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Elected F.R.S. 1955

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ARTHUR RAMSAY was born in 1909 in Ayrshire and died with his wife on a train from Inverness to London on 5 February 1988. What he achieved in his lifetime strongly affected those who knew him and what he was and what he stood for will continue to affect us. He revolutionized comparative physiology by showing how tiny structures, organs and organisms could be handled, kept alive and analysed. He delighted in devising methods, instruments and tools for doing this and took the process on one stage further and made, for example, the machines that allowed extensive analysis of minute drops of fluid, and scissors with which one could cut open a single cell. From the results he produced with the help of this technology, he was able to provide detailed explanations of how the excretory systems of several invertebrate animals function. Building on this he came to profound insights into the functional organization of these systems; his general conclusions underlie all the modern work in these areas. He raised his eyes still further from detail and reflected on a whole range of physiological problems in animals; especially in his book, written in 1952, *A physiological approach to the lower animals*, still today remarkable for its insights and for its clarity of treatment and for the way it leads the reader to focus on fundamental questions. In his wrestling with the physics of the processes he studied, he became impatient with the way that thermodynamics was presented: he found that for a biologist the subject was very difficult to approach. His typical response was immediately to do something about this and he wrote, in 1971, *A guide to thermodynamics*, which, without losing the necessary rigour, makes large tracts of this formerly inhospitable land possible to explore for people trained to think as biologists. As an accompaniment to all these pioneering endeavours, he lectured on many aspects of zoology, armed with the conviction that any zoological subject could be absorbed and presented clearly and accurately by anyone who was appointed to a university lectureship. Not only did he lecture, but he edited for 21 years, the leading journal in comparative physiology, *The Journal of Experimental Biology*.

However, for many of us that knew him, the greatest effect he had on us came from his uncompromising, honest, direct and unswerving way of dealing with everything and everybody. This affected not only the way we did our science but for those with eyes to see and ears to hear there were clear lessons for dealing with difficulties and deciding priorities in all parts of life.

Arthur Ramsay was born in Barns Terrace, Maybole, Ayrshire on the 6 September 1909, the eldest of three children. His father, David Ramsay was a boot and shoe manufacturer in the family business, James Ramsay and Co. Ltd of Maybole. His mother was Isabella Rae Ramsay (née Garvie) daughter of R.G. Garvie, agricultural implement manufacturer from Aberdeen.

Arthur Ramsay later felt that his scientific life really took off when he went to Edinburgh University at the early age of 16. But he had been pointed this way early on, particularly by his mother, who took the view that he should be given every possible opportunity of escaping from the prospect of the family business, so he enjoyed part-time instruction at home until he was eight. He was then sent to Cambusdoon Preparatory School at Ayr for five years and on to Fettes College, Edinburgh, for three years until he was near his 16th birthday. It was clear by then that Ramsay's interest was in science but at that time science played a minor role second to Classics at Fettes. So his parents, wisely, took him from school and sent him for two years to Edinburgh University, preparatory to his going off to Cambridge.

His main subject at Edinburgh was to be chemistry, and also he took physics as a matter of course. But as he felt he could not face mathematics, he had to choose between botany, geology and zoology. His reasons for preferring zoology were typically practical. Botany was ruled out as the summer term classes began at 8.00 a.m. and Geology because it offered the prospect of carting loads of rock about on his back! So *faute de mieux*, and eventually to the great benefit of the subject, he settled on zoology. He found chemistry and physics difficult but in each of his two years he won the Class Medal in Zoology, towards which his main interest naturally gravitated. He was much encouraged in this by the then Professor of Zoology, Sir J.H. Ashworth, F.R.S. A fortunate circumstance put him in zoology classes with Stephen Whittaker, third son of Professor Sir Edmund Whittaker, F.R.S., and Lady Whittaker. They became close friends and he came to have the freedom of the Whittaker household and often stayed there. This was his first contact with an academic family and he subconsciously absorbed the academic outlook and tradition which permeated the happy and charming family circle. He was touched by the simplicity and informality of their way of life. Men of great distinction were always coming and going, with no fuss made. He once found himself sitting next to Sir Arthur Eddington, F.R.S., at lunch and they ate only stewed prunes!

Towards the end of Arthur Ramsay's second year at Edinburgh, Sir Edmund became disturbed by the idea that his son and his friend would shortly go up to Cambridge, completely ignorant of calculus. So he proposed to give them a personal course of instruction and since he was a gifted teacher, young Ramsay found it a most inspiring experience. During the last week or so, the course took on a puzzling direction which Arthur could follow but without any very clear idea of what it was about or where it was leading. Only 30 years later did he realize that it must have been thermodynamics. Perhaps, this in turn, was part of the stimulus for him soon to write his book on thermodynamics.

