



Robert K. Morton

ROBERT KERFORD MORTON

"And gladly would he learn and gladly teach" (*The Canterbury Tales*)

The tragic death of Robert Kerford (Bob) Morton on September 27th, 1963, early in his 43rd year, as the result of an accident in his laboratory three days previously, cast a shadow over the lives of his many friends and colleagues both in Australia and overseas and deprived biochemical science of one of its most brilliant exponents. He was in the full flood of his ideas and achievements, with so much still waiting to be accomplished within the framework of his clearly defined future plans.

Morton was born on August 7th, 1920, at Cootamundra, N.S.W., the youngest of seven children, to John Wilson and Catherine Elsie Morton. The family had moved from Beechworth, Victoria, where the parents were contemporary with David Rivett. In later years Sir David Rivett took a special interest in the youngest Morton, who travelled to Melbourne a short time before his death specifically to hear Sir Howard Florey deliver the First David Rivett Memorial Lecture on September 5th, 1963. It was a pleasure at this time to have had Morton to dinner, with Victorian Fellows in the presence of our distinguished visitor.

The closely-knit Morton family often went on hikes together, and it is recorded that young Robert always managed to keep up with the older members—excellent training for the subsequent scientist of unflagging energy. From this background he also developed, no doubt, his passionate love of the Australian bush.

The family eventually settled in Sydney, where Morton attended the Sydney Boys' High School. Too young to go directly to the University, he entered Hawkesbury Agricultural College in 1936 and in 1938 completed the course for the Diploma in Dairy Technology as dux of the College and Gold Medallist. Here he obtained his first insight into some of the practical problems associated with biological systems, which was further stimulated by the broad training he received during his undergraduate years at the University of Sydney, where in 1939 he enrolled in the Faculty of Agriculture. At this time he was noticed by one of his teachers, R. N. Robertson, as an unusually bright student in a class of quality and there began then a friendship which gained in strength continually over the next twenty-three years. Professor Robertson's moving tribute to his friend and colleague on the occasion of the memorial service at the University of Adelaide the day after the funeral will be long remembered by those who were present. In the latter part of his second year Morton interrupted his course to join the Royal Australian Navy, from which he was transferred, as sub-lieutenant early in 1941, for active service with the Royal Navy. Towards the end of the war he was posted as first-lieutenant on the anti-submarine frigate, H.M.S. *Ness*. Although he spoke little of his war years, it is clear that in the small ships in which he operated he was often exposed to danger and personal discomfort, but what is certain is that he would have undertaken any allotted task with the same

cheerfulness and tireless energy which were so characteristic of his subsequent scientific career. His ships were mainly on convoy duties, but he also took part in the preparations for the Normandy landings. There are extant naval certificates, equivalent to references, which were issued by the commanding officers on the occasions when he transferred ship. It is clear from these that he exercised a profound influence on the morale of each ship in which he served. All highlighted his striking personal qualities, two referring in almost identical words to his "infectious personality—a stimulus to his subordinates and superiors alike".

In spite of his exacting war duties, there flowed back a steady stream of letters to his family and friends, including his teachers and former fellow students at the University of Sydney. These are recalled as vividly descriptive—within the limits of war time censorship. Snatches of poetic composition, above average in style, and to which he added in later years, were often included. Morton's original intention was to carve out a career in literature in which he excelled at school and for which he won several prizes. He read widely and could recite at length the masters of English prose and poetry. He was able in later years to gratify these early desires and ambitions through the clear, concise and elegant form in which his many scientific papers were prepared for publication. It is worth quoting from one letter written to W. L. Waterhouse, with whom he had been in frequent correspondence, dated 9th September, 1945, from H.M.S. *Ness*. He referred at length to several of his fellow students, who had started the course with him, but who by then had graduated, several with distinction. "How integral a part of us become these loyalties to our institutions and associates. It is a characteristic of the British race, and it reached its height in those tragic but magnificent years between 1940 and 1944. Now that peace is with us my duty in these parts will soon be completed. I look forward to my return." Soon afterwards he was demobilized, with the reserve list rank of lieutenant-commander, and was able to return in 1946 to renew his studies at the University of Sydney. After distinguished performances in individual subjects, he graduated in 1948 with First Class Honours and the University's Gold Medal. During this period he came particularly under the influence of W. L. Waterhouse and J. M. Vincent.

Professor Waterhouse has recorded: "Of course it is impossible to put down on paper an adequate assessment of his worth. In his earliest undergraduate days my first contact with him was when he came to me to ask if he might see what I was doing in the wheat rust research. Not idle curiosity, but a clear desire to know what was involved in the research. His work at Hawkesbury Agricultural College had made him somewhat familiar with some of the problems of the wheat grower and he wanted to know what my approach to the rust problem was. Not long after, on one of his visits to the plant houses, where the first discovery of the effect of temperature changes on rust susceptibility and resistance was being demonstrated, he offered to arrange for certain rusted material to be

stored at particular temperatures at Peters Ice Cream Co., and for portions to be withdrawn for testing at successive periods. At that time no such storage facilities were available at Sydney University, and this action by Bob was most helpful. This attitude of trying to help the other chap was evidenced again and again.

It was after his return from the war and his coming into my Third Year courses that I had the day to day contacts with him. He was one of the most outstanding students who passed through my hands, top of the year in all three of my subjects. His reading was wide, and he was always inspiring in discussions, markedly alert and clear thinking in his contributions. His high standard set a pace for other students in his group.

In his post-graduate work before going abroad, he was often later than I working back in the laboratory, and I remember one of the night-watchmen, who was very friendly, telling me what a 'tiger for work' Bob was. His enthusiasm was truly remarkable.

In me he engendered a real affection and respect. I shall not forget my last walk and talk with him at Canberra, in November, 1962, when he told me of his future outlook and hopes. Amongst other things, he told me that he was planning to get down to that elusive problem of what constitutes resistance to disease in plants, a problem to which I have always maintained that the biochemist can be expected to provide the answer.

Looking back, I think that Bob was perhaps the most brilliant graduate of the Sydney University Faculty of Agriculture."

The recollections of Professor J. M. Vincent are also relevant to the formative years of a scientist of unusual perception and rare quality.

