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*J. W. S. Finkle*

## JOHN WILLIAM SUTTON PRINGLE

22 July 1912 — 2 November 1982

Elected F.R.S. 1954

By SIR VINCENT WIGGLESWORTH, F.R.S.

JOHN WILLIAM SUTTON PRINGLE was born in Manchester on 22 July 1912. He was the eldest of four brothers. His father was John Pringle, M.D. (Dublin), a well known medical practitioner in Rochdale and Manchester. The origins of the family have been traced back to one Robert de Hoppryngil, which is a hill near Galashiels from which the name Pringle was derived. They moved to Ireland in the time of Cromwell, where they became farmers and bailiffs. J. W. S. Pringle's father had come over to Manchester in 1900. His mother was Dorothy Emily (*née* Beney), whose family claimed to be of Huguenot extraction. The Scottish branch of the Pringle family produced Sir John Pringle (1707–83), the founder of modern military medicine and originator of the Red Cross idea. He secured improved ventilation in jails, ships, barracks and mines; he named influenza and defined the forms of dysentery; he eventually became President of the Royal Society. And J. W. S. Pringle had a more recent link with the Royal Society in that he shared a grandfather with the malariologist J. A. Sinton, V.C., F.R.S.

As a boy, John Pringle enjoyed a happy family life, escaping from the grime of Manchester for summer holidays in the Lake District, in Donegal and in the Alps. He was educated at home and at a local 'high school' until ten years of age. He then started attending Manchester Grammar School (1922–23) but the Manchester fogs induced broncho-pneumonia in two consecutive years and he was therefore transferred to a preparatory school, Langley place at St Leonard's-on-Sea, Sussex (1923–26). Here the teaching under W. J. Roberts was very good and he won a senior scholarship to Winchester College.

At Winchester he continued with classics and mathematics up to School Certificate and only then started scientific subjects. He always recalled the inspiration he had derived in physics from S. R. Humby and in biology from Rev. S. A. McDowell. He showed no prowess in sport, but played (violin) in the school orchestra. His interest in natural history



was much stimulated by his friendship with his contemporary Bruce (F. B. M.) Campbell, who later became well known as a naturalist on the radio and Secretary of the British Trust for Ornithology. Their joint activities with insects and birds are conspicuous in the 1927–31 Report of the Winchester College Natural History Society. In the spring of 1931 Pringle spent a fortnight at the Millport Marine Biological Station where he first met James Gray (Sir James Gray, F.R.S.) with whom he was later to be so closely associated in Cambridge.

Pringle never regretted his early classical training; he and his immediate associates, who were taking science, persuaded the Winchester authorities to let them continue with Greek for their last two years, and he got much enjoyment from reading Herodotus 'at high speed without regard for syntax'. His science consisted mainly of physics and chemistry and zoology always a poor, though favourite, third subject.

#### CAMBRIDGE, 1931–39

In 1931 Pringle won a major entrance scholarship to King's College, Cambridge. He duly gained a class I in the Natural Sciences Tripos part I in 1933 (Zoology, Botany and Physiology) and a class I in part II (Zoology) in 1934, taking this course (usually occupying two years) in a single year by omitting almost the whole of vertebrate zoology. A potent factor in preserving his interest in other branches of science was the exclusive Cambridge University Natural Science Club, where papers were read on all scientific matters by the hand-picked members (undergraduates and research students). He was also secretary of the Cambridge Natural History Society for a year and collected Diptera, but did no research as an undergraduate. In 1934 he organized and led an expedition to the Atlas Mountains to study the ecology of freshwater springs and to collect specimens in the area south of Meknes, with A. L. Hodgkin, P. T. Cotton and K. H. Chapman; however, their achievements were restricted by illness.

Pringle then held a King's College studentship (1934–37) with his sights set upon a fellowship. During his first postgraduate year he was occupied in an abortive study of chemoreceptors of freshwater molluscs by behavioural methods. But in the following year he started oscillographic work under the initial guidance of R. J. Pumphrey, originally on chemoreceptors but then on proprioception. This work continued until 1939 and demonstrated the outstanding ability of Pringle as an investigator; it was the prelude to a great research career. He served as University Demonstrator in Zoology (1937–38) and was elected to a Fellowship of King's College, 1938–44, for five years of which time he was away on war service.

In 1939 he obtained a Rockefeller Fellowship to work for a year with

D. W. Bronk in Philadelphia. He arrived in the U.S.A. in September 1939, and returned to England at once on the outbreak of war, with the intention of enlisting as a pilot in the Royal Air Force. For during his undergraduate career he had not only taken up gliding (p. 541) but he had learned to fly fixed wing aircraft.

#### WAR SERVICE, 1939–45

When Pringle presented himself to the Royal Air Force on his return from America he was not assigned for training as a pilot but was allocated to research work on airborne radar with the Telecommunications Research Establishment (T.R.E.) and thus became one of that remarkable band of biologists who were able to switch from researching in nerve physiology or ecology and capitalize their experience by studying the technicalities of communication or the assessment of tactics in warfare. Pringle moved to Perth, St Athan, Swanage, and to the headquarters laboratory at Malvern. At St Athan in the winter of 1939–40 he was one of a group that included A. C. B. Lovell, and Pringle was set to lead the team. For a time he was in charge of all airborne radar work in Britain, and after centimetre radar was split off he continued to work on  $1\frac{1}{2}$  metre radar for use by the army as a navigational aid.

Quite early in his service Pringle was sent down to Pembroke Dock to calibrate prototype airborne radar equipment destined for U-boat detection, which had just been installed in a Sunderland flying boat. The calibration involved mapping signal strength at precise bearings from the aircraft. But the Sunderland at its mooring in Milford Haven would not keep still, and accurate recordings were impossible. After taking a look at the R.A.F. Station on shore, Pringle reported to the Station Commander and asked for the 20-ton flying boat to be moved to the nearby rugby pitch. The Group Captain agreed to the young boffin's request; the Sunderland was hauled up the slipway, manoeuvred with difficulty to the rugby ground, and the calibration was done! John Pringle was greatly impressed by the enthusiasm and the immense patience of the aircrews in overcoming the endless teething troubles of new equipment. The fact that in case the equipment at last became operationally effective was largely if not wholly due to the son of Chaim Weizmann, who was a flight lieutenant with that squadron and was killed later in the war.

By the end of 1942, when the tide began to turn, he became a member of a group styled, somewhat optimistically, the 'invasion panel', along with W. B. Lewis and R. A. Smith, to consider the innumerable ways in which radar could contribute when the invasion of Europe really materialized.

Pringle was in charge of a group that developed 'responder' devices: 'Eureka', a radio beacon deposited to mark an objective for bombing or for



troop landing, and 'Rebecca', carried by the attacking bomber or the troop-carrying aircraft, which picked up the pulsed radio signals emitted by the beacon. On the whole the air force was extremely receptive to new ideas put forward by the scientists. 'Eureka' and 'Rebecca', however, had a difficult passage, but in the end they were widely accepted and used by the R.A.F. and enthusiastically later by the American Army. They played a memorable role in North Africa and when D-Day came.