Although zoology sustained him and physics was useful, he turned against chemistry, again for decidedly pragmatic reasons. Edinburgh chemistry exams always involved attempting four questions, one of them a numerical problem. For the latter, if one reached the correct answer one got 25 marks; if, however, one worked out the problem with sound logic but through arithmetical error (even in the last line) got the wrong answer, one got no marks. Ramsay reckoned that inaccuracy with figures plagued him all his life (though signs of this never appeared to us who read his papers or heard him lecture). In all six chemistry examinations he sat while at Edinburgh, he worked out the numerical problems the right way but came to wrong answers. Not surprisingly, this galled him so much that he went off to Cambridge firmly resolved not to have any more to do with chemistry.

He went up to Gonville and Caius College, Cambridge, in October 1928. This choice of College was an outcome of a lifelong friendship between his mother and Professor A.B. Soutar, F.B.A., sometime Fellow of Caius. At Caius, Sir William Hardy was Director of Studies in Natural Sciences. Ramsay said he wanted to read Zoology and also Physiology; Hardy naturally agreed to these. However, he proposed chemistry as the third subject. Ramsay replied that actually he would prefer botany, for the unrevealed reason that it would not entail solving numerical problems in examinations. Apparently, Hardy was rather a towering personality and he put, strongly, several telling arguments in favour of chemistry. I find it no surprise, however, that Ramsay's typical resolve did not waver; so chemistry lost an opportunity from the intransigence of its examiners in Edinburgh.

His first two years in Cambridge passed relatively uneventfully; physiology captured his interest but he also became aware of a subject called 'Experimental zoology' and he came to think that this was where his future lay. Work apart, he was making life-long friends and, in vacations, indulging in the thrills and joys of mountain climbing. Then in 1930 he took Part I of the Natural Sciences Tripos in Zoology, Physiology and Botany, was placed in Class I and awarded an exhibition of £40 per year; he could at last feel he was beginning to free his parents from the financial burden of his education.

A whole new world opened up to him in Part II Zoology. Quite suddenly he came in sight of the frontiers of the subject; no more grinding at text books, from then on his reading was to be of original papers. He found this wonderfully exhilarating and felt himself floating on a cloud of excitement and euphoria, inspired by the personalities he then came to know. The Professor of Zoology was then J. Stanley Gardiner, F.R.S., whom Ramsay found very good to him, but at times so unpredictable, even puckish, that he never felt completely at ease in his company. The two main influences on him were Carl Pantin and James Gray both FF.R.S. and both, later, occupants of the Chair of Zoology. Carl Pantin was, for Ramsay, the most inspiring teacher he ever knew, bubbling over with boyish enthusiasm, a lovable person, never more so than in his latter days. Of James Gray, Ramsay felt that to him more than any man he owed his academic career. More than that and perhaps because he was an expatriate Scot – though sometimes a dour one – they became closer and closer friends. Although he did not have Carl Pantin's sparkle, he was warmly encouraging and as Ramsay came to know him better, he greatly admired his strength of character and soundness of judgement. Later Ramsay and his wife numbered James Gray and his wife among their very closest friends. Of his contemporaries he found Lawrence Picken, scientist, scholar and musician to be the most versatile and gifted man he knew.

He took Part II in Zoology in 1932 and was again placed in Class I. He was awarded on the strength of this a studentship of £150 per annum by Caius, later supplemented by a research grant from the DSIR. His rock climbing had meanwhile flourished and he was secretary of the University Mountaineering Club in 1931–32.

After his undergraduate career ended, he became a research student under the supervision of James Gray. He chose to work on the evaporation of water from animals, from the list of suggestions that Gray made. He set out to build the apparatus and begin to make experiments. About once a fortnight, Gray would put his head in at the door and ask 'Are you all right in there?'. On replying that he was, Ramsay usually got the answer 'Good', and Gray would go on his way. One day, however, Ramsay was in trouble and Gray came in and listened to the problems. A few days later a card came from Sir Geoffrey Taylor, F.R.S., who wrote, 'I hear you have a problem with evaporation. Come and have tea at my house on Tuesday and we will discuss it'. That was Gray's way: leave the student on his own until he got into difficulty, then send him straight to the top.