"Bob Morton belonged to what I regard, somewhat nostalgically, as the 'golden age' of my teaching career. This was the period when we had that select group of mature men who, resuming their courses after the war, brought to their work an intensity and an enthusiasm that stimulated us all. With this there was a wonderful ability to enjoy relaxed out-of-doors comradeship. Amongst these Bob was the natural leader and in every respect outstanding.

Ordinary examination standards became pretty meaningless so far as Bob was concerned. The examiner after a while, if he had any sense, gave up looking for places where marks could be deducted, for the sake of appearances, and often found that he had before him virtually an excellent and critical review of the topic (written at fantastic speed, in a handwriting that became more nearly horizontal as the pace increased) that would have done credit to an author sitting composedly in his study.

But this was by no means the most important measure of Bob's intellectual stature. The capacity for thought, work and enthusiasm was terrific. So much was this revealed in his student days, that by the time he had completed the ordinary undergraduate course (in which, of course, he excelled), he had also done what would have been expected of an extra honours year. By the time he

finished this he was able to turn in a piece of work that was not far short of Ph.D. standard.

At the same time this was going on, Bob was enjoying life to the full. As president of the undergraduate agricultural society, he set a standard in the conduct of its meetings that has hardly been equalled; and with it all he could and did enjoy a drink with the boys, and at parties carried over plenty of that wardroom exuberance in the best naval tradition."

To this should be added the fact that he resurrected a moribund university hockey team and distinguished himself as a member of it. With a freshness that was remarkable he returned to hockey as a form of relaxation with both graduates and students during his last year at the University of Adelaide.

With Vincent, an able and enthusiastic microbiologist, Morton was able to enjoy his early experiences in research. He was the first appointee to a research fellowship supported by the New South Wales Milk Board, a position which he held while still an undergraduate and for the first part of his subsequent period overseas. Their work was concerned with factors responsible for the spoiling of milk supplies in New South Wales and led to several collaborative papers, the first of which was published while Morton was still an undergraduate. During this period Morton also learned to appreciate the importance of collaborative work with experts in other scientific disciplines, which became a feature of his later broadly conceived research projects.

Soon after graduation he became the first Gowrie Travelling Scholar—named to commemorate a much-loved former Governor-General. This was a signal honour, as he was in competition with many brilliant ex-servicemen in the several Australian universities. Then came the turning points of his life. He elected to hold his scholarship in the sub-department of enzymology, headed by the distinguished biochemist, Malcolm Dixon, within the School of Biochemistry at the University of Cambridge, and to marry and take with him a young nurse, Jessie Noelle Telfer, on what, to them, was a great adventure. Few dedicated scientists could have been more fortunate in the choice of a wife and companion. She synchronized her life completely with his, whatever the call—to assist in the scraping of yards of calf intestine at Cambridge, or at Melbourne in the preparation of a large batch of crystalline lactic dehydrogenase following the small-scale demonstration; to prepare dinner for 6.30 p.m. and to have it still appetizing after midnight following a late session at the laboratory; to enjoy with him his successes or to ease his sorrows or disappointments; to find time still to give devoted attention to their two young sons. The contributions of his wife to his outstandingly successful career as a biochemist cannot be overestimated.

Morton, now turned 28, entered into his work at Cambridge with tremendous enthusiasm and a seemingly endless capacity to endure long hours in the laboratory, frequently until well past midnight. He had the great advantage to be able to awaken refreshed with

half the normal period of sleep, a habit no doubt cultivated from the limited allowance between watches during the war. The Professor of Biochemistry at Cambridge, Dr. F. G. Young, told me in 1951 that he often thought of excluding Morton from the laboratory after midnight, although merely for the preservation of the well-being of this young enthusiast. However, Morton was able to continue this pattern of limitless activity with little ill-health up to the time of his death, with the exception of one episode in late 1961, which was of some concern to his friends and medical advisers, but which was fortunately resolved.

Morton was at Cambridge for three years, being awarded his Ph.D., in 1952, with an exceptional thesis. When he began his investigations, biochemistry was in one of its quiescent phases, although Gowland Hopkins' dictum that "protoplasm" would eventually be resolved by the application of chemical methods remained a guiding principle. Many intracellular enzymes had been purified and their kinetics studied, but others could not be brought into true solution and remained intractable to standard methods of purification through their attachment to sub-cellular particles, lipoprotein in nature. New techniques were needed and Morton found the answer in the careful use of certain alcohols, in particular n-butanol, which disrupted the lipoprotein complex and freed the enzyme. After the discovery, the method seemed too simple and obvious, as did paper chromatography when first described. In consequence, however, in Morton's hands and in those of workers in many other laboratories, the use of butanol (alternatively called "mortonol" by others) at an early stage in isolation procedures led to the purification of many critically important enzymes, previously refractory, so that their properties could then be studied in detail.

In his now classical paper (Reference 6) Morton described the application of the method to the purification of no less than eleven distinct enzymes, including a number of phosphates and succinic dehydrogenase, a crucial component of the enzyme complex catalyzing reactions within the tricarboxylic acid cycle of mitochondria and sarcosomes. Although Morton found difficulty in reproducing his results with succinic dehydrogenase, to his intense satisfaction confirmation was provided in 1955 by C. L. Tsou, who devised a suitable procedure based essentially upon the conditions as originally published. While still at Cambridge he purified milk alkaline phosphatase nearly 6,000-fold and the alkaline phosphatase of calf intestinal mucosa over 1,000-fold. The phosphatases remained an interest for many years and he and his collaborators were able to resolve many previously contentious points, including clarification of the transferase activities of these enzymes. Through this work, which was extended at Melbourne and Adelaide into other aspects of the biochemistry of phosphate and organic phosphates, Morton became a world authority in this important field and was much sought after as an author of review articles.

In 1952 he departed from Cambridge for Melbourne, leaving behind several new friends, in particular Malcolm Dixon, to whom

he often acknowledged his lasting indebtedness as having laid the foundations for his subsequent career in enzymology. Although I was able to induce the University of Melbourne to create a new senior lectureship in my Department specifically for Morton (whom I had met for the first time at Cambridge in 1951), it was typical of his sense of loyalty and affection for his Alma Mater that he insisted that he be first cleared with the Dean of the Faculty of Agriculture at the University of Sydney. He considered himself to be still on leave from the position he had previously held as New South Wales Milk Board Research Fellow. Professor McMillan replied promptly. After paying a gracious tribute to Morton, it was generously agreed that he should come to Melbourne as providing a better environment for the effective prosecution of his research interests.

