Michael Locke, who died on 20 October 2013 in London, Ontario, was among the most influential insect scientists of his generation whose work illuminated insect development and cell biology. Gifted with extraordinary intelligence, restless curiosity, and quiet determination, he was able to spot crucial lacunae in our knowledge of how insects function, to identify with great precision the appropriate questions, and, using a variety of tools, provide answers that were unfailingly provocative.

Ken MacDonald

Michael Locke
(1929-2013)

Born in 1929, Locke attended Drayton Manor Grammar School in Ealing, London, England, and, after obligatory National Service in the RAF, took up a state scholarship to Cambridge, obtaining a double first in the Natural Sciences Tripos, an early recognition of his talent. He joined the growing group of students of V.B. Wigglesworth on the top floor of the Zoology Department, obtaining his PhD in 1956. He later earned a DSc for his additional work.

The three papers from his doctoral work, published in the *Quarterly Journal of Microscopical Science* in 1958, had a fresh look at the structure and development of insect tracheae. He used electron microscopy (EM) to demonstrate that tracheoles exhibit the same taenidial structure as the rest of the tracheal system and demonstrated convincingly that the taenidia arose simply as a result of physical forces generated during development. More importantly, he identified and explored an apparent paradox: although the normal developmental pattern resulted in a series of branching tubes in each segment in which the total cross sectional area after each branching remained approximately constant (an observation first made by the Danish physiologist Krogh), the system was also capable of considerable plasticity. A series of simple surgical approaches outlined the dimensions of this plasticity and hinted at the existence of both tissue gradients and blood-borne factors. These papers are still attracting citations more than half a century after publication, a clear indication of their influence.

Michael, perhaps surprisingly, took up a position at the University of the West Indies in Jamaica. Among the consequences was his adoption of the skipper butterfly *Calpodes ethlius* as an experimental model. Easily reared, the larvae are transparent, permitting the observation of events in living specimens. He used this model to explore a paradox in the secretion of the wax layer of the cuticle. The current dogma held that this layer reached the cuticle via pore canals, but often the melting point exceeded 60°C. A paper in *Nature* showed that final synthesis of the wax occurred after secretion. Note that while the solution to the paradox was important, so also was the identification, and clear statement, of the problem.

While in the West Indies, he also took up the question of segmental developmental gradients that had been raised by his analysis of tracheal growth. In two extraordinary papers, completed while on leave in Cambridge, he used clever transplantation of *Rhodnius* cuticle and underlying epidermis, to explore the effect on cuticular pattern of rotating the transplants. While the concept of developmental gradients had been in the air for many years, these papers were the first to provide an unequivocal demonstration of their existence, and launched a renewal of interest. The papers continue to attract citations.

These early papers exemplify Locke's approach that characterized all of his work. First, identify the paradox or problem, and provide a clear analysis leading to an experimental approach to solve or at least further clarify the problem. All of this is written in unfailingly clear, simple, easily comprehended prose. Indeed, these papers could easily be used in teaching about how to write in science.

During a 6 month leave in Cambridge, Locke used the EM to explore the question of wax secretion in *Calpodes*. This marked the beginning of his use of the EM as the primary (although not exclusive) tool for his research. He was still to some degree a novice, however, and he spent the summer of 1960 in the Rockefeller Institute (now University) with Keith Porter exploring the ultrastructure of insect cuticles, particularly pore canals. By the time that the paper (which still attracts citations) appeared in 1961, Michael had been recruited by Howard Schneiderman to the faculty of the Department of Biology to join a large group of developmental biologists at Western Reserve University (later Case Western) in Cleveland. Others in the group were also former students of VBW: Tony Watson, John Edwards, Peter Lawrence, Michael Berridge. This period was enormously productive and a flood of papers appeared, mostly concerned with the tracheal system or the epidermis and cuticle. It would be a mistake, however, to regard these as simply descriptive biology. In each case, the observations were directed toward a specific problem in the cellular dynamics of the insect system. At least one of these publications, on cuticulin, was designated as a "citation classic".