The results of Ramsay's work on evaporation were published in two papers. Ramsay felt the first one, which had to do with the significance of air movement in the design and interpretation of experiments on evaporation, was the more important. But the one which aroused more interest described how a layer of grease on the cuticle of the cockroach critically limited the evaporation of water. This discovery was accidental. Ramsay had set up a cockroach to be placed in his wind tunnel when 'incautious use of a tap' caused it to be exposed to a fine spray of water. To his disgust there were minute droplets of water both on the cockroach and on its mounting and he waited for them to dry off. The drops on the mounting quickly evaporated but those on the cockroach refused to disappear. So Ramsay looked at the recalcitrant drops under a microscope, saw interference colours on their surfaces and quickly deduced that there must have been a film of grease covering them. Pasteur said that fortune favours the prepared mind. Arthur Ramsay reckoned however that his mind was not prepared, that the discovery was purely a lucky accident and that instead fortune favours the fortunate. We may disagree with this conclusion! However, it has to be said, that at least he did not take the discovery very seriously and did not follow it up. It was V.B. Wigglesworth, F.R.S. (later Professor Sir Vincent Wigglesworth and still at work in the Department of Zoology at the age of 92) who perceived its possible importance and he and J.W.L. Beament, F.R.S. (later Sir James, sometime head of the NERC and Professor of Applied Biology) demonstrated its generality and explored its mechanism. One reason why Ramsay did not exploit his discovery was that, as he was later to admit, he was getting bored with evaporation and his thoughts had turned towards neuromuscular physiology. He had his eye on a nerve–muscle preparation from the snail which he thought it would be profitable to work on. He developed the preparation, published a paper describing it, spent three years accumulating a mass of data from it and found he could interpret very little of it. Characteristically and bluntly he concluded that he had got nowhere.

However, in these three years that he felt he had largely wasted, all sorts of other things happened to him and they may have taken away from his ability profitably to pursue his research. Even before he had finished his Ph.D. work he was, in October 1934, appointed University Demonstrator in Zoology. He claimed that this was due to the recommendations of James Gray and Professor Stanley Gardiner and to the fortunate circumstance that a benefaction had come from the Rockefeller Foundation to the Department of Zoology which made possible new appointments. He felt he was once again lucky to be on the market at just the right time. Perhaps so, but we, with hindsight, can see that he was a very marketable commodity. Hard on the heels of this first appointment came his appointment to a Fellowship at Queens' College and to a College Lectureship there in Zoology. And, although he felt that his research on snail neuromuscular physiology had been of very little value, he was in October 1937, elected Hardinge Lecturer in Experimental Zoology in the University and had been made Director of Studies in Natural Sciences at Queens' and also College Steward. With his promotion to University Lecturer at the age of 28 he felt he had his foot firmly on the academic ladder.

One is struck to read of his feelings of delight or despair with intellectual matters and at the same time to hear his matter-of-fact practical realization and satisfaction at the financial consequences of his advancement in the academic world. Perhaps this came from his roots in Scottish commerce and from his early experience with people of strong intellectual leanings.

Anyway, he records that he now felt secure enough to contemplate marriage. And, in July 1939, just before the outbreak of World War II, he married Helen Dickson in Stockholm. She was the daughter of Oscar Charles William Dickson of Stockholm, nephew of Friherre (Baron) Dickson, patron of arctic exploration, and of Amelie Elisabeth Dickson, daughter of Gustar Löwenhjelm, Lord Chamberlain of the Swedish Court. In fact the Dicksons had emigrated to Sweden in the first decade of the 19th century from Montrose in Scotland, had prospered exceedingly and married into the Swedish nobility. His feelings of joy at his marriage, too personal to be included here, again illustrate the diverse apparently incompatible, parts of Arthur Ramsay's character: the extremely romantic and warm, yet intensely practical man with a keen eye for securing a safe financial basis for himself and his family. Food for thought.

Further involvement with zoological interests were promptly ruled out by the outbreak of war. Ramsay enlisted in an anti-aircraft battery, but at the beginning of 1940 he was sent to Watchet to be instructed in radar. By the early summer he was posted to the Coast and Anti-Aircraft Defence Experimental Establishment, at first in the Isle of Wight, later in Llandudno in North Wales. His army career, which ended with him as Major R.A., he felt to be unheroic but both profitable and interesting. Profitable because he acquired the rudiments of electronics, and interesting, as this was a relatively new field in which theory was lagging behind observation so that one did not need to be a physicist to make a contribution to it. M.V. Wilkes (later F.R.S.) was one of his colleagues and, after the war, they published a joint paper on the performance of radar on ship targets. In 1945 he was made M.B.E.

Readjustment to University life after the war was more difficult than Ramsay expected. He knew what reading to do to catch up but had no idea as to where he should direct his research effort. He had no wish to pursue snail neuromuscular physiology any further and so he spent the better part of a year casting around before he decided to settle on the osmotic relations of the earthworm, in some ways harking back to his earlier studies on water loss in organisms. It was also at this time that he became associated with the *Journal of Experimental Biology*, first as editorial assistant to James Gray, then as joint editor with him and later as joint editor with V.B. Wigglesworth.