Here he began five years of almost feverish activity. Apart from research he accepted readily the additional obligation of his first academic appointment—namely, teaching, in which he excelled. His lectures were always well-prepared and in delivery clear and stimulating. He was ever ready to take on extra duties, which could contribute to the welfare of the department. Thus, he played an important part in the planning for the new biochemistry building at the University, The Russell Grimwade School of Biochemistry, which, however, was not completed until after he had joined the Waite Institute at the University of Adelaide.

At Melbourne he extended and consolidated some of his Cambridge findings, in particular those related to alkaline phosphatase of milk and its association with milk microsomes. The identity of these particles with the microsomes of mammary tissues was clearly established by careful comparisons at the enzyme and coenzyme level. His interest in lipoprotein particles in both animal and plant tissues led to a profitable collaboration with the electron microscopist, A. J. Hodge. From these observations Morton became convinced of the essential need to correlate the anatomy of the cell with its dynamic properties. In consequence structure and function became inseparable in his thinking, when planning and defining the objectives of all his future major research projects.

Perhaps the contributions for which he will be best remembered, in the annals of biochemistry, lie in a series of brilliant studies of the enzyme, yeast lactic dehydrogenase, which occupied a considerable part of his time in the years 1953–1963. It is sad to recall that it was while working on an improved method for the purification of this enzyme, involving large volumes of acetone, that an explosion occurred which resulted in his fatal injuries. This important work will, however, continue with the co-operation of some of his former colleagues, both at the University of Adelaide and overseas.

Dixon and colleagues had shown that the enzyme, which they partially purified, but as an unstable preparation, was associated with a haem protein (which they called cytochrome b_2). It was uncertain, however, whether the cytochrome was in fact the dehy-

drogenase, i.e., reacting directly with lactate, or an essential intermediate carrier of electrons to cytochrome *c*. At the suggestion of Dixon, Morton undertook to continue further purification studies of the enzyme at Melbourne and, if successful, to make a detailed examination of its properties. He began soon after arrival and was joined early in 1953 by C. A. Appleby, who was seconded from the C.S.I.R.O. to enter the course leading to the Ph.D. degree. Dr. Appleby has kindly supplied me with notes to assist in the recollection of an evening in November, 1953, when lactic dehydrogenase was first crystallized and I was the third person to observe it under the microscope as beautiful square-shaped pink crystals. There was great excitement, their laboratory finally shutting down at 2 a.m., with the bench as clean and tidy as when the day had started. Morton always placed great importance on laboratory neatness and himself set the example. In the purification procedure, butanol, followed by acetone fractionation, had been applied, and a large batch at this stage was ready for passage through a column of ion-exchange resin, IRC 50, which in tests had been shown to enhance the purification factor considerably. Appleby had removed the enzyme solution from its dialysis sac and placed it in a bucket of ice some hours before Morton had the column ready. Consternation reigned when the enzyme was observed to be out of solution as a red sludge at the bottom of the tube; Appleby was chided for leaving the enzyme too long, but then there was almost immediately a characteristic shout of joy from Morton as, on shaking the tube gently, he noticed the sheen of protein crystals. Dame Fortune does occasionally smile on the prepared mind and diligent investigator.

Crystallization increased ten-fold the specific activity of the enzyme, which proved to be in many ways a unique homogeneous protein in that it contained two different prosthetic groups, both essential for enzyme activity, protohaem and a flavin (flavin mononucleotide), in one to one ratio. It is thus a flavohaem protein or a "flavocytochrome", being incidentally the first cytochrome to be crystallized. The enzyme was intensively studied by Morton in conjunction with Appleby and subsequently with other associates at the University of Adelaide. In addition to the two prosthetic groups, the enzyme was found always to crystallize with a constant proportion of a small molecular weight DNA (deoxyribonucleic acid), which did not, however, contribute to the activity of the enzyme and could be separated from it. This observation excited great interest, particularly in overseas laboratories, owing to the low molecular weight of the component and its non-nuclear origin. Collaborative studies in which distinguished biochemists in both the United States and England have participated, with the ultimate aim of elucidating its sequence and structure, are still in progress.

Morton's interest in cytochromes was extended in Melbourne to include those of animal and plant tissues and was continued at the University of Adelaide. He and his colleagues made many import-

ant contributions to our understanding of these essential intermediates in electron transport.

In 1954 Morton turned his attention to the challenging problems of tumour growth, following the demonstration by Bittner of a milk factor in strains of mice genetically susceptible to tumours of the mammary gland. Fortified by his knowledge of the biochemistry of milk and mammary tissue, studies of enzymic changes which might accompany tumour development were initiated. He believed that the key to the problem of abnormal cell division would be found in the nucleus. With Marjorie Branster (Mrs. Jago) he isolated nuclei from lactating and non-lactating mammary tissue and from tumours, using two strains of mice, one with low and the other with high tumour incidence. The enzyme which catalyzes the synthesis of coenzyme I (nicotinamide adenine dinucleotide—NAD), a highly important cofactor in cellular metabolism, is located in the nucleus and it was found that the rate of synthesis of NAD by tumour nuclei is only about one-fifth that of nuclei from lactating mammary glands. These investigations were subsequently considerably extended at the University of Adelaide.

Morton received rapid promotion, first to reader and then to associate professor of plant biochemistry, but he was not to be held. He received an invitation from the Director of the Waite Institute at the University of Adelaide, Dr. Melville, to the Chair of Agricultural Chemistry, which he eventually accepted, though not without reluctance. His years at Melbourne had been most fruitful and he and his family were happily established. However, he wisely considered the advantages in being able to develop his own research school in a position of independence, while the opportunity to return to a faculty of agriculture gave added attraction. He made the right decision, although I had much cause for regret. We had become close friends and he had played a major part in the development of our graduate school.

On one of his too infrequent vacations we had gone together to Gippsland. We travelled one afternoon to the upper reaches of the Timbarra River beyond Buchan, intent on trout fishing early the following morning after a rest under the stars, as we had no camping equipment. Instead, torrential rain forced us to spend the night cooped up on the front seat of an old Morris Oxford. For me it was an exhilarating experience to be with such a delightful companion. Apart from cat-naps, the conversation never flagged and ranged from biochemistry through literature to philosophy and religion. Trout were forgotten.

