

within the oceanic plates. Yet the plates remain essentially undeformed over life-spans of 100 to 200 million years, whereas North America is straining at a rate of  $10^{-15}$  to  $10^{-16} \text{ s}^{-1}$  in response to forces of the same magnitude. These rates of strain may seem slow, but they are brisk in geological terms — they

would produce 100 per cent strain in 20 to 200 million years.

The continent of North America must be much weaker than the stiff oceanic plates, so weak in fact that it makes no sense to treat it as a plate at all. Mountains do indeed flow, though at a rate that is slow on a human timescale. Deborah, I

presume, intended her prophecy as a comment on the Lord's omnipotence; it could equally be interpreted as a comment on His longevity. □

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## OBITUARY

## Colin S. Pittendrigh (1918–96)

COLIN S. Pittendrigh, founder of the modern field of circadian biology and for many years its most articulate spokesman, died in Bozeman, Montana, on 18 March.

Pitt, as he was universally known, took a first degree in botany at the University of Durham, and in the Second World War worked on malaria control in Trinidad, studying the anopheline mosquitoes that breed in bromeliad ponds. During that period he made substantial contributions to understanding of bromeliad evolution and his interest in rhythmicity was kindled by observing the biting rhythms of malaria-carrying mosquitoes. After the war he completed a PhD under the supervision of Theodosius Dobzhansky at Columbia University, moving to Princeton in 1947. There he taught a memorable course in introductory biology, and notably, as dean of the graduate school, was instrumental in making admission to Princeton open to women. In 1969 he moved to Stanford, where he remained until his retirement in 1984.

His early and seminal insight was that the many rhythms expressed by living things in the real world are the consequence of endogenous, self-sustained biological oscillations that are entrained (synchronized) by environmental cycles. Although this view seems obvious now, it was accepted only slowly because it seemed unnecessarily complex. Why should natural selection favour an internal oscillator when the environment is replete with temporal cues? One answer was contained in the earlier research of G. Kramer and K. von Frisch on Sun-compass orientation in birds and bees. To use the Sun as a compass animals need the equivalent of a clock, and it was this work that led Pitt to the inspired guess that this same clock times many biological processes and is indeed a general property of cells and organisms.

Many clear predictions emerged from this new view of rhythmicity. In the mid-1950s, Pitt, along with his graduate students and close associate Victor Bruce, began testing them. Pitt himself concentrated on the beautifully precise

eclosion (pupal emergence) rhythm of *Drosophila pseudoobscura* and quickly verified three central predictions: the eclosion rhythm persists in the absence of temporal cues from the environment (that is, under constant conditions in the laboratory); its period varies only slightly with changes in ambient temperature (a prerequisite for accurate time-keeping); and it can be entrained by cycles of light



or temperature within a narrow range around its natural period.

Together with his long-time friend and scientific colleague, Jürgen Aschoff, Pitt led the work of the next decade which established that biological clocks with nearly identical formal properties occur in virtually all eukaryotic organisms. They provide temporal frameworks for processes as different as photosynthesis in green plants, spore formation in fungi, cell division in the ears of mice, and human cognitive performance. The recent demonstration of a clock in a cyanobacterium extends the generalization to the prokaryotes.

Although Pitt participated in one of the earliest identifications of a circadian pacemaker in a multicellular organism (in the optic lobe of the cockroach), physiology was not his *métier*. While

many in the field moved in that direction, he began to study photoperiodic time measurement, an interest that occupied the rest of his career. Building on a prescient insight of Erwin Bünning and a beautiful experiment by K. K. Nanda and K. C. Hamner, he developed a set of logically tight arguments and designed a series of elegant experiments that convincingly demonstrated that the circadian clock measures daylength and thus times many of the adaptive responses of organisms to seasonal change.

Pitt was always interested in the power of language to direct thought, and over the past few years he became convinced that the term 'biological clock' had outlived its usefulness. He perceived that the central function of the circadian system is to provide a temporal framework within the organism or cell: to emphasize this view, he preferred the term 'temporal programme' to 'clock'.

Although his experimental work was almost entirely directed at understanding circadian rhythmicity, his thinking was dominated by evolutionary considerations. In one of his papers — which is still well worth reading — he originated the concept of 'teleonomy' as a necessary and respectable alternative to 'teleology' with its unacceptable baggage (Chapter 8 in *Behavior and Evolution*, Yale University Press, 1958).

By force of intellect and personality, Colin Pittendrigh exerted a profound influence on the development of a field which, very early on, he realized is central to our understanding of biological organization. It has taken many years for biologists generally to catch up with his vision, but it is now clear that he was right and the hunt is on for underlying circadian mechanisms at the cellular and molecular levels. Those of us — and there are many — who were privileged to know and work with Pitt will never forget him as a scientist or as a man.

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