Ramsay's work on earthworm osmoregulation naturally directed his interest to the role of the nephridia. He needed to measure the osmotic concentration of fluids in the lumen of these structures. The Hill–Baldes thermal method, which he had begun by using, needed about a microlitre of fluid and did not seem capable of being adapted to a significantly smaller scale; the freezing-point method was held to be unsuitable for small volumes because of the latent heat of ice formation and the difficulty of inducing nucleation. Crucially it occurred to him that the latter difficulty would disappear if he observed the melting-point instead of the freezing-point. Further, if he made the sample smaller, the more rapidly would thermal equilibrium be achieved and the less would the latent heat protract the observation of the melting-point. Almost at a stroke he was able to reduce the volume of the sample by 10 000 times. He soon made a machine to use these ideas, copies of which a whole generation of physiologists used to measure osmotic concentrations of tiny drops of fluid. Similar lines of thought and the way he could translate those thoughts into working, easily used devices were extremely impressive and essentially revolutionized research on the physiology of small organisms, tissues and organs. Even here, however, he showed a slightly pessimistic, fatalistic streak which is difficult to reconcile with the success of many of his battles with problems of measurement. He came to think that he had been extremely fortunate in the first stage of developing, what later we called the Ramsay Osmotic Pressure Machine, memories of which, with its liberal use of alcohol and dry ice, come easily and happily to mind. To measure the temperature at which his samples melted he used a Beckmann thermometer, one of three in the department's stores. It worked beautifully. Much later he had occasion to use a second Beckmann which gave very poor, inconsistent results; so also did the third. He later asked many users of these thermometers whether they also had encountered the phenomenon; none had. He was haunted by the thought of what might have happened had he started with one of the unreliable thermometers, and wondered again whether Pasteur was right in supposing that fortune favoured the prepared mind or was much more random in distributing its favours.

He was by now committed to work in the field of salt–water balance and osmoregulation. With a method able to measure one of the relevant parameters on samples in the nanolitre range, he was soon on the lookout for others. The flame photometer, then coming on the market, made it possible to determine the quantities of sodium and potassium in drops, down to about 1 μl. By Ramsay's standards this was extremely extravagant of fluid. Again a wonderfully simple idea came to him. Instead of measuring a steady emission of light as fluid is steadily introduced into a flame, why not devise a method to collect and measure all the light available from a sample. He excitedly took this idea off to the Cavendish Laboratory, to Dr S.W.H.W. Falloon and Dr K.E. Machin. Ken Machin was later to transfer to the Zoology Department and help illuminate, with mathematical and physical methods and in characteristic style, much of the new research going on there. Ramsay remarks that he believed that the willingness of physicists and chemists to put their precious time at the disposal of biologists was unique to Cambridge, probably a spin-off from the College system. Anyway, his two new colleagues thought that something might be done and sent him away to await progress. A week or two later he was bidden to the Cavendish where an ancient spectrometer stood smothered in brown paper and was connected to an untidy group of electronic components on the bench beside it. As a test, they took a platinum wire, dabbed it on the tongue and held it in a bunsen flame in front of the apparatus. There was a short burst of light and a meter sprang from a zero reading to a new higher steady level. 'Would this be of any use?' he was asked. He took it off there and then and set himself to work it up into a serviceable method. With the benefit of his war experiences with electronics he developed and built the rather complicated electrical side of the apparatus with his own hands; any faults that appeared he could therefore quickly rectify. The machine worked well and he could easily measure both sodium and potassium simultaneously on a nanolitre sample. To round off this series of micromethods he developed a very simple and elegant method for determining chloride in similarly small nanolitre samples. Dr R.H.J. Brown was a most helpful collaborator in the development of all these micromethods; he had the enviable gift of seeing how best ideas could be turned into functioning hardware.

With this arsenal of micromethods available, the purposes to which they could be put were almost without limit. One might have thought that he would have taken on a research group or a series of research students to help gather in the harvest of results, while he set about organizing funding and collating their results. But he always saw his research as a personal contest between himself and his problem. He could, just about, have accepted the services of a purely technical assistant and, on occasion, did collaborate with colleagues, but he was never willing to stand back and watch someone else getting to grips with an opponent he considered as his own.