I was to reinforce on many subsequent occasions my assessment of his fine qualities of character. Meanness of any sort was foreign to him, as befitted one who was by nature a leader. He urged on his colleagues and his younger associates, as himself, with a tremendous driving force, occasionally much to their dismay, but looking back it is certain that all of them would have considered it to have been a privilege to have once worked with him. He enjoyed life to the full, both when relaxed or intent upon a problem. He was gay

and gracious, with a ready wit, but sensitive to the feelings of his friends and colleagues; though possessing the spark of genius he was full of the spirit of charity, humility and sense of service. Not a regular churchgoer, his life was nonetheless founded on strong Christian principles and he was a devoted family man. While in Melbourne, Morton and his wife became attracted by the teachings of The Reverend Lyall Dixon, Minister of Collins Street Independent Church, and a firm friendship developed with him and Mrs. Dixon.

Morton never sought rewards for his work, although when recognition came he was appreciative. He could, however, be distressed at over-emphasis of the importance of his scientific observations, as on the occasion of sensational reports of his cancer investigations, which appeared in the newspapers while he was at the University of Adelaide. He was so concerned that he thought seriously of abandoning all research related to cell division.

In 1957 for his contributions to the advance of biochemical knowledge while at Cambridge and Melbourne, he was elected to Fellowship of the Academy. This gave him great satisfaction, but was doubtably just one of the many honours that would have come his way had he lived. With M. R. Lemberg and J. E. Falk he organized, on behalf of the Academy and the International Union of Biochemistry, a most successful symposium on haematin enzymes, which was held in Canberra in 1959. A senior American biochemist, who had been a participant, described the conference subsequently as the most important meeting he had attended. The published proceedings is still an authoritative monograph in this field.

Morton played a leading part in the foundation of the Australian Biochemical Society and was its President in 1958-9. He was also in 1961 President of Section N of the Australian and New Zealand Association for the Advancement of Science. His presidential address, "New Concepts of the Biochemistry of the Cell Nucleus", was brilliantly conceived and delivered and was received with enthusiasm by the large audience.

Morton's five years at the Waite Institute was a period of incredible activity and output. He accepted his triple obligation as professor—teaching, research and administration—with the energy of three men and yet somehow managed to achieve a sound integration of his efforts. With the encouragement of the Director and financial support from many sources, both local and overseas, he rapidly equipped his Department with a range of modern biochemical apparatus and he soon assembled a group of dedicated young post-graduate workers from various parts of Australia. It was not long before applicants from abroad began seeking the opportunity for association with his exciting investigations.

As at Melbourne, he pursued several lines of research simultaneously. He continued his studies of the enzymology of normal and malignant cells within the thesis that cell division was controlled by the rate of synthesis of nicotinamide nucleotide coen-

zymes. Nicotinamide, a precursor of coenzyme I (NAD), was found to cause a significant decline in the extent of cell division in a number of types of animal cells grown in tissue culture. This inhibitory effect of nicotinamide was confirmed elsewhere for other types of dividing cells. Japanese workers in particular accepted his ideas and towards the end of 1962 he made a visit to Japan, which was both profitable and enjoyable. The nuclear enzyme responsible for the final stage of coenzyme I (NAD) synthesis, nicotinamide mononucleotide adenylyltransferase, was extensively purified and crystallized from pig liver nuclei by Morton and colleagues and its properties studied in detail. In expansion of his investigations on tumour growth Morton initiated in his Department an extensive programme of organic chemical synthesis, as many of the compounds needed were not available commercially. Although he did not have a background of chemical training, an omission which he often regretted, he knew what he wanted, his penetrating mind seeing the objectives more clearly than the experts. In much of his work on cancer and other investigations, his principal associate was M. R. Atkinson, senior lecturer and subsequently reader in the Department at the Waite Institute. Dr. Atkinson had come from the University of New South Wales with considerable experience in organic and physical chemistry. He was a joint author with Morton in eighteen publications.

Towards the close of his career Morton diverted from his hypothesis of nuclear control of cell division into a new direction, with studies of the mechanism of action of the anti-leukaemic drug, 6-mercaptopurine. He published a suggested pattern of chemical compounds, which could be converted *in vivo* into active antimetabolites by cells which had become resistant to mercaptopurine. Shortly before his death he was gratified to receive a report from the United States that a substance belonging to a class within his list, a phosphodiester of thioinosinic acid, was an effective inhibitor of the division of resistant cells. This promising result will no doubt lead to further examination of his original proposals.

In spite of his continuing interest in cell division and in his favourite research topic, cytochrome b_2 , Morton found time to embark on two major projects of direct agricultural importance. Five papers were published on the biochemistry of the noxious weed, *Oxalis pes-caprae* (L). It was shown that oxalic acid accumulation in *Oxalis* may be an effective method of metabolizing glyoxylic acid which, unless removed, would inhibit aconitate hydratase and thus prevent normal functioning of the tricarboxylic acid cycle, essential for the life of the plant. The detailed studies of the enzymes concerned in the origin and fate of glyoxylic acid in *Oxalis* led to the hypothesis that it should be possible to develop enzyme inhibitors which would cause the plant to accumulate glyoxylic acid and thus lead to its elimination.

Morton always took a keen interest in the subsequent careers of his former students and he would thus have been delighted to have known that his junior collaborator throughout the *Oxalis* investiga-

tion, Dr. J. R. E. Wells, was awarded this year one of the first Queen Elizabeth II Fellowships.

The other project, and one to which he found himself committed on arrival at Adelaide, was concerned with the proteins of the wheat grain. Although he appreciated the complexity of the problem, he organized with characteristic vigour a collaborative effort involving the combined resources of electron microscopy, physical chemistry and enzymology. The success of this venture was beyond his expectations. In eight papers published in 1963 and one posthumously, an entirely new approach to the question of protein biosynthesis in the wheat grain, and probably one of more general application, was revealed. It was shown that specific granules (proteoplasts) in the wheat endosperm are concerned with the incorporation of amino acids into proteins and that the energy for the synthetic process is provided at the expense of phytic acid.