Pringle visited the United States and the Mediterranean war theatre as Squadron-Leader (hon.) in 1942 to observe these communications systems at work. Shortly before the war ended he was seconded to the Ministry of Transport as secretary of a committee to assist the introduction of wartime radar aids to the Merchant Service Navy. He found this fascinating work and was tempted to stay on after the war, but in the end Cambridge prevailed.

For his war service Pringle was awarded the M.B.E. and the American Medal of Freedom with Bronze Palm.

#### CAMBRIDGE, 1945-61

On his return to Cambridge, Pringle was offered a lectureship in the Department of Zoology and a Fellowship of Peterhouse. Thus opened a new chapter in his career. In August 1946 he married Beatrice, widow of the late Capt. M. M. Wilson, and daughter of H. Gilbert-Carter, for many years (1922-50) Director of the Botanic Gardens in Cambridge. From that day onwards a happy family life added a new dimension to the figure of John Pringle. They had a son and two daughters, together with the daughter of Mrs Pringle's first marriage.

Pringle was very active in college affairs, becoming Tutor in 1947 and Senior Tutor in 1949 until 1957, then Senior Bursar of Peterhouse 1957-59 and Librarian 1959-61; he also undertook college teaching in biology. All of these duties he is reported to have carried out most competently and conscientiously. In the Department of Zoology he had his university lecturing and was for many years Administrative Officer, thus relieving Professor Sir James Gray of many administrative duties. And yet, despite this heavy load, throughout the fifteen years from 1946 to 1961, single-handed (for by his own choice he took on almost no research students) he was producing research results of the highest quality and originality (p. 533).

Most of the time was spent in Cambridge, but in 1953 he had six months sabbatical leave in Ceylon with a Leverhulme Research Fellowship, studying the physiology of singing in cicadas, and working in the Department of Physiology of the University of Ceylon in Colombo. In 1955, having armed himself with an Sc.D. so that he would not be discounted as plain Mr Pringle, he spent a couple of months in the



summer at Woods Hole working on proprioception in *Limulus* and including visits to Oregon and California. Finally in 1960–61, Pringle served for a year on the General Board of the University. This gave him a great interest in and liking for university government. He put his weight behind the organization of a science course that could be taken by Arts men at Cambridge. As a member of the Library Syndicate he campaigned for a Science Library in Cambridge. This was not achieved but the Science Periodicals Library established some years later probably met the wishes of most of the scientists.

James Gray retired from the Chair of Zoology in 1959, to be succeeded by Carl Pantin, and John Pringle was made Reader in Experimental Cytology (1959–61). It seemed that he was well set to continue his distinguished career in Cambridge with such appointments as the Chair in Zoology or perhaps the Mastership of Peterhouse before him. But in December 1960 he was surprised to receive an unsought offer of the Linacre Chair of Zoology at Oxford. A prolonged correspondence with the Registrar followed, in which he was assured that the building of a new zoology laboratory was to begin in 1964, that an architect had been appointed and that Professor Sir Alister Hardy was resigning from the Chair two years before the retiring age to allow his successor to plan the new developments from the outset. The correspondence ended with Pringle's acceptance of the offer in June 1961.

Why did he embark on this move, which would mean abandoning the beloved gliding club which still needed his continued help, leaving a house and garden to which he had become greatly attached, and many friends and a progressing research group, combined with a probable financial loss? But he was urged by James Gray that it was a duty to British zoology; he was attracted by the challenge of rescuing a depressed laboratory, and building on small resources; and by the adventure for his wife and himself of a new life.

We in Cambridge had no illusions about the troubles that lay ahead; we knew that Pringle would have a rough passage. In the battles that followed he found his inspiration well expressed in the closing lines of Lermontov's poem 'Paris' (1832), which Pringle himself translated thus:

A lonely sail gleams white upon the blue mists of the sea.

What does he seek in a distant land? What has he left in his own country?

The waves gambol, the wind whistles and the mainmast bends and creaks.

Alas! T'is not from joy he hurries; t'is not happiness he seeks. Beneath, a streak of brightest azure; above, the sunshine's golden ray.

But he, rebellious, woos the tempest, as though in storms lay sanctuary.



## OXFORD, 1961–79

So Pringle moved to Oxford in the autumn of 1961, becoming M.A., D.Sc. (Oxon.) by incorporation, and a Fellow of Merton, where he was already known since Merton is the sister college of Peterhouse. Already, early in Michaelmas Term 1961, difficulty arose over the site for the new laboratory; and by the time in Hilary Term when the Resolution came before Congregation it was evident that this was the only chance of keeping the clear promise he had received of construction of the new laboratory starting in 1964. By this time Pringle had come to feel very bitter that so many people were prepared to disregard the promise given in good faith by the Vice-Chancellor and Registrar. But support was forthcoming in high quarters, notably from Oakeshott, another Wykehamist, and a Resolution allocating half an acre in the Parks for the new laboratory was approved (March 1962).

Pringle and all concerned now believed that the way was clear. With Peter Chamberlain as architect he designed the building in detail. The site was so small that it had to be a tall tower. But to design a laboratory in this form was a challenge that John Pringle and his architect met with enthusiasm. They incorporated many novel features of engineering and layout, including a paternoster lift which would be continually in motion, carrying passengers in both directions, and slowing down as it passed the landing stages on each floor. I well remember Pringle's enthusiasm in describing how it was all going to work—but I fancy that after the novelty had worn off it could have been an exasperating place to work in.

All might have been well if a visit by Princess Margaret had not made it necessary to postpone the debate on the decree confirming the site, so that it had to be taken at the same time as a second decree approving the building. By this time opposition was well organized, composed of those who deplored either the encroachment on the Parks or the interference with the skyline, and those who opposed the expansion of science in general or of zoology in particular. (For an inborn opposition to science did still exist in Oxford. Only a few years earlier I had served on an appointment committee for a professorial election, and had been unwise enough to recommend my favoured candidate on the grounds that he could be relied upon to develop his subject and put Oxford 'on the map' in respect to his branch of learning. But the Vice-Chancellor (Professor Stallybrass), who was in the chair, at once pointed out that I misunderstood the situation: science in Oxford had been expanding; it was continuing to expand; that had got to stop; and this was where it was going to stop!) The first decree, confirming the site, was lost, and the second decree about the building could not therefore be put to the vote.

Pringle was in the depth of despair and so were his friends and supporters. He even considered bringing an action for breach of contract against the University; but the legal advice he received was that he had



only a slender chance of winning such an action. Pringle had served two years on the General Board in Cambridge, but evidently not long enough to learn that in the ultra-democratic universities of Oxford and Cambridge it is impossible for the authorities making an appointment to give a guarantee that a promise made to a new member of staff will not be overturned by the popular vote in the Senate or Congregation when the time for implementation arrives.