His chosen opponents were the Malpighian tubules of insects. These are long slender tubes whose walls are one cell thick; they secrete a steady flow of fluid into the alimentary canal which further processes this fluid before it is eliminated. He soon developed a method, used to this day, of isolating tubules into drops of physiological saline under liquid paraffin on a wax base. He found the tubules would secrete fluid if the saline were mixed with insect blood and so he could analyse this fluid and compare it with the composition of the bathing fluid. He could also measure its rate of production and, by using microelectrodes, measure the trans-epithelial electrical potential difference. There followed a stream of papers, mostly using the tubules from the stick insect, *Dixippus* (now *Carausius*) *morosus*. He showed that the tubules produced an almost iso-osmotic fluid, much richer in potassium than the bathing saline, and did so at a rate dependent on the potassium concentration of the bathing saline (almost no fluid was secreted in potassium-depleted media). He found that the lumina of most tubules was at a potential positive to the bath, so it was clear that potassium transport into the lumen moved, thermodynamically, very much uphill. Potassium transport, he showed, was the driving force behind the secretion of fluid. Virtually all of the remaining wide range of solutes that he measured showed a concentration in the secreted fluid less than that in the bathing medium. To his surprise, even useful compounds such as sugars and amino acids appeared in the secreted fluid. From this he came to one of his more insightful general conclusions: all excretory systems have to allow solutes from the blood unselective entry into the primary excretory fluid, as only in this way will toxic compounds not previously encountered be automatically eliminated. He clearly saw that there had to be further selective recovery of useful materials from the flow of excretory fluid before its elimination and showed that this had to occur in the insect hindgut. This picture of how

Malpighian tubules operate has since been refined and added to, but not fundamentally altered, and Ramsay's views about the essential features of excretory systems are still as valid as when he formed them.

His last serious paper on insect Malpighian tubules appeared in 1958. There was still, he felt, a very great deal that he wanted to do but a difficulty stood in his way. As first observed by V.B. Wigglesworth, Malpighian tubules do not survive well in artificial media, so that in all his work Ramsay had to use media which incorporated at least some insect blood and were therefore not completely defined. He set out to isolate, or at least concentrate the factor necessary for functional survival of the tubules but, for once, as he would have put it, fortune did not go with him, and after three years of effort he decided to admit defeat. With hindsight it was unfortunate that I did not discover until 1963 the potent diuretic hormone of *Rhodnius*, one of the insects that he had worked on. But by this time he had taken up a much more ambitious project and did not turn back.

He resolved that if failure was to be his lot – it is remarkable how the fear of failure haunted and drove him on – then he would fail on some problem that was really worthwhile attacking. He chose to study the rectal complex of the mealworm which he saw as a real challenge. The story of his success in unravelling how this very impressive system can perform the feat of extracting water vapour from air at relative humidities as low as 88%, is fascinating. The picture that finally emerged is intricate, beautiful, immensely pleasing and intellectually satisfying and remains an absolutely classic instance of investigation in comparative physiology.

What he found was that the last part of the hindgut in the insect is closely invested with a set of six Malpighian tubules, each tightly meandering its way along the outside of the rectum. Holding these on to the surface is a thin tunic consisting of many extremely flattened cells, their cell membranes making the structure almost impermeable. There are serially repeated openings in this barrier, where the underlying tubules have direct contact with the surrounding haemolymph. The particular small cells (called leptophragma cells) that occupy these openings are extremely modified and very thin (only 0.25 μm deep). He found that through these leptophragmata potassium chloride is taken up at *very* high concentration (up to 3 $\mathrm{mol\,l^{-1}}$) but very little water enters. These very high concentrations of KCl in the tubular lumina draw water osmotically from the space round the rectum in which the tubules lie. A special protein there, acting as an osmotic filler, becomes concentrated and passes on the osmotic drying effect to the contents of the rectum, drying completely the fluid that enters the anterior end and extracting water vapour from air admitted at the posterior end. Because of the uptake of water vapour from this air, the entire insect can gain water whenever it needs to (provided the surrounding air is moister than 88% relative humidity).

