothly. Each of the three older journals had its loyalists; many of them felt let down and upset by what they saw as an attempt to deprive them of their legitimate territory. Shekhar was taken aback to find that some of the reaction was directed at him personally. It needed all his diplomatic skills for the new, broad-based *Journal of Biosciences* gradually to gain acceptance. One of the aims that he set for the journal was that it should attract a reasonable proportion of the best work carried out in India. The older journals had achieved this in some measure; they catered to well-defined communities – roughly speaking, of botanists, zoologists and biochemists. With hindsight, it is evident that for a generalist journal of biology to succeed in this sense, it has to overcome the handicap of not ‘belonging’ to any defined area.

Shekhar had always been a votary of biology as a unified science and had fought against narrow compartmentalization whenever he could.

**Bangalore (1996–2009):** Following an invitation from Professor C N R Rao, Shekhar left Madurai and joined the Jawaharlal Nehru Centre for Advanced Scientific Research in Bangalore. There he built up the Evolutionary and Organismal Biology Unit. In this a pair of much younger and congenial colleagues, initially Amitabh Joshi



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and later Vijay Kumar Sharma, ably assisted him. The position of Head, Academic, Fellowship and Exchange Programmes meant that administrative responsibilities occupied much of Shekhar's time in the J N Centre. His approachable nature led young people to often come for advice and support when things were not going well for them. He was never short of time to talk to others. Still, he managed to contribute to significant experimental findings. The eclosion rhythm in *D. melanogaster* persisted after as many as 600 generations in an aperiodic environment, hinting that a lapse from rhythmicity – or something with which it was tightly correlated – was strongly disfavoured (Sheeba *et al.* 1999). Observations on the rhythm of oviposition pointed to the presence of at least three different circadian oscillators underlying locomotor activity, eclosion and oviposition respectively (Sheeba *et al.* 2001).

He soon added German to his repertoire of languages, to the extent of being able to appreciate the special qualities of Robert Musil and Joseph Roth.

**The Person:** For someone whose mother tongue was Tulu and higher education had been in English, Shekhar's mastery of the Tamil language and its literature was remarkable even to scholars in the area. He was apt to pepper his remarks by quoting from the Tirukkural. His fondness for – and skill in using – the English language was no less; his writings were marked by a spare elegance. He was equally crisp in scientific communication. Once he was asked after a talk, “Do bats ever fly during the day?” (by Francis Crick, as it happens). The response was in words that remain vivid for the way they encapsulate what biology is all about: “Only on islands that lack birds”. Going to Germany gave him the opportunity to immerse himself in an entirely new culture. He soon added German to his repertoire of languages, to the extent of being able to appreciate the special qualities of Robert Musil and Joseph Roth. The identification with Germany and things German was such that on one occasion, often recollected by his friends, he asked a visitor from another part of the country, “What do you have against us Swabians?” [He was referring to the part of Germany where Tübingen was situated.] A sense of attachment to Tübingen, its University and its cafes lasted all his life.

With students, what he valued most was their motivation. As a lecturer he had the knack of keeping things simple and making

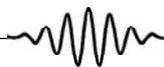


research sound like fun. He used to regret that contemporary science had become a grim affair and its practitioners, one-dimensional creatures. He believed in communicating science in the manner of a story that could be understood by anyone. To those who worked closely with him he conveyed a sense of manual dexterity. His philosophy about how to nurture a good department was that one should hire first-rate people and then leave them alone, something that he practised in his own leadership style. He was passionate about universities, especially state universities, and worried over how they had been allowed to decay. In the meticulousness with which he wrote papers, he remained very much an old fashioned scientist. Few things bothered him as much as the contemporary tendency to assess the worth of a publication more by where it was published than what it contained. Along the same lines, he despaired about the fatuity of judging science and discriminating between scientists on the basis of quantitative assessments.

He was a man of enormous culture and charm, but because of a fundamentally shy personality it took people a while to realise this. However unexpectedly you dropped in on him, he managed to convey the impression that he had been waiting for you, had all the time in the world and wanted to discuss precisely the subject that was uppermost in your mind. Within a matter of minutes anyone meeting him for the first time was made to feel comfortable and at home. There was hardly anything that he was not interested in. He could hold his own on topics ranging from popular cinema to Chola bronzes. He had an uncanny memory of people, events and places. Thirty and more years later he could recollect the time of day and place where a certain encounter had taken place and who had said what to whom. He explained this trait by saying that on account of shyness he tended to keep his eyes and ears open and mouth closed. A keen observer of humans no less than of bats and mice, he made the perceptive remark that scientists go through two phases of imprinting during which they unconsciously assimilate behavioural traits. The first (like everyone else) is when they are growing up; the second phase occurs when they are much older,

Shekhar was passionate about universities, especially state universities, and worried over how they had been allowed to decay.

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and the imprint is derived from their research mentors. A fine mimic, he had the ability to spot the funny side of any situation or incident and to describe it in an inimitable deadpan style. His takes on the Panjandrums of Mylapore were unforgettable. It is telling of the sort of person Shekhar was that when his friends talk about him (and this was true even in the early days after his passing), the mood of gloom is brightened by bouts of laughter.

Shekar passed away after a brief illness on July 2, 2009. He had been unwell for some months and did not recover from a seizure that occurred while he was at work the day before. At the time of his death he held the position of Honorary Professor in the Evolutionary and Organismal Biology Unit of the Jawaharlal Nehru Centre for Advanced Scientific Research, Bangalore, the unit which he had established in 1996. His wife, Shashikala, and daughters Sujata and Sonali survive him.

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In preparing this tribute, the biggest help came from Shekhar's own reminiscences, partly published (Chandrashekar 1998, 2005) and partly in manuscript form. Thanks are due to the many people who contributed their recollections. Wolfgang Engelmann and Gottfried Wiedenmann described the Tübingen days; Hans-Willi Honegger wrote about Tübingen and Berkeley, R Jayaraman and G Marimuthu about the Madurai period and Amitabh Joshi and Vijay Kumar Sharma told me about life in EOBU. The photographs were kindly provided by Shashikala Chandrashekar (Figure 1), Wolfgang Engelmann (Figure 2) and Vijay Kumar Sharma (Figure 3). Durgadas Kasbekar and H Sharat Chandra made helpful comments on an earlier draft.

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