

Michael Abercrombie (1912-1979)

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Michael Abercrombie was born on August 14th 1912, one of the four children of Lascelles Abercrombie, a poet, who later became Professor of English at Leeds University. Michael was educated at Leeds Grammar School and at Oxford University where he read Zoology and came under the influence of G.R. (later Sir Gavin) de Beer who introduced him to experimental embryology, and J.Z. Young; (an account of these early days was given by Medawar, 1980). These contacts were to stand him in good stead in later years.

His research career began in earnest in 1934 when, having obtained a first class degree in Zoology at Oxford, he moved to The Strangeways Laboratory in Cambridge, attracted by the exciting work being carried out there by Waddington on the chick embryo. This was the time when biologists were thrilled and inspired by the great achievements of Spemann on the embryonic 'organiser'. A major technical problem had been that most of the experiments had been performed on amphibian embryos and it was not clear whether an 'organiser', or something comparable, was active also in other classes of vertebrates. But Waddington had recently developed a new technique for explanting and maintaining chick blastoderms in culture and had shown (1932) that Hensen's node (the anterior end of the primitive streak) possessed many properties in common with the dorsal lip of the blastopore, the site of the amphibian organiser. Michael was keen to explore the possibilities that had opened up. In comparison with later modifications (e.g.,

New, 1955), this original technique was a crude and difficult one and Michael received little guidance from Waddington, who was preoccupied with other activities at that time. Nevertheless, two important papers were published. Both were concerned with the effects of inserting grafts of epiblast (Abercrombie, 1937) or of primitive streak (Abercrombie and Waddington, 1937) beneath the primitive streak of another (host) embryo. The first of these led Abercrombie to conclude that all parts of the epiblast at the primitive streak stage (i.e., about stage 3 of Hamburger and Hamilton, 1951) could be induced to differentiate into neural tissue; certainly, even today, there is good evidence that most, if not all, of the epiblast has this ability.

In the second paper (Abercrombie and Waddington, 1937), he noted a series of effects of the host on the graft, perhaps the most interesting being that the anterior-posterior orientation of the graft was altered to conform with that of the host, and in both papers he drew attention to the elongation of the graft, brought about by the influence of the cell migrations of the host tissues. Some fifteen years later he followed this up with two further papers which showed that when the primitive streak (Abercrombie, 1950a) or part of it (Abercrombie and Bellairs, 1954) was removed from a chick embryo and replaced so that Hensen's node was relocated to the posterior end of the area pellucida, the head of the embryo did not develop in association with the transplanted Hensen's node; instead, it formed near the anterior end of the area pellucida,

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just as it did in unoperated control embryos. These papers were the earliest to demonstrate that the role of Hensen's node, the so-called chick organiser, was subservient to the influence of the area pellucida as a whole. They were also critical in establishing Michael's interest in cell locomotion.

In 1938 he obtained a lectureship in the Zoology Department in the University of Birmingham, where he met and subsequently married M.L. (Jane) Johnson. His interest in the chick embryo was however interrupted by the second World War. Never robust in health, he was declared physically unfit for military service and instead returned to Oxford to join a team led by J.Z. Young carrying out research on nerve regeneration and wound healing, topics of great practical importance in war time. He became particularly interested in Wallerian degeneration, publishing several papers in collaboration with M.L. Johnson and continuing with this topic when he returned to Birmingham in 1943. Perhaps the most enduring result of this period of his research is that, thanks to the influence of J.Z. Young, he came to appreciate the importance of a quantitative approach to experimental work. The collection of large amounts of data and their statistical analysis was to become a characteristic of all his future work. He was justly suspicious of conclusions based on a minimal, or even undisclosed, number of experiments. This insistence on a statistical approach, together with the rejection of all anecdotal evidence, featured largely among the important values that he inculcated into his research students.

In 1947 the Abercrombies moved to University College London, initially to the Department of Anatomy and Embryology to join his former Oxford tutors. Professor J.Z. Young had recently been appointed head of the Department, and Professor G.R. de Beer was head of the sub-department of Embryology. Michael was elected a Fellow of the Royal Society in 1958 and succeeded de Beer in 1960. Subsequently (1962), he became head of the Department of Zoology at University College London but during his last few years he returned to the Strangeways Laboratory in Cambridge, where he succeeded Honor B. Fell as Director.