It may have been a surprise to the Vice-Chancellor and Registrar, when Pringle saw them three days later, that he did not propose to resign; instead he presented them with a complete plan for the University to purchase Merton playing fields for laboratories and, meanwhile, to put the old Zoology Laboratory in order. Since the Warden of Merton had at that time nearly succeeded in getting agreement to a 'package deal' with the University and Rhodes House that would have effectively prevented the southward enlargement of the Science Area, he offered his resignation as a Fellow of Merton—which the Warden declined to accept (June 1962).

Later, in August, he made a well prepared and forceful speech at a meeting of the Governing Body, and the College agreed to sell whatever land was recommended by Sir William Holford, whom the University was to be asked to bring in as an independent consultant. This was agreed by the University, but Holford was unable to report quickly and by November the general run of feeling in the University made Pringle doubt again whether there was indeed the will to act. Because of this continuing uncertainty he was unable to recruit staff or plan the much-needed expansion of research. He therefore decided on an ultimatum.

In a long letter to Council (in the drafting of which he had the assistance of Norrington, by this time retired as Vice-Chancellor) he asked for public confirmation of the intention to build a large new laboratory when a site was available, for a doubling of the existing space for Zoology (which was practicable through the impending move of Biochemistry) and for funds to put the old laboratory in order. He prepared a full account of the whole affair for the national press and let it be known that he was going to California on 4 December. One week before this, the new Vice-Chancellor (Oakeshott) agreed to all his requests.

Holford reported in the following May and on 18 June his recommendation was accepted by Congregation, that the Science Area should be expanded across South Parks Road on to the Merton land. Zoology duly occupied the old Physiology Laboratory when Biochemistry moved out and, with the help of his administrator Miss Helen Statham, Pringle was able to put the old laboratory in order at a cost of £40 000. The equipment grant for this, and support from the Agricultural Research Council and other Research Councils, enabled him to get research going for all members of the staff so inclined.



The design of the new laboratory meant a new start from scratch, with a building of more orthodox form. Pringle would have liked to work again with Peter Chamberlin, but the Council had recruited Sir Leslie Martin for the whole area. To describe as 'orthodox' the new Zoology Department as it eventually emerged is misleading. Pringle put an immense amount of detailed work into it, including in the design all the features which he felt desirable. The staff moved in in October 1970 and it was officially opened in 1971. It is a very impressive laboratory to visit. After some twelve years of operation the occupants of course suffer from the endemic faults that appear inevitable in modern buildings of this kind; but the flat roof does not yet leak, so in that respect at least they may consider themselves fortunate.

The work involved in getting the laboratory designed and built was formidable; but the worry was at an end. At last Pringle could concentrate on the planning and execution of teaching and research. He organized a large new subdepartment of Molecular Biophysics led by D. C. Phillips, with finances from the Medical Research Council and the Nuffield Foundation. With support from the Agricultural Research Council, who set up a Research Unit of Muscle Biophysics and Insect Physiology in the Department, he recruited a group of biochemists, a physiologist, a physicist and an engineer to work on insect flight muscle, in the hope ultimately of understanding the mechanism of contractility. The Zoology Laboratory already had well-known groups working on animal behaviour (ethology) and ecology, and on population genetics. Pringle did his utmost to encourage the continued success of work in these fields.

And he was largely instrumental in organizing a powerful group in the University resolved to introduce Human and Social Biology into the undergraduate curriculum (see below). He completely reorganized on modern lines both the first-year course (which became a joint Biology Preliminary based on genetics, cell physiology and ecology) and the Honours School of zoology. As he expressed it himself in 1965: 'It has taken me three years to get Oxford into a state where I can live and work in it, but I do not regret the effort.'

Before his retirement in 1979 he deposited in the University Archives all the relevant documents concerning this stormy period in the history of Zoology in Oxford together with his own history of the laboratory as given in a lecture to the Department on 28 May 1979.

#### 'HUMAN SCIENCES'

In his inaugural lecture of 24 October 1963, under the title 'The two biologies', Pringle had divided the subject into 'organismic' biology, concerned with ecology, evolution, behaviour and genetics, which were already well represented in Oxford zoology, and 'atomistic' biology, which included physiology and biochemistry, and which had recently



been expanding prodigiously in the guise of molecular biology—with, of course, a broad no man's land between, where the two became indistinguishable. His reorganization of the department had provided for a large measure of reinforcement to the atomistic side. But he still felt that there was another frontier at the upper limit of organismal studies, that is to say the study of man and his societies; a study that would be based on ideas coming from animal behaviour, psychology, anthropology, geography and genetics.

Like many others in the early 1960s he was intensely conscious of the dual threat to the human race from the exhaustion of natural resources on a global scale and from the explosion of human populations. Extensive publicity about these matters, which some regarded as 'alarmist', had attracted much attention. By his own assessment of himself Pringle was not an evangelist and he had no liking for publicity. His conception was that the weapon to use in the campaign for the ultimate survival of man was not propaganda but education.

In an after-dinner discussion in the Common Room of Linacre College in the autumn of 1963, with Dr Henri Tajfel of the Department of Social and Administrative Studies and others, the conversation turned on C. P. Snow's book *The two cultures and the scientific revolution*, in which the author deplored the divergence in outlook between science and the arts. Pringle suggested that Snow, as a physical chemist, had completely overlooked the bridging role of biology. There was a good measure of agreement from the assembled company, and as a result they got together a group of people in Oxford to explore the possibility of forming a bridge between Snow's two cultures.

The group included Dr A. H. Halsey (sociology), Professor Geoffrey A. Harrison (physical anthropology), Professor Niko Tinbergen (ethology and animal behaviour), Professor E. B. Ford (ecological genetics), Dr Michael Argyle, Dr E. W. Ardener (social anthropology), Dr K. R. Lewis and Dr Edward Houston (geography). After a series of after-dinner meetings they reached a common understanding about what should be included in a first-degree course on human science. To test their ideas, they decided to mount a series of special lectures in 1964–65 in which each contributor would indicate how he thought the special interests of his studies could be integrated into the new system. Pringle gave the first of these lectures with the title 'Can there be a scientific study of man and society?'

It is interesting to recall that Thomas Henry Huxley in his writings was frequently reverting to the vision of a general education based on the link between biology and the social sciences; Ray Lankester, who held the Linacre Chair of Zoology at Oxford from 1891 to 1899, went further in his Romanes Lecture of 1905 and urged Oxford to abandon its classical and historical scheme of education, which he regarded as having 'an injurious influence upon the education of the country', and to substitute a



scheme of education in the knowledge of Nature. These were visions. The human science group were out to put into operation actual teaching, in the form of an integrated course at undergraduate level. The series of special lectures was well attended and well received, in spite of the fact that they did not form part of any degree curriculum. So the group started on the long task of getting agreement to the introduction of a new Honour School, which involved cooperation between six Faculty Boards, on each of which there was perhaps only one member who was really sympathetic to the idea. Indeed the general attitude in the University was extremely hostile.