In 1963 he was joined for a few months by the distinguished physical biochemist, Professor Julian Sturtevant of Yale University, whose arrival was preceded by his stopped flow spectrophotometer, which was allowed to remain at the Waite Institute. This instrument enabled critical studies to be made of the mechanism of action of the enzyme, lactic dehydrogenase. This association proved a most happy and profitable experience for both. The important results obtained are in process of publication.

Prior to this event he had been on sabbatical leave during the whole of 1962 as Commonwealth Visiting Fellow at the University of Nottingham in the Department of Professor E. G. Hallsworth, one of his former teachers in the early years at the University of Sydney. Here and on visits to other universities the Morton family was able to live together in a relaxed atmosphere, which gave great joy to all. Then at the height of his powers, Morton received many invitations to lecture. Although much of his important work had already been published, other exciting investigations were nearing completion and were new to his audiences, who found his lectures fascinating.

He returned to Adelaide to take over the Chair of Biochemistry, to which he had been invited. It was not easy for him to make this decision, but he was prevailed upon to believe that his acceptance would be in the best interests of Australian biochemistry. He continued, until the accident which ended his life, to administer the department at the Waite Institute while engaged on the affairs of his new appointment. His life's work is preserved in the scientific literature to which he and his collaborators contributed one hundred and ten highly original papers (with some still to be submitted), the outcome of but fourteen years of inspired laboratory effort.

Occasionally a very bright star has passed across Australia's scientific firmament. Morton was one of these and his friends and colleagues are deeply saddened that his passage was so short. Tri-

butes and condolences have come to his family from all parts of the world. Mrs. Morton and young Robert and Graham can rest assured that their distinguished husband and father will be long remembered with respect, admiration and deep affection.

V. M. TRIKOJUS.

PUBLICATIONS

1. The Bacteriological Grading of Milk in New South Wales. *J. Aust. Inst. Agric. Sci.*, 13, 125 (1947). With J. M. Vincent.
2. Influence of Time and Temperature of Storage on Dye-Reduction Tests in Milk. *Nature*, Lond., 162, 415 (1948). With J. M. Vincent.
3. Dairy Research and Australian Progress. A Review. *J. Aust. Inst. Agric. Sci.*, 14, 53 (1948).
4. The Influence of Time and Temperature of Storage on Dye-Reduction Tests in Milk. I. Reduction of Methylene Blue. *J. Dairy Res.*, 16, 310 (1949). With J. M. Vincent.
5. Aspects of Dye-Reduction Methods for the Bacteriological Grading of Milk. 1. Time and Temperature of Storage as Factors in Dye-Reduction Tests. 2. Physico-Chemical Methods for the Study of Dye-Reduction Mechanisms. Thesis, Faculty of Agriculture, University of Sydney (1949).
6. Separation and Purification of Enzymes Associated with Insoluble Particles. *Nature*, Lond., 166, 1092 (1950).
7. An Improved Temperature-Compensated Test for the Grading of Milk. *Dairy Industries*, 16, 3 (1951). With J. T. Feagen and J. M. Vincent.
8. The Transferase Activity of Hydrolytic Enzymes. In Symposium on Phosphorus Metabolism, Vol. 2, p. 125 (1952). The Johns Hopkins Press, Baltimore, U.S.A.
9. Phosphatases and Phosphotransferases. Thesis, University of Cambridge (1952).
10. Transferase Activity of Hydrolytic Enzymes. *Nature*, Lond., 172, 65 (1953).
11. Microsomal Particles of Normal Cow's Milk. *Nature*, Lond., 171, 734 (1953).
12. Alkaline Phosphatase of Milk. 1. Association of the Enzyme with a Particulate Lipoprotein Complex. *Biochem. J.*, 55, 786 (1953).
13. Alkaline Phosphatase of Milk. 2. Purification of the Enzyme. *Biochem. J.*, 55, 795 (1953).
14. The Lipoprotein Particles in Cow's Milk. *Biochem. J.*, 57, 231 (1954).
15. The Purification of Alkaline Phosphatases of Animal Tissues. *Biochem. J.*, 57, 595 (1954).
16. Crystalline Cytochrome b_2 and Lactic Dehydrogenase of Yeast. *Nature*, Lond., 173, 749 (1954). With C. A. Appleby.
17. Enzymic Iodination of Milk Proteins. *Nature*, Lond., 173, 305 (1954). With Mary T. McQuillan, P. G. Stanley and V. M. Trikojus.
18. Some Properties of Alkaline Phosphatase of Cow's Milk and Calf Intestinal Mucosa. *Biochem. J.*, 60, 573 (1955).
19. The Substrate Specificity and Inhibition of Alkaline Phosphatases of Cow's Milk and Calf Intestinal Mucosa. *Biochem. J.*, 61, 232 (1955).
20. The Action of Purified Alkaline Phosphatases on Di- and Tri-Phosphopyridine Nucleotides. *Biochem. J.*, 61, 240 (1955).
21. Methods of Extraction of Enzymes from Animal Tissues. In Methods in Enzymology, edited by S. P. Colowick and N. O. Kaplan. Vol. 1, p. 25 (1955), Academic Press, New York, U.S.A.
22. Phosphomonoesterase of Milk. In Methods in Enzymology, edited by S. P. Colowick and N. O. Kaplan, Vol. 2, p. 533 (1955), Academic Press, New York, U.S.A.
23. Transphosphorylation by Phosphatases. In Methods in Enzymology, edited by S. P. Colowick and N. O. Kaplan, Vol. 2, p. 556 (1955), Academic Press, New York, U.S.A.