With this successful elucidation of the complex and involved workings of the cryptonephridial system of *Tenebrio*, Ramsay reached retirement age. His attitude to this was most revealing; retirement had come not a moment too soon, he thought. In his early days he had been free to devote himself exclusively to research and, broadly speaking, that was all he asked of his life as an academic. Increasingly, however, he found that he had to recognize that other duties and responsibilities had to take precedence. Research became more and more a part-time activity, to be pursued on Saturdays and Sundays when he could hope to be free from interruption. He found it increasingly difficult to retain what he had read and he felt he had lost touch with everything except his own immediate problem. Enthusiasm had been replaced by frustration. He went on trying to do research because he felt he could not admit to himself that he was no longer up to it. Retirement gave him an acceptable reason for giving up. He asked me to read his final paper and to give my comments on it. He agreed with my suggestions but said that he did not propose to change what he had written because it was his last paper and he lacked the spirit to work on it further. So it was with relief that he entered retirement, left science and went off, as he put it, 'to build a road to a croft in the Highlands'. As proprietors of the *Journal of Experimental Biology* we tried to persuade him to take a free subscription to the journal, but he would have none of it. He wanted to change his goals completely so we came to the happier solution of sending him a bottle of Glenmorangie Malt Whisky from time to time! To the Department he left, as an irreverent parting gift, a year's subscription to a highly popular magazine which delighted or embarrassed users of the Department's communal tea room!

Ramsay worked continuously until two years before his retirement, without taking any of the sabbatical years away that others take. Discovering that the University regulations forbade him taking his last year as sabbatical, and very practically wishing to try out his scheme to become a crofter on retirement, he spent his penultimate year in the Highlands. He returned convinced that his plans were sound and as soon as possible he left for his croft at Abriachan in the hills above Loch Ness, and spent 12 very happy years there.

During his later scientifically active years in Cambridge, he was successively appointed as Reader in Comparative Physiology (1959) and, in 1969, to the pleasure of those that knew of the quality of his work, he was made Professor of Comparative Physiology (*ad hominem*). Later still, his College, Queens', recognized his achievements by electing him to an Honorary Fellowship (1977).

During his academic career, Arthur Ramsay concentrated first and foremost on research and because he enjoyed teaching (he tried hard to give value) he took an active role in lecturing in many different courses. Apart from these activities which, because they involve the generation and dissemination of new knowledge, are central to academic matters, he did (in his own eyes) relatively little. He did act as administrative officer for the Department of Zoology under James Gray for many years but this, like the editorship of the *Journal of Experimental Biology*, he undertook to supplement his income and because it could be done in his own time. He was happy to serve his College in the offices of Director of Studies, Steward and Vice-President, but he never wanted a position of authority. Above all he wished to avoid taking responsibility for the welfare and career prospects of other people, for this, he felt, would have made him a slave to his own conscience and would have bowed him to the ground. Shortly after he was elected to a Fellowship at Queens', he was pressed to become a tutor, but rather than take this post he offered to resign his Fellowship.

He never allowed his name to be put forward for election to the Presidency of Queens' or to the Chair of Zoology. He did allow himself to be persuaded by James Gray, against his own inclination, to chair a government sub-committee on the hazards to the aquatic environment of radio-active fallout; but after two years, he decided it was a waste of time and withdrew.

Election to the Fellowship of the Royal Society was never a goal that he consciously set himself to achieve, but when it came it meant more to him than he could say. Most of all, he felt it was a reassurance that what he had set out to do in research had been endorsed by the scientific community. And when he walked through the Society's rooms and passed the portraits of the great men of the past, it thrilled him to feel that he had been considered worthy of admission to a company of which they too had been members. It also gave him great pleasure to be elected to an Honorary Fellowship of Queens' College and he was surprised and delighted when his scientific friends presented him with a Festschrift entitled 'Transport of ions and water in animals'. We who contributed to this latter were greatly relieved at his reaction; he hated any fuss to be made over him.

To today's more frenetic generation his output of scientific papers might seem sparse. But a high proportion of his papers were seminal; the sort of papers one keeps returning to, both for the detail and for the general conclusions. It is probably safe to say that anyone setting out to investigate the physiology of an organ or tissue from a small animal (particularly an insect) would be a fool not to consult Ramsay's papers. There he would almost certainly discover useful techniques and important guidelines as how best, in general terms, to grapple with his problem.

One of the most impressive things about Arthur Ramsay was his gift for writing. For example, he wrote his book, *The experimental basis of modern biology*, as a single draft! The results of his writing seemed so effortless. I recall with pleasure seeing proofs of my own papers appearing in the *Journal of Experimental Biology* and being pleasantly surprised at how well I had written them. But on comparing the proof with my original typescript, I soon discovered what had happened; the Ramsay magic had been applied to what I had written, superfluous words removed, inelegant ones replaced, tortuous passages straightened and the result immeasurably improved. It always appeared (and I suspect it was so) as if he had spent just ten minutes on the job. There was never any improvement to be made on his corrections; his aim was unerring.