Finally Pringle got himself elected to the General Board and was able to persuade them to put the proposal to Congregation. The *University Gazette* of 7 August 1969 carried a lucid and persuasive statement for the ensuing debate on the desirability of this development—which must surely have been drafted by Pringle himself—stating: ‘The syllabus of the proposed course, which has been deliberately designed to draw almost entirely on existing courses of lectures and practical classes, is intended to cover the biological and social aspects of the study of man, and to this end the relevant elements of genetics, ethology, ecology, psychology, geography, sociology, and anthropology will be brought together in logical order.’

¶The final approval by the University was not without opposition; and although the vote in Congregation went in favour of starting the course, the feelings of some people were so strong as to demand, for the first time, the use of a postal vote. Grounds for opposition were that this type of course could not be tutored in colleges by one man; for some physicists it was not science and should not be so called; some thought it too superficial and others too difficult; some medical physiologists argued that their subject was the only true human biology. The first undergraduates to read human science were admitted in October 1970. The new Honour School had been started without any new University appointments.

Experiments along somewhat similar lines had been started in other universities, and Pringle made a point of studying their plans and giving lectures in other universities on the arrangement in Oxford. He favoured the idea of experiment and diversity, and deplored any suggestion that the Oxford plan should be deliberately copied elsewhere. At Oxford, as an alternative to the classical Greats and history, there had emerged P.P.E. (philosophy, politics and economics), the academic basis of the forces that were shaping the new world. In his most optimistic moments Pringle saw the new child, the Human Science School, some day attaining similar authority. Today, some twelve years after its establishment, the degree in human science is well regarded by University and Colleges; the subject has its own building and a group of staff who are completely dedicated to it.



## SCIENCE IN THE 'THIRD WORLD'

Pringle's interest in the problems of science in developing countries was first inspired by Professor P. M. S. Blackett's Presidential Address to the British Association in Dublin in 1955. His own experience of the tropics, his six months' sabbatical leave in Sri Lanka (p. 527) and his expedition in Trinidad to secure a source for the large belostomatid bugs needed for studies of muscular contraction, had not been concerned with the local scientific activities of the countries visited. His interest was stirred by attending the conference of commonwealth scientists organized by Blackett (then P.R.S.) in 1967, where the contribution by Professor Goma, Vice-Chancellor of the University of Zambia, brought home to him the difficulties experienced by postgraduate students from developing countries in pursuing their scientific research, initiated in the universities of a developed country, when they returned home.

A few years later Pringle was able to visit the Serengeti Research Institute in Tanzania (which had close links with his own department in Oxford) and to appreciate the very great difficulties in the way of coordinating the activities of expatriate research workers with the science departments in the University College at Dar-es-Salaam. Similar difficulties were experienced in the research institutes in the Queen Elizabeth National Park in Uganda and the Tsavo Research Centre in Kenya. All this was happening in the period of rapid transfer of government into African hands. The same difficult transfer was occurring in the research centres for agriculture and veterinary science, but in these more 'applied' fields of science the tension was less and cooperation was easier.

In 1969 T. R. Odhiambo of the University of Nairobi, who had studied for his Ph.D. in the Zoology Department in Cambridge a few years earlier, secured the cooperation of Karl Djerassi of Stanford University and the American Academy of Arts and Sciences in putting forward a scheme for an International Centre for the Study of Insect Physiology and Ecology (I.C.I.P.E.) in Nairobi, involving the close cooperation of scientists from developed countries with African scientists. The American Academy proposed that the scheme should be under the guidance of a 'consortium' of national academies world wide. This proposal was received with varying degrees of support and doubt by entomologists in Britain; but it made an immediate appeal to Pringle who was enthusiastically in favour of it from the outset, and in a contribution to the composite volume *Insect biology in the future* (1980) he gave some account of I.C.I.P.E. and of his own contribution to its activities.

In the early years (1969-77) the chief agents in the running of the centre in Nairobi were a number of experienced directors of research who undertook to visit the centre from time to time and guide research in specified fields that had a potential importance for application in agricul-



ture or public health. These same Directors of Research undertook to receive promising young African graduates in their laboratories for research training with a view to producing recruits for research in I.C.I.P.E. or in other establishments in Africa.

Both the research and the educational sides of the enterprise made a strong appeal to Pringle. The specific problem with which he was concerned was that of the migratory activities of *Spodoptera exempta*, the moth whose gregarious caterpillars constitute the African armyworm; a problem that gave rise to very diverse lines of research in the field and in the laboratory. Indeed he was surprised by the range of 'interesting scientific problems that arise from the study of an insect pest'. And in the laboratory Pringle was responsible for the organization and equipping of the section dealing with the electrophysiology programme. Pringle took my place on the Board of Governors of I.C.I.P.E. in 1972 and succeeded Caryl Wilson as Chairman, retaining this office until 1978. His abilities in laboratory planning, in the organizing of the finances, and the experience of Nairobi and of East Africa in general, which he had acquired during the six months (1972–73) that he spent as a Royal Society Visiting Professor in the University of Nairobi, were all devoted to the development of I.C.I.P.E. He established very good relations with William T. Mashler of the United Nations Development Programme (U.N.D.P.) and the Consultative group on International Agricultural Research (C.G.I.A.R.) and was thus extremely helpful in securing funds for I.C.I.P.E. during its first decade. He reorganized the financial administration of I.C.I.P.E. and was very active in supervising the laboratory construction.

Indeed at one period he seriously contemplated early retirement from his Chair in Oxford and devoting himself entirely to the welfare of I.C.I.P.E. But as time went on, the African Director, Professor Odhiambo, found himself in an increasingly difficult relationship with the visiting Directors of Research, who had extensive and ill-defined powers of administration. It was not only the natural desire to increase the African role in the running of this African centre that finally led to the abolition of the system of visiting Directors of Research and their replacement by permanent staff aided by outside consultants. At the same time the research programme had swung more towards immediate problems of pest control. These changes have weakened the tie between the national academies, including the Royal Society, and I.C.I.P.E.; but ways are still being sought to maintain these links to fulfil the original objective of ensuring the high scientific standard of research at the Centre to which Pringle had been so wholeheartedly devoted.

Aside from the hard work he put into I.C.I.P.E., John Pringle always looked forward to the prospect of escaping 'into the bush' and enjoying the birds and beasts. On one of these occasions he contracted a severe and prolonged attack of malaria. I twitted him with sleeping in the open





Professor J. W. S. Pringle with Professor T. R. Odhiambo (Director of I.C.I.P.E.) and Mr J. H. O. Omino (Permanent Secretary, Ministry of Natural Resources, Kenya) in Nairobi in 1977.

without a net; it turned out that he had surrendered his mosquito-netted bed to an unprovided lady in the party. He defended himself on the grounds that he was regularly taking his antimalarial pills; he did not know that the open markets of East Africa are flooded with these pills, which are voraciously consumed by all and sundry, so that many strains of *Plasmodium* are totally resistant to them.