24. Cytochromes of Microsomal Particles. Cytochrome b_5 of Microsomes from Animal Tissues. *Nature*, Lond., 176, 111 (1955). With Margot Bailie.
25. Cytochromes of Microsomal Particles. Cytochrome b_3 of Microsomes from Plant Tissues. *Nature*, Lond., 176, 113 (1955). With E. M. Martin.
26. The Heart-Muscle Succinic Dehydrogenase and Yeast Lactic Dehydrogenase Systems. In The Silver Jubilee Volume, Society of Biological Chemists, India, p. 117 (1955).
27. The Group-Transferring Activity of Certain Hydrolytic Enzymes. In Discussions of the Faraday Society on Physical Chemistry of Enzymes, p. 149, The Faraday Society, London (1955).
28. Enzymic Properties of Microsomes and Mitochondria from Silver Beet. *Biochem. J.*, 62, 696 (1956). With E. M. Martin.
29. The Chemical Composition of Microsomes and Mitochondria from Silver Beet. *Biochem. J.*, 64, 221 (1956). With E. M. Martin.
30. Enzymic and Chemical Properties of Cytoplasmic Particles from Wheat Roots. *Biochem. J.*, 64, 687 (1956). With E. M. Martin.
31. Comparative Rates of Synthesis of Diphosphopyridine Nucleotide by Normal and Tumour Tissue from Mouse Mammary Gland: Studies with Isolated Nuclei. *Biochem. J.*, 63, 640 (1956). With Marjorie V. Branster.
32. Appendix to above paper: A Simply Constructed Tissue Homogenizer. *Biochem. J.*, 63, 647 (1956). With H. Kamphausen.
33. Effects of the Physical Environment on Some Lipoprotein Layer Systems and Observations on Their Morphogenesis. (Conference on Tissue Fine Structure.) *J. Biophys. Biochem. Cytology* 2, Supp. 221 (1956). With A. J. Hodge, Marjorie V. Branster, E. M. Martin, J. D. McLean and F. V. Mercer.
34. Haem Pigments of Cytoplasmic Particles from Non-Photosynthetic Plant Tissues. *Biochem. J.*, 65, 404 (1957). With E. M. Martin.
35. The Structure of Cytoplasmic Components of Plant Cells in Relation to the Biochemical Properties of Isolated Particles. *J. Biophys. Biochem. Cytology*, 3, 61 (1957). With A. J. Hodge and E. M. Martin.
36. The Kinetics of Hydrolysis of Phenyl Phosphate by Alkaline Phosphatases. *Biochem. J.*, 65, 674 (1957).
37. Isolation of Intact Liver Cells. *Nature*, Lond., 180, 1283 (1957). With Marjorie V. Branster.
38. Enzymic Synthesis of Coenzyme 1 in Relation to Chemical Control of Cell Growth. *Nature*, Lond., 181, 540 (1958).
39. Comparative Properties of Microsomes from Cow's Milk and from Mammary Gland. 1. Enzymic Activities. *Biochem. J.*, 69, 35 (1958). With Margot J. Bailie.
40. Comparative Properties of Microsomes from Cow's Milk and from Mammary Gland. 2. Chemical Composition. *Biochem. J.*, 69, 44 (1958). With Margot J. Bailie.
41. The Phosphotransferase Activity of Phosphatases. 1. Spectrophotometric Methods for the Estimation of Some Phosphate Esters and Other Compounds. *Biochem. J.*, 70, 134 (1958).
42. The Phosphotransferase Activity of Phosphatases. 2. Studies with Purified Alkaline Phosphomonoesterases and Some Substrate-specific Phosphatases. *Biochem. J.*, 70, 139 (1958).
43. The Purification and Properties of Yeast Cytochrome c . *Aust. J. Sci.*, 21, 119 (1958). With J. McD. Armstrong and J. H. Coates.
44. The Phosphotransferase Activity of Phosphatases. 3. Comparison of Enzymic Catalysis by Acid Phosphatase with Non-Enzymic Catalysis at Acid pH Values. *Biochem. J.*, 70, 150 (1958).
45. The Cytochromes. *Rev. Pure and Applied Chem.*, 8, 161 (1958).
46. The Preparation and Properties of Nicotinamide Mononucleotide. *Aust. J. Sci.*, 21, 119 (1958). With M. R. Atkinson and J. F. Jackson.
47. Equilibrium Constant of the Galactokinase Reaction and Free Energy of Hydrolysis of Adenosine Triphosphate. *Nature*, Lond., 184, 1925 (1959). With M. R. Atkinson and Eleanor Johnson.
48. Lactic Dehydrogenase and Cytochrome b_3 of Baker's Yeast: Purification and Crystallization. *Biochem. J.*, 71, 492 (1959). With C. A. Appleby.

