Obituary

Thomas Cavalier-Smith

(1942–2021)

Polymath of cellular evolution who shaped understanding of the tree of life.

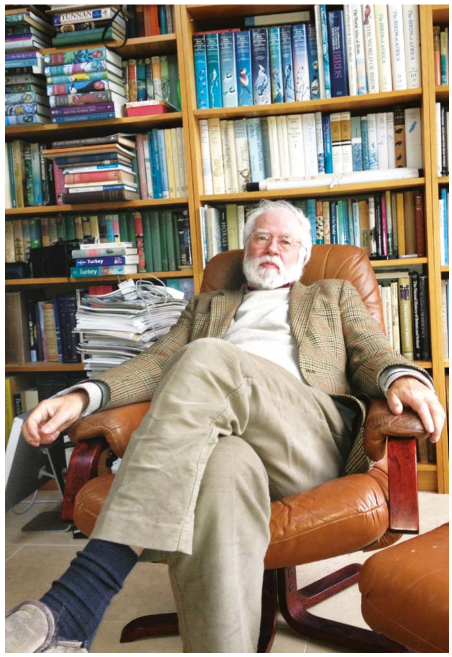
Since Charles Darwin first proposed his theory of evolution, biologists have struggled to fit all life forms – from the tiniest bacterium to the blue whale – onto a tree of life that explains their ancestry. The tree, it turned out, was more of a web. Branches were fused by the demonstration that endosymbiosis can lead to the integration of a microbial cell into another cell to form a discrete compartment passed from generation to generation over hundreds of millions of years. Thomas (Tom) Cavalier-Smith played a crucial part in understanding major transitions in evolution, including the role of endosymbiosis. He has died, aged 78.

Cavalier-Smith's aim was to understand the rise of the eukaryotes – organisms with complex, compartmentalized cells, including plants, animals and fungi. His passion was the huge diversity of single-celled eukaryotes – the protists. His ideas were based on the thesis that we cannot grasp evolutionary history without understanding how all dimensions of a cellular system – function, structure, biochemistry, economy and spatial organization – arose. How this network varies across the tree, he argued, defines the tree.

Historically, the study of microbial forms focused on interpretations gleaned from light microscopy. With his second wife and colleague Ema Chao, Cavalier-Smith rationalized the comparative study of protists. He and Chao combined light and electron microscopy with genetic analysis to construct a new systematics for the eukaryotes and to pursue a unified taxonomy for all life.

Cavalier-Smith was born in London in 1942. He studied at Gonville & Caius College at the University of Cambridge, UK, and completed a PhD at King's College London in 1967, with the biophysicist John Randall. When Cavalier-Smith turned to electron microscopy, he began to reveal the diversity of protists and algae and the complexity of organelles such as mitochondria and chloroplasts, the products of endosymbiosis.

After postdoctoral studies at the Rockefeller University, New York City, Cavalier-Smith returned to King's in 1969 as lecturer, and then reader, in biophysics. He moved to the University of British Columbia in Vancouver, Canada, in 1989. Observing that some living protists seemed to lack mitochondria, he suggested that the eukaryotes originated before the endosymbiotic event that led to mitochondrial



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evolution. He placed these intermediate forms in a new kingdom, the Archezoa, developing a scheme for the stepwise evolution of cellular complexity in eukaryotes.

Another of his hypotheses proposed that a huge branch of eukaryotic life, including large multicellular forms such as the seaweed kelp, were the product of endosymbiosis between one eukaryote and another, much earlier than

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had been suggested. In the group he designated the chromalveolates, this event left behind a chloroplast – the cellular compartment for photosynthesis. The group contains lineages as divergent as marine phytoplankton (such as diatoms) and the malaria parasite, whose chloroplasts are colourless and non-photosynthetic.

These hypotheses represented confident strides towards an evolutionary synthesis that was new in two ways. They were detailed, but spoke of billion-year timescales; and they offered testable predictions. He gave the infant field of evolutionary cell biology a common language and a set of ideas to either work with or to disprove.

Cavalier-Smith's ideas were indeed challenged and subject to extensive revision. Nobody championed these revisions more than he, with, for example, the ultimate demise of the Archezoa. The idea that a scientist (indeed any intellectual adventurer) could not completely restructure their understanding, or even destroy their own previous synthesis in response to new data, was anathema to him.

In 2000, he returned to the United Kingdom as professor of evolutionary biology in the Department of Zoology at the University of Oxford. He made fundamental contributions to understanding the origins of sexual reproduction, the origins and diversification of prokaryotes (bacteria and archaea), genome structure, and the evolutionary history of almost every eukaryotic organelle.

Influential examples I often re-read include his works on the relationship between the size of an organism's genome and the volume of its cells, and how an early organism could arise from the interaction of a self-replicating nucleic acid and a proto-membrane. These contributions again brought the multiple dimensions of a cellular system to an evolutionary problem.

A highlight of his many honours was the International Prize for Biology, received from the Emperor of Japan in 2004. I remember the day he told me of this award, announcing that he was learning parts of his speech in Japanese – further evidence of his many intellectual gifts.

Time with Tom was precious yet given generously. Debates at conferences were robust, but his attention and interaction with all were unbounded. He grilled graduate students and eminent professors alike, offered advice and radiated enthusiasm. Supervisions would often last for six hours: discussion would roam over the whole of biology. We might not all have agreed with Tom all the time – many of us argued with him again and again – yet at every turn he was there, providing ideas, hypotheses accurately framed to test, syntheses to absorb and data to digest. His mark on the field is indelible. Evolutionary biology will miss him greatly.

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