## RESEARCH

### *Proprioception in insects*

Pringle's first year of research was devoted to an abortive attempt to learn about the sensory perceptions of molluscs by behavioural methods. But in the following year, under the guidance of R. J. Pumphrey, who introduced him to oscillographic methods, he turned to the study of proprioception in insects. In 1928–33 B. H. C. Matthews had published a series of papers on proprioception in vertebrates based on the electrical responses of nerves, disconnected from the central nervous system, when appropriate stimuli were given to the receptor organs. Pringle employed the methods of Matthews, recording impulses in the cut sensory nerves by means of platinum wire electrodes, a four-stage condenser coupled amplifier and a Matthews oscillograph, together with a loudspeaker.

The first organs studied were the joints of the maxillary palps of the cockroach *Periplaneta*. Passive movements at the joints gave rise to a stream of impulses, particularly if there was resistance to movement, whereas free active movements by the muscles themselves produced very little excitation. The sensory endings were located in the groups of campaniform sensilla in the cuticle just below the joint. They responded to bending of the cuticle at these points. Adaptation was slow and incomplete. Pringle concluded that the campaniform sensilla are 'stress receptors' responding to strains in the cuticular skeleton, in contrast to the tension receptors of vertebrates (1938a).

Weinland in 1980 and Demoll in 1917, from considerations of their structure, regarded the campaniform organs as responding to bending of the cuticle and inferred that their elongated shape enabled them to detect the direction of the stress. But Pringle's work was on a different level. In the second paper (1938b) he exhibits the qualities that characterize all his original researches. Turning to the legs of the cockroach he makes a meticulous study of the distribution and orientation of the elongated campaniform organs. He confirms the electrical response to compression force, showing that they are so placed that they will be subject to compression in the standing insect. Having arrived at this conclusion he adopts an engineering approach and goes more deeply into the mechanical forces involved. He argues that the response is not to 'bending', as had been supposed, but to the shear forces acting in the plane of the elastic cuticle; and, a final characteristic of his methods, he constructs a model



campaniform organ and by means of an electrical resistance device he measures the vertical movement (and so the tension exerted on what would be the nerve ending) in response to the compression force.

He observed the synchronous discharge in the nerve from multiple receptors, and believed that there was fusion between individual neurons. But the methylene blue method of staining was not adequate for such a conclusion. It has since been shown by improved fixation and staining, and particularly by the electron microscope, that no such fusion occurs: the number of axons in the insect sensory nerve is equal to the number of receptors.

The third paper (1938*c*) deals with the proprioceptive function of the 'hair plates' associated with the leg joints of the cockroach. These were regarded by Lowne as having a proprioceptive function in the blowfly *Calliphora*. In the cockroach they are mechanical sense organs with a slow rate of adaptation, the excitation varying with the position of the joint. They are regarded by Pringle as 'position' sense organs.

(Pringle did not deal at all with the chordotonal organs, which are important proprioceptors in insects and are often closely associated with the muscles to form tension receptors with some resemblance to those of vertebrates.)

Many years later Pringle returned to the study of proprioception in the appendages of other Arthropoda in the lyriform organs of arachnids, when working in Ceylon (1955*a*), and proprioceptors in *Limulus*, at Woods Hole (1956*c*). But his major contribution to proprioception was his classic work on the halteres or 'balancers' of Diptera (p. 535).

Pringle extended his work on *Periplaneta* to studies of the motor mechanisms and reflex mechanisms of the leg (1939, 1940). Extensive work had already been done in this field so that these papers deal with modifications of existing knowledge rather than the breaking of new ground. He recognized the distinction between nerves with a 'fast' action on the muscle contraction and nerves with a 'slow' action, but was unable to find a third or inhibitory nerve in the cockroach. He produced good evidence that the same muscle fibres were involved in each response, but the slow nerve brought only a few fibres into action. The earlier experiments on campaniform sensilla had shown that they are excited when the insect is standing on the ground in the normal position. They were now shown to be responsible for the reflex influence on the tone of the depressor muscles, thus completing the objective proof of the existence in the insect of a proprioceptive mechanism analogous to that of vertebrates.

A much later study (1952) of the response of a tactile spine on the femur of *Periplaneta* was an exercise to demonstrate the possibility of using engineering control methods in observing the mathematical relations between stimulus and response. The procedure was simple but ingenious, and it showed that when the spine was exposed to a harmonic



(sinusoidal) mechanical stimulus, which involved changes in tension without movement of the spine, the peak frequency of the nerve impulses precedes the maximum tension of the stimulus. This result is the corollary of the adaptation shown by the sensory response to a transient stimulus. The adaptation in this sense organ is slow compared with that in mechanical receptors in vertebrates as studied by E. D. Adrian.

### *The gyroscopic mechanism of the halteres of Diptera*

It had long been believed that the reduced hind wings of Diptera served in some way to secure the equilibrium of these insects in flight. Jousset de Bellesme in 1879 had shown that the flight of *Calliphora* or *Eristalis* became disorganized if the halteres were removed, so that they crashed to the ground like a kite without a tail; but they maintained their equilibrium if a small weight was attached to the abdomen. He inferred that, by some means, the halteres conveyed nervous information that led to the control of the wing movements. These conclusions were supported by Weinland in 1890. It was well known that the base of each haltere had a dense array of elongated campaniform organs, and also chordotonal organs, but their precise relation to the problem of equilibrium was quite unknown.

In 1938 Pringle conceived the novel idea that certain of the groups of elongated campaniform organs were so placed that they would not be exposed to stress during the normal vibration of the halteres through a vertical angle of about  $150^\circ$ , in harmony with the wings beating at about 200 times per second. But he opined that the rapidly oscillating haltere will act as an alternating gyroscope, and if the insect in flight rotates in a plane different from that of the oscillation, gyroscopic torques will be set up in the cuticle at the base of the haltere, about an axis at right angles to the plane of oscillation, and the resultant strain would be detected by the oriented campaniform sensilla.

This idea was published in a preliminary note by Fraenkel & Pringle (1938*d*). But the complete experimental analysis was not published by Pringle until after the war, in 1948. This paper is a classic of beautifully delicate work. It is argued from physical considerations that it is improbable that gyroscopic torques in the halteres will afford useful information with regard to pitching and rolling rotations. It is in the yawing plane that they will give exact information. And flash photographs of a haltere-less fly showed that the instability occurred mainly in the yawing plane. He made a detailed re-examination of all the groups of sensilla concerned, and confirmed the predictions of the gyroscopic theory by oscillographic records from the haltere nerve when in free movement and when the fly is rotated in yaw or roll. There is stimulation, probably of the dorsal and ventral scapel plates, during normal oscillation; this provides a sensory background against which the gyroscopic



torques, which stimulate the Hick's papillae and other campaniform organs, will be perceived. Video tapes of *Eristalis* in flight without halteres confirmed that it was in the yawing plane that reflex stabilization is required.