49. Oligosaccharide Synthesis in the Banana and Its Relationship to the Transferase Activity of Invertase. *Biochem. J.*, **72**, 340 (1959). With R. W. Henderson and W. A. Rawlinson.
50. Lactic Dehydrogenase and Cytochrome b_2 of Baker's Yeast: Enzymic and Chemical Properties of the Crystalline Enzyme. *Biochem. J.*, **73**, 539 (1959). With C. A. Appleby.
51. Free Energy and the Biosynthesis of Phosphates. In *Comparative Biochemistry*, Vol. 2, Chapter 1. Edited by M. Florkin and H. Mason, Academic Press, New York (1960). With M. R. Atkinson.
52. The Respiratory Chain of Beetroot Mitochondria. *Aust. J. Biol. Sci.*, **13**, 109 (1960). With J. Wiskich and R. N. Robertson.
53. The Kinetics and Inhibition of Adenylyl Transfer to Pyridine Nucleotides. *Aust. J. Sci.*, **22**, 414 (1960). With M. R. Atkinson and J. F. Jackson.
54. The Effect of Oxygen and of Thiol-Binding Agents on Cytochrome b_2 of Yeast. *Aust. J. Sci.*, **22**, 418 (1960). With J. McD. Armstrong and J. H. Coates.
55. Lactic Dehydrogenase and Cytochrome b_2 of Baker's Yeast: The Amino Acid Composition of the Crystalline Enzyme. *Biochem. J.*, **75**, 72 (1960). With C. A. Appleby and D. H. Simmonds.
56. Lactic Dehydrogenase and Cytochrome b_2 of Baker's Yeast: The Deoxyribose Polynucleotide Component and the Physicochemical Properties of the Crystalline Enzyme. *Biochem. J.*, **75**, 258 (1960). With C. A. Appleby.
57. Flavin Dissociation and Inactivation of Cytochrome b_2 by Oxygen. *Nature, Lond.*, **186**, 1033 (1960). With J. McD. Armstrong and J. H. Coates.
58. Chemical and Physical Properties of the Small Deoxyribonucleic Acid Component of Crystalline Cytochrome b_2 . *Nature, Lond.*, **187**, 916 (1960). With M. D. Montague.
59. Synthesis of Nicotinic Acid Nucleotides. *Nature, Lond.*, **188**, 58 (1960). With M. R. Atkinson.
60. Effects of α -Lipoic Acid on the Respiratory Chain of Plant Mitochondria. *Nature, Lond.*, **188**, 658 (1960). With J. T. Wiskich.
61. Equilibrium Constant of Phosphoryl Transfer from Adenosine Triphosphate to Galactose in the Presence of Galactokinase. *Biochem. J.*, **78**, 813 (1961). With M. R. Atkinson and R. M. Burton.
62. Equilibrium Constants of Phosphoryl Transfer from C (1) to C (6) of α -D-Glucose 1-Phosphate and from Glucose 6-Phosphate to Water. *Biochem. J.*, **79**, 12 (1961). With M. R. Atkinson and Eleanor Johnson.
63. Nicotinamide Mononucleotide Adenylyltransferase of Pig Liver Nuclei: The Effects of Nicotinamide Mononucleotide Concentration and pH on Dinucleotide Synthesis. *Biochem. J.*, **80**, 318 (1961). With M. R. Atkinson and J. F. Jackson.
64. Properties of Crystalline Cytochrome b_2 (L-Lactate Dehydrogenase) of Baker's Yeast. *Aust. J. Sci.*, **24**, 137 (1961). With J. McD. Armstrong.
65. Substrate Specificity of Nicotinamide-Adenine-Dinucleotide Pyrophosphorylase. *Aust. J. Sci.*, **24**, 137 (1961). With M. R. Atkinson and J. F. Jackson.
66. Nomenclature of CO-binding Pigments. In *Haematin Enzymes. A Symposium of the International Union of Biochemistry organized by the Australian Academy of Science, Canberra*. Edited by J. E. Falk, R. Lemberg and R. K. Morton, p. 432 (1961), Pergamon Press, London.
67. Synthesis of Nicotinic Acid Nucleotides and of Nicotinamide Nucleotides by Liver and by Maize Roots. *Aust. J. Sci.*, **24**, 138 (1961). With M. R. Atkinson, P. Caiger and C. V. Ramakrishnan.
68. The Extraction and Fractionation of Protein in Developing Wheat Endosperm. *Aust. J. Sci.*, **24**, 132 (1961). With J. S. D. Graham and D. H. Simmonds.
69. Oxalate Formation in *Oxalis pes-caprae*. *Aust. J. Sci.*, **24**, 140 (1961). With Adele Millerd and J. R. E. Wells.
70. The Chemical and Enzymic Properties of Crystalline Cytochrome b_2 of Baker's Yeast. In *Haematin Enzymes. A Symposium of the International Union of Biochemistry organized by the Australian Academy of Science,*

- Canberra. Edited by J. E. Falk, R. Lemberg and R. K. Morton, p. 501 (1961). Pergamon Press, London. With J. McD. Armstrong and C. A. Appleby.
71. Comparative Properties of Cytochrome *c* from Yeast and Heart Muscle. In Haematin Enzymes. A Symposium of the International Union of Biochemistry organized by the Australian Academy of Science, Canberra. Edited by J. E. Falk, R. Lemberg and R. K. Morton, p. 385 (1961). Pergamon Press, London. With J. McD. Armstrong and J. H. Coates.
 72. The Contribution of the Prosthetic Groups to the Absorption Spectrum of Cytochrome *b₂*. In Haematin Enzymes. A Symposium of the International Union of Biochemistry organized by the Australian Academy of Science, Canberra. Edited by J. E. Falk, R. Lemberg and R. K. Morton, p. 567 (1961). Pergamon Press, London.
 73. The Bonding Between the Flavin Group and Apoprotein of Cytochrome *b₂*. In Haematin Enzymes. A Symposium of the International Union of Biochemistry organized by the Australian Academy of Science, Canberra. Edited by J. E. Falk, R. Lemberg and R. K. Morton, p. 569 (1961). Pergamon Press, London. With J. McD. Armstrong and J. H. Coates.
 74. Cytochromes *c₁* and *b₂* of Particulate Components of Plants. In Haematin Enzymes. A Symposium of the International Union of Biochemistry organized by the Australian Academy of Science, Canberra. Edited by J. E. Falk, R. Lemberg and R. K. Morton, p. 498 (1961). Pergamon Press, London.
 75. Biosynthesis of Pyridine Nucleotide Coenzymes. Fifth Internat. Congr. Biochem., Moscow. Abstr. of Comm., p. 157 (1961). Pergamon Press, London. With M. R. Atkinson.
 76. Structure and Properties of the Flavohaemoprotein, Cytochrome *b₂* (L(+)-Lactate Dehydrogenase of Baker's Yeast) and of Haemoprotein, Flavoprotein and Apoprotein Derivatives. *Nature*, Lond., 192, 727 (1961).
 77. Crystallization of Cytochrome *b₂* Free of the Deoxyribonucleic Acid Component. *Nature*, London, 192, 639 (1961). With Kathryn Shepley.
 78. Substrate Specificity and Inhibition of Nicotinamide Mononucleotide-Adenyl Transferase of Liver Nuclei: Possible Mechanism of Effect of 6-Mercaptopurine on Tumour Growth. *Nature*, Lond., 192, 946 (1961). With M. R. Atkinson and J. F. Jackson.
 79. New Concepts of the Biochemistry of the Cell Nucleus. (Presidential Address to Section N of A.N.Z.A.A.S., 1961.) *Aust. J. Sci.*, 2, 260 (1961).
 80. Nicotinamide 6-Mercaptopurine Dinucleotide and Related Compounds; Potential Sources of 6-Mercaptopurine Nucleotide in Chemotherapy. *Nature*, Lond., 196, 35 (1962). With M. R. Atkinson, J. F. Jackson and A. W. Murray.
 81. Role of Isocitrate Lyase in Synthesis of Oxalic Acid in Plants. *Nature*, Lond., 196, 955 (1962). With Adele Millerd and J. R. E. Wells.
 82. Protein Bodies and Protein Synthesis in Developing Wheat Endosperm. *Nature*, Lond., 196, 967 (1962). With Janet S. D. Graham, A. C. Jennings, B. A. Palk and J. K. Raison.
 83. Changes in Carbohydrate, Protein, and Non-Protein Nitrogenous Compounds of Developing Wheat Grain. *Aust. J. Biol. Sci.*, 16, 318 (1963). With A. C. Jennings.
 84. Changes in Nucleic Acids and Other Phosphorous-Containing Compounds of Developing Wheat Grain. *Aust. J. Biol. Sci.*, 16, 332 (1963). With A. C. Jennings.
 85. Studies of Proteins of Developing Wheat Endosperm. Fractionation by Ion-Exchange Chromatography. *Aust. J. Biol. Sci.*, 16, 350 (1963). With Janet S. D. Graham and D. H. Simmonds.
 86. Studies of Proteins of Developing Wheat Endosperm. Separation by Starch-Gel Electrophoresis and Incorporation of (³⁵S) Sulphate. *Aust. J. Biol. Sci.*, 16, 357 (1963). With Janet S. D. Graham.
 87. Cytological Studies of Protein Bodies of Developing Wheat Endosperm. *Aust. J. Biol. Sci.*, 16, 366 (1963). With A. C. Jennings and B. A. Palk.
 88. Isolation and Characterization of Protein Bodies from Developing Wheat Endosperm. *Aust. J. Biol. Sci.*, 16, 375 (1963). With Janet S. D. Graham and J. K. Raison.