During this period, a new interest in the movement of protein within and between tissues developed, exemplified by a series of five papers using the fat body of *Calpodes* (including one in Science and another in Nature) with his student, Janet Collins.

In 1971, Michael was attracted to the University of Western Ontario to be chair of the Department of Zoology. It was perhaps an odd appointment, given his commitment to research, but he remained as chair for 14 years with external reviews every 5 years. During all of this time, he continued his personal research program, working personally at the bench, providing leadership by example. Given a granting system that rewards professors as managers, directing the research of others, it is a remarkable achievement. His interests in the cell biology of epidermal cells and fat body were undiminished, and papers on a wide variety of problems emerged. Of particular note are those on the beads of the Golgi complex, and the exploration of ferritin. The Golgi beads were at first challenged, informally and amusingly, by those who regarded insects as "lower" organisms and hence not particularly relevant to "real" (mammalian) cells. Michael extended the reach of his research and showed that they were observable in mouse testes.

As always, however, he remained close to the organism. An example is the remarkable discovery of the tracheal lung in *Calpodes*, stemming from his recognition that, although every cell in an insect received a direct supply of oxygen via the tracheal system, there was one exception: the blood cells. Generations of insect scientists had failed to recognise this problem. Michael did, and the transparent *Calpodes* was the ideal organism to answer the question. I suspect that I was not the only scientist to feel a little foolish for having missed that anomaly. Curiously, others have not taken up this interesting and important question. Although *Calpodes* has a specialised tracheal structure, that is not the case in all insects. The fundamental question, identified by Michael, remains: how do blood cells get their oxygen?

Michael was frequently at his best as a synthesizer of a field. Those papers, often invited, are not simply the recitation of his research, but develop new insights. The paper "What every epidermal cell knows" in the Festschrift for Wigglesworth marking his formal "retirement" in 1967 is still relevant, as is his contribution to the remarkable volume he developed with David Smith to celebrate Wigglesworth's 80th birthday 13 years later. For several years in the 60s, he served as editor of the annual Symposium of the Society of Developmental Biology and Growth (now the Society of Developmental Biology).

Like most academic scientists, he leaves the legacy not only of a body of papers (about 200 in all) and several books, as author or editor, but also a legacy of students. Among his doctoral students from the time in Cleveland were Joan Lai Fook (faculty at University of Toronto), Susan Bonner-Weir (faculty at Harvard), Joseph Kunkel (faculty at the University of Massachusetts), and Eugenia Wang (faculty at the University of Louisville). At Western, his doctoral students included Reddy Palli (faculty at the University of Kentucky), Jan Ryerse (faculty at St Louis University), Helen Nichol (faculty at the University of Saskatchewan), David Brodie (pharmaceutical industry), Tim Brac (Brac Scientific Consulting), Oana Marcu (SETI Institute), and Alan Tuck (faculty in Medicine, Western). Among the post docs at Cleveland were Michael (now Sir Michael) Berridge and Peter Lawrence, both of whom returned to Cambridge, and at Western, David Carter (UC Riverside), Cheryl Ketola (Fanshawe College) and Rob Dean (faculty, Western).

Various honours recognized his achievements: Fellow of the Royal Society of Canada, Fellow of the Entomological Society of Canada and of the Entomological Society of America, Honorary Fellow of the Royal Entomological Society, Killam Fellowship. The award by the RES of the Wigglesworth Medal and Lectureship at the International Congress of Entomology in Brazil gave him great pleasure, since Wigglesworth was his inspiration.