Almost all the lower Diptera have elongated abdomens and are stable in flight without their halteres. Pringle suggested that this inherent stability was a hindrance in making rapid turns—hence the short abdomen in the higher flies and the increase in haltere efficiency.

Since the publication of that paper further work, notably by G. Schneider and by R. Faust, has strongly suggested that the gyroscopic mechanism *can* operate also for stabilization in pitch and roll, and that both vision and sense organs responding to air currents play an important role in stabilization. In his monograph *Insect flight* (1957c) Pringle accepted some of these conclusions; others remained the subject of an exchange published in *Nature* (1958).

### *Insect song*

As will be related in the next section, Pringle turned to the cicada as an experimental animal for the purpose of studying the properties of the tymbal muscles, but at the same time he took the opportunity of exploring the physiology of their production of sound. By amplifying the output from a microphone and connecting to an oscilloscope he was able to obtain immediate photographic recordings of the sounds.

The normal song, produced by the vibration of the tymbals, which excites the resonance of the tracheal air cavities in the abdomen, consists of a train of damped oscillations at a fundamental frequency of about  $4500\text{ s}^{-1}$ , the frequency of repetition of the pulses being about  $390\text{ s}^{-1}$  ( $120\text{--}600\text{ s}^{-1}$ ), the pulse frequency being determined by the rate of contraction of the tymbal muscles.

The chordotonal sensilla associated with the tympana (the organs of hearing) are extremely sensitive to high-pitched sounds, and when the song of another cicada is played back through a loudspeaker the impulse pattern in the auditory nerve corresponds to the pulse modulation envelope, as had been pointed out by R. J. Pumphrey for other insect ears. The insect ear is little affected by changes in other qualities of the sound, such as pitch and tone, which are far more noticeable for the human ear than the modulation frequency.

The curvature of the tymbals can be increased by contraction of accessory tensor muscles and this controls the loudness of the sound. Some species emit a regular succession of pulses; others have a slow pattern to their song controlled by a pattern of nervous stimuli (1953b, 1954c).

During his visit to Ceylon in January to June 1953, Pringle made field recordings of the songs of 9 of the 19 species recognized in Ceylon



(including two new species that he himself described). He brought together all existing knowledge about Ceylon cicadas and their songs and habits (1955*b*). In another paper (1957*b*) Pringle described the anatomy and the organs of sound production and hearing in the two species of *Tettigarcta*, primitive cicadas from Australia, from which he concluded that tymbals and their muscles are developments of the first abdominal segment and he suggested that the system may have originated from movements made during copulation and not from flight muscles.

### *Insect flight muscles*

In 1949 Pringle published his first paper dealing with the excitation and contraction of flight muscles in insects (1949). During his work on the halteres he had noticed by chance that in some preparations, when the nerve to the haltere muscles had been cut, the haltere could still be induced to vibrate by an oscillatory activity of the muscles. Since the haltere is a reduced wing, it was this curious observation that induced him to tackle the mechanisms of flight muscle.

He studied the indirect fibrillar muscle of the blowfly *Calliphora* and he found that its behaviour was quite different from that of any known muscles. It appeared that an impulse in a nerve fibre supplying this muscle sets up an electrical 'spike' over the fibres and that as a result the myofibrils are brought into a state of excitation in which they contract actively when stretched. Their contraction stretches the antagonist muscles, which then contract in turn, and thus a myogenic rhythm is set up requiring only intermittent nervous stimuli to sustain the activated state; the rate of wing beat is determined not by the frequency of nerve stimuli but by the elastic properties of the thorax and the inertia of the wings. In *Calliphora* the motor nerve fibres discharge at a regular  $3\text{ s}^{-1}$ , and maintain wing beats of  $120\text{ s}^{-1}$ , although no reflexes of any sort are present. In this myogenic rhythmicity there are no synchronous potential changes in the fibre membranes.

This paper was the source of a stream of publications on insect flight muscle, which flowed from the efforts of Pringle and his colleagues (and many others) until the end of his career. Attempts to elucidate the mechanism of the rhythmic activity in *Calliphora* failed because the response did not occur when the flight muscle was isolated. Pringle therefore turned his attention to the sound-producing tymbal muscles of cicadas of the genus *Platypleura*, which have a similar histological structure and were found to have similar properties (1953*b*, 1954*b*).

The song of the cicada is produced by a pair of slightly convex drums or tymbals, which are operated like a tin lid pressed inwards by the finger. The isolated tymbal muscle gives normal twitches little faster than those of the frog sartorius, with similar mechanical summation and tetanus. But in their normal site they behave like the indirect wing muscles: provided



that the muscles receive nerve impulses from time to time, they show myogenic rhythmic activity, and contract and relax causing the tymbal to click in and out and so to generate the natural vibration responsible for the song. A single stimulus to the nerve will produce a series of clicks, and at 50 stimuli per second the muscle goes into rhythmic activity at a high frequency unrelated to that of the nerve impulses.

On this material it was possible to show that the myogenic rhythm of activity was maintained, not through 'excitation by stretch', as supposed in *Calliphora*, but through 'deactivation by release'.

In 1952 Boettiger & Furshpan had shown that in the higher Diptera the movement of the wings also is associated with a series of 'clicks'. During the almost isometric contraction of the indirect wing muscles, energy is stored in the elastic exoskeleton until suddenly released with a click and dissipated in wing movement. This sudden release occurs in both directions of the wing stroke. This mechanism must induce a very abrupt drop in tension and Pringle proposed that, as in the muscles of the cicada, the indirect flight muscles are deactivated by release (1957a). This response, together with the absence of synchronous potential changes during myogenic rhythmicity, were new properties for striated muscle and they raised the question whether such properties were latent in all striated muscle.

In the deactivated state the fibrillar muscles can be passively extended by a small force (such as the residual elasticity of the tymbal skeleton) and a sudden stretch at the end of the deactivation interval perhaps aids the redevelopment of tension. In his contribution to the Oregon symposium (1957a) Pringle reviews the state of knowledge about myogenic rhythms. He noted that myogenic rhythmicity in insects, correlated with the fibrillar structure, has evolved independently several times for flight and sound production. He put forward some tentative hypotheses about the nature of deactivation by release. In most insects the nervous activity of flight muscle is of the usual character with one nerve impulse for each contraction; from which there has been a gradual evolution of partial deactivation by release leading to a myogenic rhythm.

In the same year that the Oregon symposium paper appeared Pringle's monograph on *Insect flight* was published. This is a fine work with meticulous anatomical detail and such critical assessment of the published work reviewed that it sometimes seems to have the character of original work. It is still invaluable today. (It was updated in 1968c.) He also produced an animated film to explain the complicated linkages that operate in the wings of the bee.

A notable advance in the study of the myogenic rhythm in fibrillar muscle was the 'discovery' of the basalar flight muscle of lamellicorn beetles, notably the large rhinoceros beetle *Oryctes*. This muscle is connected to the wing by a cuticular apodeme, which makes it possible to isolate the muscle and use it for all kinds of experiments *in vitro*.



