

Obituary

Arthur James Cain (1921–99)

The 1950s and 1960s saw a flowering of experiments on natural populations. Many evolutionary biologists tried to detect and measure natural selection, and to interpret evolution through the mathematics of R. A. Fisher, J. B. S. Haldane and Sewall Wright. The majority unequivocally supported a Darwinian view of the natural world. By the 1970s, however, uncertainty had set in. Studies of variation in proteins and DNA seemed to favour an alternative — that most evolutionary changes have little or no effect on survival or reproduction. A schism arose between ‘selectionists’ on one side and ‘neutralists’ on the other. The former often came from the ecological parts of the subject, and the latter from the molecular parts. The argument between them was long and hard, and still continues. Arthur Cain, who died on 20 August at the age of 78, was a standard-bearer for the selectionists.

Cain was educated at the Lawrence Sherriff school, Rugby, England, from where he won an open scholarship to Magdalen College, University of Oxford. There, in the 1950s, with Philip Sheppard he carried out a classic study of land snails whose colour polymorphisms had been widely cited as neutral in terms of natural selection. In an elegant series of observations and experiments, the two collaborators showed that the different colours and patterns strongly affected the likelihood of being eaten by predators. This work convinced Cain that it is always a mistake to assume a character to be selectively neutral without a careful study of its interactions with the ecology and habits of the organism. Indeed, it is a double mistake because it discourages further observation and experiment.

These conclusions inspired him to accumulate evidence about the power and delicacy of natural selection. The result was a trenchant paper, “The Perfection of Animals”, first published in 1964 and reprinted in the *Biological Journal of the Linnean Society* in 1989. It is still necessary reading for nascent biologists. It is sad that Cain’s last illness prevented him from learning about the recent evidence for selection acting on supposedly ‘trivial’ variants of protein and DNA.

Following up the work with Sheppard, Cain joined John Currey to produce the first description of ‘area effects’, parts of the range of a species where particular genetic variants are found at high frequencies in many adjacent populations,



Naturalist and doughty Darwinian

apparently regardless of habitat, separated from other such groups of populations by steep gradients in gene frequency. In 1963, Cain and Currey argued that these patches were caused by cryptic environmental selection. The work has given rise to much argument in the realms of phylogeography.

Cain’s interest in evolution was wide. An early expedition to the Solomon Islands, and later ones to British Guiana (as it then was) and the Dominican Republic, reinforced his fascination with the processes by which species come about. He produced a seminal book, *Animal Species and Their Evolution* (1954, reprinted by Princeton University Press in 1993), and worked on the evolution of fruit pigeons, parrots, ducks, earthworms, fruit flies, sea anemones, microbes and plants. He developed an extraordinary breadth and depth of knowledge about animals and plants, and an uncanny acuteness of biological understanding. He was, in the very best sense of that word, a naturalist, perhaps the most accomplished of his day.

Early in the 1960s, Cain also became a leader in the theory of classification, and a pioneer of numerical methods in taxonomy, although his approach became superseded by that devised by Robert Sokal and Peter Sneath. His work on speciation led him to investigate the history of the species concept, and he grew interested in Linnaeus, about whom he wrote several papers. He branched out into other aspects of scientific history, ranging from Aristotle to Darwin.

Cain loved to campaign as much as he loved to argue. He had an incendiary enthusiasm for evolutionary biology, a tendency to wrathful indignation, and a deep contempt for administrators, particularly those who had once been scientists. When in 1985 he was awarded the Linnean Society’s Gold Medal, he took the opportunity to attack the current vogue for appraisal and assessment. When a paper from his doctoral thesis on the staining of lipids became a ‘citation classic’, he responded by writing a thinly veiled attack on quantitative measures of merit.

After Oxford and four years in Manchester, Cain moved to the University of Liverpool in 1968. When he became chairman of the Department of Zoology there, he circulated an edict that members of staff should come to his office or laboratory only to discuss science. Matters of administration would be settled over morning coffee or afternoon tea. He wrote a book on Erasmus Darwin that never saw the light of day, for reasons very much in character. Apparently he submitted the manuscript to a well-known publisher, whose editor said that they would be delighted to accept it, but that it contained too many quotations. Would Cain care to reduce their number? He would not. In high dudgeon he submitted it to another publisher, with the same result. After that he became exasperated and decided not to publish it at all. He put it in the university library at Liverpool, where it still lies.

His combative style and changeable moods made Cain some enemies as well as friends — which perhaps accounts for his rather late election to the Royal Society in 1989. On his good days he could charm anybody and on his bad days he could offend anybody. Nonetheless he gained the lasting respect, affection and gratitude of many students and colleagues. He had a sort of passionate innocence that was very appealing. At a meeting in the 1980s it was estimated that about 120 (40%) of those attending were his academic descendants (students, or students of students, or students of students of students). Their company included many figures who are now prominent in evolutionary biology. Few of them will forget Arthur Cain’s unique combination of enthusiasm, encyclopaedic knowledge, intelligence, encouragement, irascibility and disapproval. That particular mixture had a lasting influence on the growth of his subject.

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