I think it is important that I should say something about Michael, Cambridge and Wigglesworth. Being a student in that environment was clearly a defining experience in Michael's life, as it was in mine. Certainly it changed my life. VBW was required to take on students as a condition of the Quick Professorship that he occupied. Once he was satisfied that you had selected and defined a worthwhile problem, you were left to get on with it, leaving Wigglesworth free to get on with his research, his consuming interest. This single-minded commitment to, and personal involvement in, research at the bench impressed Michael and he tried, successfully in my view, to emulate that behaviour within the constraints of a very different academic environment in North America. For students of Wigglesworth, the dissertation was YOURS, the papers were YOURS. There were no committees to satisfy, no course work required, and Wigglesworth refused to read the dissertation or drafts of the papers. But that did not imply indifference. Because I had the privilege of returning to the group as a Fellow, and because I visited VBW at least once per year until the late 80s, I was able to observe him more closely. He was certainly aware of what the students were doing, and while he would never intervene directly, he might ask about progress, implying perhaps that you had better get on with it. He also followed the progress of former students. VBW had a strong preference for students from Canada, a strategic move designed to strengthen insect science in Canada, and he took a great interest in what he referred to as his Canadian mafia. He was thus pleased that Michael had taken on the job at Western and often asked about his progress. Incidentally, Michael was the second Wigglesworthian to serve as chair of Zoology at Western. A.W.A. Brown, who was chair during my time at Western, had worked his way across the Atlantic in a cattle boat to work with VBW in the late 30s while he was still at the London School of Hygiene and Tropical Medicine.

And that brings me to Michael the man. He was, as already noted, blindingly bright, unswervingly principled and above all, rational. He set very high standards for himself (and others!): good enough was not in his vocabulary. At the same time, he was also entirely self-contained: extrovert is not a characteristic that leaps to mind. All of that sounds cold and humourless, and first encounters could be daunting or even terrifying.

He was in fact a man capable of great generosity and kindness, particularly for the young. Evidence of that can be found in the acknowledgments of his help by many authors from what might be regarded as competing labs. He was generous about recognising the contributions of others to his thinking and about authorship: his long-time assistant at Western was a co-author on many of his papers.

Although he served as chair for 14 years, he regarded most "administrators" in universities as superfluous, and he frequently turned his devastating sense of humour in their direction, often in the form of a carefully crafted bit of writing. I wish that I had retained one piece, written when he was dealing with bowel cancer. He compared the administrative process in universities to the fascination of the aged with their own digestive process: "a far too careful inspection of the product combined with an excessive use of paper". He even managed to insert a bit of invective in his address for the Wigglesworth Medal, published in the *Journal of Insect Physiology.*

Michael married Audrey in 1953, before beginning his doctoral work. They had four children. In 1980, Michael married his former student, the formidable Janet Collins, who left a position in Biology at Dalhousie to join him in London. She entered law school at Western, qualified as a lawyer, and served on the Board of Governors at Western.

He was, for a supposedly entirely logical predictable man, capable of great surprises. On one occasion, he took me after dinner to the basement where he revealed the equipment he used in lapidary. He explained that since he no longer had the time to cut sections, he found that he needed something to do with his hands. (I note that VBW produced soapstone carvings, often of *Rhodnius*). As in his science, lapidary was done at a level of perfection matched only by the best professionals. Michael was incapable of superficiality. The lapidary led him to an interest in objects fashioned from bone, and eventually ivory and horn. He developed so much expertise that he was consulted about antiquities made from these materials. Typically, his examination of bone identified some questions about the details of the accepted structure, and a paper in the *Journal of Morphology* resulted. Similarly, he investigated the structure of ivory from a wide variety of animals. That study also resulted in a paper in the *Journal of Morphology* that included characteristic sketches that clarified the apparent complexity. A book on bone, ivory and horn appeared at the end of 2013, after his death.

He and Janet shared an interest in gardening, and the garden at the back of their home in London was a perfection, whether it was dominated by flowers or, as happened suddenly, converted to a vegetable garden, including a miniature swamp, fed by run-off from the roof.

It has been, by any measure, an extraordinary life that has enriched our science, and the lives of many students. For me personally, I have often remarked that I have led a life full of good fortune and great privilege. That life has been enhanced by the privilege of having Michael Locke as a friend.

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