cytochrome c_1 ($M_r = 62K$); cytochrome b ($M_r = 39K$); and the Fe_2S_2 protein ($M_r = 20K$). The much larger size of the cytochrome c_1 polypeptide suggests that its sequence encompasses some of the components found as individual polypeptides in mitochondrial bc_1 .

The notion that bacterial complexes are generally simpler than their mitochondrial counterparts was supported further by a comparison of *Escherichia coli* cytochrome d terminal oxidase (R.B. Gennis, University of Illinois) with the cytochrome oxidase of mitochondria (T.G. Frey, University of Pennsylvania). The former complex is made up of one copy of cytochrome c_1 and two of cytochrome d , whereas the mitochondrial complex contains six to twelve different polypeptides. Structural information on two-dimensional crystals of the mitochondrial complex is available at a resolution of 20–30 Å, but the question of whether mitochondrial cytochrome oxidase is a dimer or monomer *in vivo* remains unanswered.

In the examples described above, the distinctive spectroscopic properties of the multiple prosthetic groups provide direct access to information bearing on the consecutive steps in the electrogenic reactions which these complexes perform. Unfortunately, this is not the case with the next group of transmembrane complexes discussed — for example, the H^+ -translocating ATP synthases, ($Na^+ + K^+$)ATPase and Ca^{2+} ATPase. Consequently, speculation still occupies centre stage in proposals for the detailed mode(s) of action of these complexes.

Common mechanism

There is increasing evidence that all of the synthases which react with ATP to form a covalent β -aspartyl phosphate (D^*) intermediate may share a common mechanism of action. For example, the sequence CSD*KTGTLT (single-letter code) is fully conserved in the H^+ ATPase of *Neurospora* and *Saccharomyces cerevisiae*, the ($Na^+ + K^+$)ATPase of sheep kidney and the Ca^{2+} ATPase of rabbit muscle. Moreover, a 15-residue sequence near the carboxy terminus of these enzymes shows variation in only three positions. The sequences of all three enzymes give rise to very similar hydrophathy plots (C.W. Slayman, Yale University). In contrast, enzymes of the bacterial phosphotransferase system, enzyme II^{int} and enzyme II^{ext} — enzyme III^{ext} , which phosphorylate and transport mannitol and glucitol, respectively, show no significant sequence homology (M. Saier, University of California, San Diego).

R.M. Macnab (Yale University) presented the latest chapter in the continuing saga of studies of the bacterial flagellar motor. Genetic and biochemical studies have focused on five polypeptides which are not integral components of the basal

Robert Day Allen (1927–1986)

ROBERT DAY ALLEN, who died at home on 23 March after an intense one-year fight with pancreatic cancer, was one of the modern founders of the field of cell structure and motility, an area that he investigated during his entire career.

After a doctoral dissertation under L.V. Heilbrun on the nature of artificial activation of clam eggs, Allen continued basic studies on the structure of egg cytoplasm and pronuclear movements at the Wenner-Gren Institute, the Kristinebergs Zoological Station in Sweden, followed by a period at the University of Michigan and then at Princeton University. It was during this period that he evolved two major concepts that stayed with him during his entire research career. One concept was that living cells could yield important information about basic biological processes; the other that light optical methods in concert with electronic control and detection devices could yield molecular information in living cells. Allen was clearly one of the pioneers in applying quantitative light microscopy to basic questions in cell and molecular biology.

He next combined the use of biophysical techniques, especially light microscopy, to test the prevailing dogma on the mechanism of amoeboid movement. A combination of studies on living cells and isolated cytoplasm led him to re-examine the tail contraction model. He demonstrated that cytoplasm was not a newtonian fluid and possessed structure as evidenced by its optical polarization properties and ability to transmit applied tension. His observation, in 1955, that isolated cytoplasm from single cells could continue to generate motile forces ultimately led to the preparation of motile cell extracts that continue to yield important biochemical information today.

This early work demonstrated, experimentally, two fundamental concepts that had been discussed previously with much less experimental evidence: first, that cytoplasm can exist as both a medium of weak structural properties (sol) and as a viscoelastic solid (gel); and second, that the elements responsible for the generation of contractile forces exist in the cytoplasm. Allen's research on the structure and motility of cytoplasm led him to propose the frontal contraction model of

body. Two of these, MotA and MotB, appear to be circumferentially arranged about the basal body and involved in interaction with other components of the motor to transduce proton potential into torque. The rest, Fla AII.2, FlaQ and FlaN, are important for assembly, rotation and switching. Deletion mutants in the corresponding genes do not assemble any detectable flagellar structure. Mis-

amoeboid movement, still used as a valuable guide in the design of experiments for testing mechanisms of this type of movement.

In the late 1960s and early 1970s, at the State University of New York at Albany, Allen assembled his first electro-optical microscope. The phase-modulated microspectrophotometer enabled him to measure separately the optical polarization properties of linear birefringence, linear dichroism, optical rotation and circular dichroism in tissue sections, muscle fibres and solutions of proteins.

The last part of Allen's career was probably the most important in that he had a seminal influence on the development and use of video-enhanced contrast microscopy in cell and molecular biology. This method allows large increases in optical contrast which facilitates the detection of structures well below the limit of resolution of traditional optical microscopy. At the Marine Biological Laboratory in Woods Hole, Massachusetts, Allen and his many collaborators investigated fast axonal transport in squid axons and in isolated axoplasm. The fundamental discovery was that particles are transported along single microtubules. Furthermore, individual microtubules can exhibit motility along glass substrates. This exciting discovery has stimulated research in several fields where microtubules have been implicated in motile events.

Robert Allen loved the challenge and thrill of performing basic research and communicating the results. He was particularly interested in seeing the same kind of enthusiasm and drive in students. A major part of his interest in science was in communicating facts and concepts in novel ways. He produced many educational movies and pioneered the use of video disks as a medium for publishing results in the journal *Cell Motility* which he founded. His uncanny intuition in both biological processes and in optical methods was expressed repeatedly in his work on the structure and motility of cytoplasm, organelles and whole cells. The fluid nature of his scientific thought and experimental approach was undoubtedly influenced, in part, by his abilities as a concert cellist. His extraordinary talents will be missed, but his impact will long be felt.

D. Lansing Taylor

sense mutants, depending on the allele, may be Fla⁻, Mot⁻ or Che⁻. The available evidence suggests that these switch proteins form a complex that is peripheral to the membrane and may be associated with the M-ring of the basal body. □

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