Moreover this muscle combines the function of supplying power to the wings with that of a graded effect on the wing movements (1959*a*). The mechanical properties of the basalar muscle are those seen in the fibrillar muscles of *Calliphora* and the tymbals of the cicada but the control of frequency and amplitude and other properties could now be studied systematically (1959*b*). The effect of sinusoidal changes in length (1960*a*) and the effect of temperature on the capacity for oscillatory work, and the integration of these parameters with the mechanically resonant system to which the muscle is connected (1962*a*) were the subjects of successive papers.

Using a length clamp to open the closed loop normally responsible for the oscillation of the muscle-load system, Boettiger had shown that, in fibrillar muscle, applied quick-stretch and quick-release produced respectively a rise or fall of tension after a delay. Machin & Pringle (1962*a*) used the same technique to measure the phase lag (between length change and tension change) to which this delay gives rise, if the applied changes of length are sinusoidal. They utilized for physiology the Nyquist plot, long used by engineers to display the results of sinusoidal studies of control systems. This enables the whole of the dynamic properties of the oscillatory contractile mechanism to be accurately visualized in a single graph. 'When joined to a vibrating effector system such as the wings, the work output of the muscle per cycle will be proportional to the negative viscous modulus. The greatest work will be obtained when the frequency of oscillation is equal to the frequency at which this viscous modulus has its maximum negative value.' This frequency depends on temperature, and the physical properties of the flight system in *Oryctes* match the physiological properties of the flight muscle only at a temperature of about 40 °C, which must be close to the intrathoracic temperature during flight in the tropics. 'The fitting of all these results into a useful model is proceeding; the conclusions of this analysis will be reported in a subsequent paper' (1962*a*). This paper marked the end of the Cambridge era.

At the time of his move to Oxford in 1961 Pringle planned to keep the study of muscle contraction as the base of his research interests. The Agricultural Research Council established a research unit of 'muscle biophysics and insect physiology' with Pringle as honorary director. He recruited a team of biochemists, a physiologist, a chemist, two zoologists, a physicist and an engineer. A stream of publications followed, many of which of course did not bear the director's name.

In 1967 Pringle published a detailed review, with full acknowledgements to his colleagues, on the contractile mechanism of insect fibrillar muscle (1967*a*). By this time the large belostomatid bug *Lethocerus* had been discovered as a source of large and long fibrillar muscles with the same characteristic properties; and sources of supply in India, Uganda and the West Indies had been located (1966*a*). And it had been shown by



Jewell & Rüegg that isolated glycerinated fibres with myofibrils freed from mitochondria and other components still retained oscillatory contractile activity when stretched in an appropriate solution of ATP and calcium ions (1964*d*). The sinusoidal (inertial) and pulsed mode of operation of insect fibrillar muscle are alternative ways in which oscillatory activity can be generated. They result from a single property of this type of muscle and occur when it is coupled, respectively, to an inertial or to a clicking load (1965*c*).

In this review (1967*a*) Pringle developed a model of muscle contraction that would conform with most of the properties of the system in insect fibrillar muscle and in vertebrate striated muscles. As in all such descriptions the key element, the molecular nature of the force involved, is missing; but because of the spontaneous oscillation of the glycerinated fibrils on stretching in an activating medium he considered this insect material more suitable than vertebrate skeletal muscle for study of the nature of the elementary contractile process (1967*c*, 1968*b*, 1969).

Insect fibrillar muscle at rest differs from vertebrate striated muscles in the high degree of its elasticity. This was attributed by Pringle to the presence of a hydrated gel joining the end of the myosin filaments to the Z-line. Filaments become visible in this material only after stretching (1974*b*, 1981*b*). Pringle contributed suggestive ideas on the physical and chemical aspects of the operation of the cross bridges in the contraction of striated muscle (1968*d*, 1975*b*).

The extensive researches of the Oxford team are well represented in the Proceedings of an Oxford Symposium held in April 1977 and edited by Richard T. Tregear under the title *Insect flight muscle*, to which Pringle himself made two contributions (1977*a*, 1977*b*).

A fitting climax to this thirty years' campaign was Pringle's Croonian Lecture on stretch activation of muscle (1978), from which I have made the following, more or less verbatim, notes. His swan song was his Bidder Lecture in 1980 on the evolution of fibrillar muscle in insects (1981*d*).

'Current theories about the mechanism of muscular contraction suppose that the level of enzymic and contractile activity is controlled by the intracellular concentration of calcium ions, the degree of overlap between the myosin and actin filaments, and the rate of relative sliding of the filaments.

'It is now known that in most or all muscles there is a further direct influence of mechanical conditions, usually called stretch activation; changes of length lead to a delayed change of active tension. The effect is large and functionally significant in insect fibrillar flight muscle and in mammalian heart muscle; it is present, but small, in vertebrate skeletal muscle, which probably accounts for its late discovery.

'In insect fibrillar flight muscle, the delayed tension is responsible



for the rhythmic mechanical activity during flight. In mammalian heart muscle it may play a role in Starling's law. In insect fibrillar muscle, extension produces a maintained increase in actomyosin ATPase and active tension; in vertebrate skeletal muscle, stretch activation is a transient phenomenon.

'The effective mechanical parameter is not overall strain but is probably the strain on an internal structure related to overall stress. Various lines of evidence point to the myosin filament as the location of the sensor.

'The phenomenon of bridge synchronization is probably of functional importance in the living insect. Unlike other striated muscles, which are required to generate steady tensions or a smooth shortening, the power-producing flight muscles must deliver their energy discontinuously at each wing stroke. This is most efficiently done if the rate of molecular activity of the cross bridges is matched to the frequency of wing beat, and if the bridges operate synchronously.

'Effectively, the enzyme is being driven by the mechanical input because of the phenomenon of stretch activation. This direct control of the energy source by the demands of the energy consuming system of the wings, perhaps constitutes the most remarkable functional adaptation in the whole range of phenomena involved in "local motion" in the animal kingdom.'

#### SPORT AND PASTIMES

In his school days Pringle did not achieve distinction in the usual sports. He preferred to pursue field natural history; this interest continued into his time in Cambridge where he became secretary of the C.U. Natural History Society. But in his third year as an undergraduate he had stayed with some cousins in Ireland and had taken up gliding. Back in Cambridge he became a member of a group, with John Paget as President and Pringle as Treasurer, which founded the Cambridge University Gliding Club in 1935; in fact it now includes a majority of non-University members. Almost from the outset the club, operating from a flat site, became famous for its winch launching and soon set up a national height record for this style. As the Editor of *Sailplane* wrote in 1937: 'The first cross-country flights from the Cambridge University Gliding Club site are notable events, in that the club has no hill for soaring, and has to rely entirely on thermal currents rising off a flat field.'