It was this quiet and effective skill that kept happy a whole generation of authors who wrote in the *Journal of Experimental Biology*. Mind you, if you consulted him at an earlier stage in your writing, you could get unconventional and fairly blunt advice. Dr Helen Skaer recalls him weighing 'Introduction' and 'Discussion' sections of her paper, one in each hand, and telling her to cut the 'Discussion' by half. The same bluntness could be applied to a manuscript before acceptance. My first paper came back from the Journal with a note from its other editor, Sir Vincent Wigglesworth, in which Ramsay is quoted as saying that he hated to see such good work so poorly presented. Sir Vincent added that he was bound to agree. Characteristically, there were suggestions for improvement which helped the paper and indeed has helped me in my subsequent writing. I suspect many scientists who published in the Journal could tell of lessons in writing they learned at his hands.

Stories about Arthur Ramsay abound. Any two biologists, who knew him, on meeting one another will inevitably compare their favourites. It would be easy to run on for pages. I can hear his editorial pen preparing to slash any such attempt!

He believed that the brain worked better at low temperature so he kept his rooms in Queens' virtually unheated. Unfortunately this slowed up the rest of his body so he acquired an electrically heated pilot's suit from World War II. This typically neat solution backfired on him when, on one occasion the suit set itself on fire. The Professor of Sanskrit next door, called on the College porters to put it out.

To concentrate the minds of undergraduates on their responsibility to come prepared with questions to discuss for supervisions with him, he would let the unprepared dry up and then sit in stony silence dropping a coin every ten seconds or so into a metal waste paper container to impress on them how much their silence was costing them.

Arthur Ramsay loved to play the bagpipes. However, recognizing that not everyone shared his tastes, he would practise his playing at 5 a.m. He reckoned that anyone awake at that time would already be feeling so bad that the noise of the pipes would not make much difference.

As he liked to construct his own equipment he was often to be found in the Zoology Department's workshops. People who did not know him, were amazed when they met what they thought was a laboratory assistant, dressed in a ragged filthy laboratory coat, with glasses perched on the end of his nose and the colourful invective that followed deflections from steady progress. Of course, they were even more struck when they found out who he actually was.

In spite of what many thought to be a crusty exterior, he was actually a very warm person when the crust was broken, and there are many stories of his great generosity to colleagues and to students.

What will live longest in the minds of those that knew him, I suspect, was the way in which he would fearlessly and directly do whatever he thought was the right thing. He took very little account of what others might think of such directness – though of course in arriving at what he proposed, he took advice from his friends and colleagues and he was very rarely unkind – but once decided, he would proceed with great sureness and firmness. Good things got done.

This method of facing up to problems and dealing with them carried through to and indeed contributed to the end of his life.

He and his wife, Helen, at the ages of 78 and 76 respectively, had become increasingly aware that their health was irreversibly declining. Arthur had worsening arthritis and could no longer play the bagpipes and found more and more difficulty in doing the routine maintenance jobs on the home they had created from a crofter's cottage. Worse, he found his mind going, leaving him often confused and forgetful. Helen Ramsay's health was also deteriorating.

One can easily understand their response to this distressing decline. They quietly decided to bring their lives to an end. And, because of how they ran their lives, they planned this over four months. First they had their elderly labrador dog put down (it had been suffering from cancer). They cancelled newspapers, arranged for detailed instructions as to how they wanted the whole range of domestic and financial matters to be settled. They sent registered packages to their children with letters for relatives and friends, and explained to their neighbours that they were going away for a few days. On the evening of Thursday, 4 February 1988, they made their way to Inverness and took the evening sleeper train to London. They were discovered next morning dead from poison they had taken. With them were letters for their two children explaining their actions, also an explanatory note for the police and one addressed to the steward apologizing for his inevitable distress.

By taking their lives on a train, the Ramsays made sure that their end was clean, that the shock to their relatives and friends was minimized and that they would immediately be put into official hands. How typical of them that all this should have been done with such directness, such careful attention to detail and such consideration of the effects of their actions on others.

We that knew them are left sadly accepting their decision; their best memorial is that many people will examine the way they run their own lives and apply some of the same criteria to them.

Near the end of his life, Arthur Ramsay concluded that, all in all, life had treated him better than he had any right to expect.

BIBLIOGRAPHY

(1) 1935 Methods of measuring the evaporation of water from animals. *J. exp. Biol.* **12**, 355–372.

(2) The evaporation of water from the cockroach. *J. exp. Biol.* **12**, 373–383.

(3) 1937 (With S.M. MANTON) Studies on the Onychophora. III The control of water loss in Peripatopsis. *J. exp. Biol.* **14**, 470–472.

(4) 1938 (With C.G. BUTLER & J.H. SANG) The humidity gradient at the surface of a transpiring leaf. *J. exp. Biol.* **15**, 255–265.

(5) 1940 A nerve–muscle preparation from the snail. *J. exp. Biol.* **17**, 96–115.