During his period at University College he briefly returned to the chick embryo but soon his main interests shifted to the behaviour of cells in tissue culture. This shift is clearly illustrated by his publications which, abandoning the chick embryo, range from wound healing and nerve regeneration to the behaviour of both normal and malignant cells in culture. Yet in all these apparently disparate topics there is one unifying theme, cell locomotion and cell interaction. This move into the field of tissue culture was partly due to the frustrations he had experienced in trying to study cell migration directly in whole organisms, but also to the fact that he was enchanted by the beauty and simplicity of tissue culture. He had acquired the then current procedures whilst at the Strangeways laboratory from one of the great practitioners, Honor B. Fell. The great care and attention to detail that she demanded struck an echo in Michael's own attitude to science, and the almost ritualistic precautions that she instilled to avoid infections, were subsequently transmitted to his own students. I recall an amusing incident at University College when we were attempting to teach some undergraduates the rudiments of culturing embryos. One of them seemed oblivious to our instructions about sterile precautions and was seen to wipe his forceps repeatedly on his pocket handkerchief! After the students had departed for the day, Michael said that the only way for the boy to learn was for his cultures to become infected, and forthwith he raided the incubator, removed

the lids of that student's petri dishes and breathed hard on the preparations. Despite this, the embryos developed magnificently and did not become infected and the student was most proud of his achievement!

Among his later papers (e.g., the Croonian Lecture, 1980) he repeatedly emphasised the fact that the role of cell locomotion had not been appreciated in the late nineteenth and early twentieth centuries and that many of its effects had then been attributed to localised regions of differential mitosis. He pointed out that this misinterpretation was to some extent generated by the excitement at the end of the nineteenth century of the discovery of mitosis and also by the fact that embryologists made their deductions about development primarily from the study of fixed and sectioned material where the beauty of the mitotic spindles is apparent but the migration of cells cannot be seen. Even when time-lapse cinematic techniques were available, many scientists had ignored the extensiveness of cell locomotion in living embryos and preferred to cling to the traditional view of differential mitosis. He quotes (1977b) some amusing examples of explanations of how mesoderm cells were thought to form in the chick embryo.

The major part of his tissue culture work was carried out using fibroblasts obtained from the hearts of chick embryos incubated for 7-10 days. These were either explanted in nutrient medium as small pieces of tissue on glass or plastic (e.g., Abercrombie and Heaysman, 1953) or later as single cells (e.g., Abercrombie and Dunn, 1977). Once the fragment of tissue had settled onto the substratum cells migrated forming a halo. This useful fact had long been known to investigators studying cells in tissue culture, but Abercrombie's genius lay in his exploitation of the technique. The cells that migrate out are known as fibroblasts, but typically, in his 1976 paper with Dunn and Heath he refers to 'the fibroblast, or more cautiously, the fibroblast like cell'. Such caution is well founded for the true identity of these cells is even today not established. Michael and his collaborators tackled this difficult question in the same paper, where they state: 'There is an *in vitro* fibroblast phenotype'. In other words, the designation of a cell as a fibroblast is from its shape and general morphology rather than its molecular structure. He enquires in the same paper, 'Are the cells that emerge as tissue-culture fibroblasts equivalent, regardless of what organ they came from?' and answers his own question with, 'Unquestionably, they are not – the fibroblast of the tissue culturist is evidently a genus of many species'. This is a scrupulous point seldom made in the general literature.

Probably the most significant papers of his whole career were those of Abercrombie and Heaysman (1953, 1954a), which later culminated in the concept of 'Contact Inhibition of Locomotion' (Abercrombie and Ambrose, 1958). The impact of these papers is shown by the fact that they were so extensively quoted in years following their publication that they featured in the Current Contents Citation Index. Abercrombie and Heaysman made time-lapse films of fibroblasts migrating from the explant, examined the paths taken by individual cells and then statistically analysed the way that each cell changed direction as it made contact with other cells. The fibroblasts grew as a monolayer on glass, a situation that made the filming possible. The leading edge of each cell extended forward as a lamella and from this a ruffled membrane rolled backwards over the upper surface of the cell. They found that the path taken by each cell was initially random until it made contact with another cell; the leading edge then ceased to protrude, the ruffling stopped and

locomotion in that direction was halted. This was the process they called contact inhibition of locomotion. If a new lamella formed elsewhere on the surface the cell tended to break away and migrate in a new direction, but if a cell was contacted all around its periphery, no new lamellae could form and the cell ceased to move.