89. Amino Acids and Protein Synthesis in Developing Wheat Endosperm. *Aust. J. Biol. Sci.*, 16, 384 (1963). With A. C. Jennings.
90. A Complete Intracellular Unit for Incorporation of Amino Acid into Storage Protein Utilizing Adenosine Triphosphate Generated from Phytate. *Nature*, Lond., 200, 429 (1963). With J. K. Raison.
91. Physicochemical Studies on Cytochrome b_2 . Sedimentation, Diffusion and Electrophoresis of the Crystalline Deoxyribonucleoprotein. *Biochem. J.*, 86, 136 (1963). With J. McD. Armstrong and J. H. Coates.
92. Physicochemical Studies on Cytochrome b_2 . Some Properties of Modified Forms of the Enzyme and of the Deoxyribonucleic Acid Component. *Biochem. J.*, 88, 266 (1963). With J. McD. Armstrong and J. H. Coates.
93. The Flavin and Haem Prosthetic Groups of Cytochrome b_2 (L-Lactate Dehydrogenase of Yeast). *Biochem. Z.* (Warburg Festband), 338, 122 (1963). With Kathryn Shepley.
94. Flavin-Haem Interaction in Crystalline Cytochrome b_2 (L(+)-Lactate Dehydrogenase of Yeast). In Symposium on Intracellular Respiration, Proc. Fifth Internat. Congress of Biochem., Moscow, 1961, 5, 213 (1963). Pergamon Press. With J. McD. Armstrong.
95. The Preparation of Crystalline Forms of Ferricytochrome b_2 and Ferrocyclochrome b_2 . *Biochem. J.*, 89, 257 (1963). With Kathryn Shepley.
96. A Comparative Study of Nicotinamide Nucleotide Coenzymes During Growth of the Sheep and Rat. *Biochem. J.*, 85, 351 (1963). With P. Caiger, O. H. Filsell and I. G. Jarrett.
97. Nicotinamide Nucleotide Coenzymes and Glucose Metabolism in the Livers of Foetal and New-Born Lambs. *Biochem. J.*, 89, 92 (1963). With O. H. Filsell, I. G. Jarrett, M. R. Atkinson and P. Caiger.
98. Inhibition of Inosine 5'-Phosphate Dehydrogenase from Ehrlich Ascites-Tumour Cells by 6-Thioinosine 5'-Phosphate. *Biochem. J.*, 89, 167 (1963). With M. R. Atkinson and A. W. Murray.
99. Oxalic Acid Synthesis in Shoots of *Oxalis Pes-Caprae*. *Biochem. J.*, 86, 57 (1963). With Adele Millerd and J. R. E. Wells.
100. Oxalic Acid Synthesis in Shoots of *Oxalis pes-caprae*. The Precursors of Glycollic Acid and Glyoxylic Acid. *Biochem. J.*, 88, 276 (1963). With Adele Millerd and J. R. E. Wells.
101. Enzymic Synthesis of Oxalic Acid in *Oxalis pes-caprae*. *Biochem. J.*, 88, 281 (1963). With Adele Millerd and J. R. E. Wells.
102. Oxidative Phosphorylation and Related Processes. *Nature*, Lond., 200, 221 (1963). With M. R. Atkinson.
103. Adenosine Triphosphate-Nicotinamide Mononucleotide Adenylyltransferase of Pig-Liver Nuclei. Extraction and Purification of the Enzyme. *Biochem. J.*, 90, 433 (1964). With M. R. Atkinson and J. F. Jackson.
104. Isocitrate-Lyase and the Formation of α -Keto γ -Hydroxyglutaric Acid in *Oxalis*. *Nature*, Lond., 201, 477 (1964). With J. R. E. Wells.
105. Kinetic Investigations of Yeast L-Lactate Dehydrogenase (Cytochrome b_2). I. The Dehydrogenation of L-Lactate in the Presence and Absence of Ferricyanide as Electron Acceptor. *J. Biol. Chem.*, 239, 1614 (1964). With Julian M. Sturtevant.
106. Intracellular Components Associated with Protein Synthesis in Developing Wheat Endosperm. *Biochem. J.*, 91, 522 (1964). With B. A. Palk and J. K. Raison.
107. The Separate Incorporation of Amino Acids into Storage and Soluble Proteins Catalyzed by Two Independent Systems Isolated from Developing Wheat Endosperm. *Biochem. J.*, 91, 528 (1964). With J. K. Raison.
108. Enzymes and Ribonucleic Acid Associated with the Incorporation of Amino Acids into Proteins of Wheat Endosperm. *Biochem. J.*, 91, 539 (1964). With J. K. Raison and J. R. Smeaton.
109. Phosphatases. In Comprehensive Biochemistry, Vol. 16. Hydrolytic Reactions; Cobamide and Biotin Coenzymes, Chapter II. Edited by M. Florkin and E. H. Stotz. Elsevier Publishing Co. (In preparation.)
110. Inhibition of Adenylosuccinate Synthetase and Adenylosuccinate Lyase from Ehrlich Ascites-Tumour Cells by 6-Thioinosine 5'-Phosphate. *Biochem. J.* (Accepted for publication.) With M. R. Atkinson and A. W. Murray.