(6) 1946 The vertical distribution of radar field strength over the sea under various conditions of atmospheric refraction. Report of Conference on Meteorological Factors in Radio-wave Propagation at Royal Institution. 8 April 1946.

(7) (With M.V. WILKES) A theory of the performance of radar on ship targets. *Proc. Camb. philos. Soc.* **43**, 222–231.

(8) Role of the earthworm nephridium in water balance. *Nature, Lond.* **158**, 665–666.

(9) 1949 The osmotic relations of the earthworm. *J.exp. Biol.* **26**, 46–56.

(10) A new method of freezing-point determination for small quantities. *J. exp. Biol.* **26**, 57–64.

(11) The site of formation of hypotonic urine in the nephridium of *Lumbricus. J. exp. Biol.* **26**, 65–75.

(12) 1950 Osmotic regulation in mosquito larvae. *J. exp. Biol.* **27**, 145–157.

(13) The determination of sodium in small volumes of fluid by flame photometry. *J. exp. Biol.* **27**, 407–419.

(14) 1951 Osmotic regulation in mosquito larvae: The role of the Malpighian tubules. *J. exp. Biol.* **28**, 62–73.

(15) (With S.W.H.W. FALLON & K.E. MACHIN) An integrating flame photometer for small quantities. *J. scient. Instrum.* **28**, 75–80.

(16) 1952 The excretion of sodium and potassium by the Malpighian tubules of *Rhodnius. J. exp. Biol.* **29**, 110–126.

(17) *Physiological approach to the lower animals.* Cambridge University Press.

(18) 1953 (With R.H.J. BROWN & S.W.H.W. FALLOON) Simultaneous determination of sodium and potassium in small volumes of fluid by flame photometry. *J. exp. Biol.* **30**, 1–17.

(19) Exchanges of sodium and potassium in mosquito larvae. *J. exp. Biol.* **30**, 79–89.

(20) Active transport of potassium by the Malpighian tubules of insects. *J. exp. Biol.* **30**, 358–369.

(21) 1954 Active transport of water by the Malpighian tubules of the stick insect *Dixippus morosus* (Orthoptera, Phasmidae). *J. exp. Biol.* **31**, 104–113.

(22) Movements of water and electrolytes in invertebrates. *Symp. Soc. exp. Biol.* **VIII**, 1–15.

(23) 1955 The excretory system of the stick insect *Dixippus morosus* (Orthoptera, Phasmidae). *J. exp. Biol.* **32**, 183–199.

(24) The excretion of sodium, potassium and water by the Malpighian tubules of the stick insect *Dixippus morosus* (Orthoptera, Phasmidae). *J. exp. Biol.* **32**, 200–216.

(25) (With R.H.J. BROWN & P.C. CROGHAN) Electrometric titration of chloride in small volumes *J. exp. Biol.* **32**, 822–829.

(26) 1956 Excretion by the Malpighian tubules of the stick insect, *Dixippus morosus* (Orthoptera, Phasmidae): calcium, magnesium, chloride, phosphate and hydrogen ions. *J. exp. Biol.* **33**, 697–708.

(27) 1958 Excretion by the Malpighian tubules of the stick insect, *Dixippus morosus* (Orthoptera, Phasmidae): amino acids, sugars and urea. *J. exp. Biol.* **35**, 871–891.

(28) 1961 The comparative physiology of renal function in invertebrates. In *The cell and the organism* (ed. Ramsay & Wigglesworth). Cambridge University Press.

(29) (With J.A. RIEGEL) Excretion of inulin by Malpighian tubules. *Nature, Lond.* **191**, 1115.

(30) 1964 The rectal complex of the mealworm *Tenebrio molitor* L. (Coleoptera, Tenebrionidae). *Phil. Trans. R. Soc. Lond.* B **248**, 279–314.

(31) 1965 *The experimental basis of modern biology*. Cambridge University Press.

(32) 1968 (With A.V. GRIMSTONE & ANN M. MULLINGER) Further studies on the rectal complex of the mealworm *Tenebrio molitor*, L. (Coleoptera, Tenebrionidae) *Phil. Trans. R. Soc. Lond.* B **253**, 343–382.

(33) 1971 Insect rectum. In *A discussion on active transport of salts and water in living tissues* (ed. R.D. Keynes) *Phil. Trans. R. Soc. Lond.* B **262**, 251–260.

(34) 1971 *A guide to thermodynamics*. Chapman and Hall Ltd.

(35) 1976 The rectal complex in the larvae of Lepidoptera. *Phil. Trans. R. Soc. Lond.* B **274**, 203–226.