These findings on the interaction of individual fibroblasts stimulated similar analyses on the behaviour of cells at the edges of sheets of epithelial cells growing in culture (Middleton, 1982). These were also found to exhibit ruffled membranes and contact inhibition of locomotion.

Such findings would be of limited interest if they applied only to cells in culture but Abercrombie's aim was to explain how cells moved *in vivo* and how they ceased to migrate once they reached their destination. In several papers (e.g., 1967a) he proposed that contact inhibition worked just as well in the embryo as in culture. Indeed, it seemed such a valuable explanation that it has been utilised by many investigators to account for naturally-occurring cell migrations in living organisms. Abercrombie suggested that if cells in the embryo were surrounded on all sides by other cells or by basement membrane, they would not move, but that if such contacts were lost in one place the cell would begin to form lamellae and ruffled membranes and would start to migrate away from adjacent cells. This in turn would have a similar 'knock on' effect on the neighbouring cells which were now no longer surrounded on all sides and they too would begin to migrate. Such a sequence might lead to a mass migration, as in gastrulation.

How well has this concept stood the test of time? There are two questions to consider. First, do migrating cells in the living embryo put out lamellae at the leading edge and show ruffled membranes like the fibroblasts in tissue culture? This has been difficult to demonstrate because most vertebrate embryos are opaque, which makes filming difficult, but fortunately the early embryos of teleosts are transparent and Trinkaus (1984) was able to show that the deep cells of *Fundulus heteroclitus* behaved in this way. Bellairs *et al.* (1969) filmed the edge cells of the chick blastoderm migrating over its natural substrate, the vitelline membrane, and recorded similar activities, whilst Keller and Hardin (1987) using time-lapse studies of explanted segments of *Xenopus* embryos found that the deep cells underwent repetitive blebbing and retraction. In general, therefore, it appears that many cells use the same methods of locomotion *in vivo* as *in vitro* though they tend to be flatter *in vitro*, probably because they adhere more firmly to the substrate.

The second question is whether there is contact inhibition of locomotion in the embryo, as Abercrombie supposed, or whether this is just an effect displayed by cells under tissue culture conditions. Again, the clearest examples come from studies of the events in young teleost embryos, which being both small and transparent lend themselves to time-lapse filming investigations. Lesseps *et al.* (1979) showed that as the so-called 'deep' cells of *Nothobranchius korthausae* migrate away from the blastoderm they form a monolayer over the yolk mass and exhibit contact inhibition of locomotion, although after they have covered the entire yolk surface they abandon this behaviour and cease to be monolayered. Other examples were reported for *Fundulus* embryos (Trinkaus, 1984) but otherwise there appear to be few direct observations on living embryos.

Against these examples we must consider certain aspects of development within an embryo that do not slot comfortably into the concept of contact inhibition of locomotion. Apart from simple



Michael Abercrombie (left) in 1970.

epithelia, such as the endothelium of early blood vessels, few cells in an embryo are present as a monolayer so that cell-cell relationships tend to be more complex than in simple tissue culture. Even within an epithelium, where each cell is closely in contact with its neighbours, the cells are not necessarily stationary, as the rules of contact inhibition would predict, but may frequently change their position and their contacts, e.g., during shape changes in an organ, or during the elongation of the embryonic ectoderm in the later stages of vertebrate gastrulation. At the time when the concept of contact inhibition of locomotion was put forward, the importance of the extra-cellular matrix and the molecular role of the cell itself were appreciated but little understood. With our present knowledge, contact inhibition now seems too simple a concept to apply as a generalisation to cells in the embryo even though it may indeed play a role in certain specialised situations like that of teleost epiboly.

An interesting diversion from the studies on fibroblasts was the work of Abercrombie and his collaborators (especially Heaysman, Karthaus, Pegrum) on the behaviour of various malignant cell lines in culture. Malignant cells were found to behave rather differently from normal cells and not to be so strictly controlled by contact inhibition of locomotion. This initially caused great excite-

ment and, although it was never claimed by Abercrombie and his co-workers, it seemed possible that lack of contact inhibition might be the distinguishing feature of malignant cells. Alas, this turned out to be too simple an explanation, different tumour cells showing different degrees of contact inhibition (Heaysman, 1978).

Abercrombie's interest in the fibroblast was unabated however, and together with others, especially J.E.M. Heaysman, S.M. Pegrum, G.A. Dunn and J.P. Heath, he turned his attention to the nature of the locomotory process itself, publishing a series of important papers on the role of cell membranes and their ruffling activities together with the relationships between cells growing in tissue culture and their substrate. Much of this work is summarised in his Croonian lecture (1980).

Perhaps because of his early interest in embryonic induction, he was always keenly attracted by the interactions between cells. In 1959 he stated that 'Directly or indirectly it seems that all cells must influence each other, so that each is informed of its relative position in the system', an interesting forerunner of the concept of 'positional information.' But although Michael's interests were mainly on the behaviour of cells in tissue culture, it would be a mistake to think that he neglected other interesting fields. His work in collaboration with D.W. James and M.H. Flint (1954, 1956, 1957) on wound healing is still regarded as a classic, whilst his interest in liver regeneration is evidenced by his 1950 papers with R.D. Harkness.

Michael's perfectionism extended to his writing. Each sentence was carefully constructed to express precisely and concisely the meaning he wished to convey. He was fortunate in his wife, a populariser of science and a communicator of the highest order and under her influence he developed an easy style. His later writing owed much to her helpful criticisms and, for example, his 1977 paper 'Concepts in Morphogenesis' is a model of simple and stylish exposition that is a pleasure to read.

Michael's services to Developmental Biology were not restricted to his own special interests. Many overseas visitors spent sabbatical periods in his laboratory. He supervised many PhD students, including R. Bellairs, A.S.G. Curtis, G.A. Dunn, A. Middleton, D.A.T. New, T.A. Partridge and R.A. Weiss and, whilst he undoubtedly influenced and guided them, he always encouraged them to pursue their own paths. His personality was a reserved one though by no means intimidating; he was greatly loved and respected by all who worked with him.

Together with M.L. Johnson and G.J. Hickman he compiled 'A Dictionary of Biology', a task that appealed to his love of detail. He honed his skills as an editor with an innovative series, *New Biology*, thirty one issues of which were published between 1946 and 1963. Each book provided about six or seven popular accounts of topics of wide general biological interest. For example, vol. 2 contains articles on rodents as pests, sewage disposal, whales, micro-organisms, weeds in cornfields, bat radar and wound healing in a cut finger. *New Biology* was immensely and deservedly popular at a time when few popular science publications were available.

In 1949 he was a founder member of the Embryologists' Club, a small group of enthusiasts drawn from the colleges and medical schools of London University, which met regularly for the presentation of seminars. Later he played a major role in transforming this club into the present British Society of Developmental Biology, so helping to bring together developmental biologists throughout the British Isles and beyond.

His editorial experience stood him in good stead when he later undertook more specialised editing. In 1953 he played a central

role in the founding of the *Journal of Embryology and Experimental Morphology* (renamed *Development* in 1987) and was its first editor. This journal has always been primarily a vehicle for the publication of original research, but Michael, sensing the need for a journal specialising in reviews of a developmental nature, was instrumental in establishing 'Advances in Morphogenesis' and, together with J. Brachet, edited the early volumes. It is difficult to over-emphasise the importance of these developments in the early post-war years. Specialist meetings were then hardly known but the editorial board of the *Journal of Embryology and Developmental Morphology* introduced and supported the idea of embryological conferences, not only in Great Britain but also throughout Europe. In those days, when international collaboration in embryological research was infrequent and international travel mainly the prerogative of the distinguished minority, the importance of the role of the *Journal of Embryology and Experimental Morphology* in enabling junior research workers to make contact with colleagues both abroad and in this country cannot be too strongly stressed.

I have concentrated in this account entirely on Michael Abercrombie's scientific life, but music and literature also played an important part. He took a keen interest in politics though always retained a strong sceptical attitude to it.

I think it is true to say that Michael was an 'ideas' man rather than a dedicated bench worker. Though a most careful and painstaking experimentalist he was happiest at his desk or slumped in an armchair with a pile of journals around him. His knowledge of the literature was outstanding. I visited him during his last illness shortly before he died and found him engrossed in the latest issue of *Current Contents*, marking off the papers he still hoped to read.

A series of scientific conferences bear his name. The first (Bellairs, Curtis and Dunn, 1982) was held shortly after his death and had originally been planned to mark his retirement, but this has been followed by others, the fourth and most recent in 1997. Michael was a modest man and would have been astounded that his name should be honored in this way nearly twenty years after his death, many of the participants being too young to have ever known him.

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