During World War II the club naturally collapsed, but one of the first things Pringle did on his return to Cambridge in the middle of 1945 was to rescue the 'Cambridge I' glider that was in storage in a barn near Dunstable and fly it from Heston to soar for three quarters of an hour over London (something that could not be done today!). Training started



again at Caxton Gibbet and 'Marshall's' (Cambridge Airport) in 1946. In 1949 Pringle set a new British record for an out and return flight in a two-seater glider. And in 1960 he gained Gold height, reaching 14 500 ft (*ca.* 4.4 km) over Marshall's airfield. Pringle had a remarkable eye for assessing country in gliding terms; a gift that is characteristic of glider pilots of international standard. His colleagues always felt that if he had set his mind to it he could have attained that standard. He became President of the resuscitated Cambridge club soon after the war and remained so until shortly before his death. He was chief test pilot of the British Gliding Association no. 2 test group. As President he seemed to the younger members a rather distant and austere figure with a reputation for firm and decisive action. But all his colleagues in the gliding club have the happiest recollections of John Pringle in action, in gliding clothes, completely relaxed, and far 'less formidable' than he seemed in every day life. There are countless anecdotes of their light-hearted escapades that commonly show John 'pressing on' regardless—sometimes with unfortunate consequences, but always with complete dominance over people and affairs.

Gliding is a seasonal sport, but Pringle devised a game known as 'thermal dice' by which it is possible to recapture some of the excitement of gliding during the closed season. The game rests on the general principles of 'snakes and ladders', in which thermals are chance events generated by dice. 'Altimeter' and 'variometer' readings are given by throws of dice, red for 'sink' and green for 'lift'; and the aim is to compete in making an agreed flight on the map. But this is no mere game of chance; the decisions made from the readings of the dice are based on experience and will depend on the type of machine that is being flown. By introducing additional hazards the game can be made more realistic and can become highly complicated and very exciting.

Thermal dice was originally conceived 'for amusement only', and Pringle was persuaded to write up and publish an account of the game in *Sailplane and Gliding*, volume 11, pages 18–19 (1960), in which he offered to supply a pair of coloured dice for one shilling in stamps. But constituted as he was Pringle could not prevent science creeping in. In 1977 Dr Anthony Edwards, who had already started putting thermal dice on to programmable calculators, discovered in correspondence that John Pringle had written an ALGOL program for thermal dice and was enjoying simulated 'cross-country flying'.

'But [writes Dr Edwards] I went a little further: it soon became obvious that one ought to be able to program the computer to take all the decisions as well, such as how fast to fly, when to circle, and so forth, and discovering the rules for these decisions led to a flurry of publications putting gliding theory on a firm mathematical basis. This happened in several countries simultaneously, but since the



British magazine *Sailplane and Gliding* is read worldwide the papers published in it were very influential and all trace back to John's idea of thermal dice.'

Pringle had many other outside interests. He was a keen gardener and beekeeper, a skilful woodworker, interested in painting, embroidery and wine-making, and concerned in the preservation of the country's canals. His interest in beekeeping had a wider impact for he was in close touch with beekeeping and bee research in both temperate zone and tropical countries and gave material service to the International Bee Research Association, as a member of Council from 1979 onwards; and to the last was occupied in the organization of the 3rd Congress on Apiculture in Tropical Climates to be held in Nairobi in 1984. It is not surprising to learn from *Bee World* that 'his incisive ability to go straight to the heart of the matter will be sorely missed at I.B.R.A. Council Meetings'.

#### PERSONALITY

John Pringle received a sincere Christian upbringing from both his father and his mother. He found no difficulty in fusing this religious teaching with the teachings of science in general and biology in particular; in 'accepting that the body and mind of man have evolved by natural selection *and* that there is an external Power from which it is possible to draw help and guidance by prayer'. Another part of Christian teaching that he could accept was 'the need for discipline, a personal need for personal discipline', and he saw much of this discipline 'as an innate inclination to conform to rules, bred into the human make-up by natural selection operating on simple communities at an early stage of development of social organization in man'. In his campaign for the teaching of human science he says: 'Science is not destructive—it is creative, and it is creative in a way that gives great hope for the future. For if man can understand himself and the society he has created, surely that is the best hope we have that he will be able to preserve and develop all that is good in it?'

Pringle had a very strong character; and with these guidelines one can understand his reactions at every crisis in his life. One can appreciate his altruistic commitment to the organization of teaching; his intense interest in 'third world science'; and his passion (it was nothing less) for creating a system of education in 'human science'. And one can perceive how he was able to battle his way to the achievement of his high objectives, free from the debilitating influence of too great a sense of humour.

During his war service he found a dictum: 'there is nothing that cannot be achieved by the man who will let someone else take the credit'. He was completely honest—too naïvely honest, I would guess, to be understood by some of his colleagues in East Africa who might have found devious



behaviour easier to comprehend. In his younger days I had admiration and respect for John Pringle, but I always thought of him as a somewhat ruthless character with a puritan interpretation of justice. He had the austere surface of the classic Wykehamist intellectual, with a contempt for stupidity and sloppy thinking. But one of those who knew him best compared him with 'an inverted *bombe surprise*—with a very thin cold layer of austerity spread over a warm and generous humanity. The outward cold soon thaws under the warmth of his smile and the charm of his family. And though he fights hard for what he believes the right objective, he does not make enemies.' I have always surmised that, as with many strong characters (if they are sufficiently fortunate) the fable of beauty and the beast contained the secret of his ontogeny. In his latter years the self-discipline was still very much in evidence; but it was a more gentle character that was revealed to the world at large.

It was characteristic of John Pringle that when his feelings were deeply moved he expressed them in verse. The few poems that I have read sometimes suffer in my judgement from hasty composition, but that does not conceal a genuine poetic feeling. Shortly before his retirement he wrote 'The red roses', which, of course, owes a debt to Ophelia, but is none the worse for that:

The red roses are gone, lady  
 The hedge is covered with grey.  
 The summer is finished and done, lady,  
 The winter has come to stay.  
 Don't grieve because of the rain, lady,  
 Do not have fear for the snow.  
 The important things remain, lady,  
 And they will never go.

John was in Nairobi in 1973 when he learned of the death of his colleague David Lack and he wrote an epitaph, which he sent to Mrs Lack. He felt that it would not be inappropriate for his own epitaph, so I reproduce it here:

If my soul return to earth  
 At the final morning,  
 Great Redeemer, give it birth  
 As the day is dawning;  
 As the music of the wild  
 Breaks in all its glory,  
 Telling for the billionth time  
 Life's unending story.

I am indebted to many persons for helpful information, notably Dr A. W. F. Edwards, Professor G. A. Harrison, Dr W. B. Lewis, F.R.S.,

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The frontispiece photograph was taken by Walter Stoneman in about 1954.

### BIBLIOGRAPHY

- 1938*a* Proprioception in insects. I. A new type of mechanical receptor from the palps of the cockroach. *J. exp. Biol.* **15**, 101–113.
- 1938*b* Proprioception in insects. II. The action of the campaniform sensilla on the legs. *J. exp. Biol.* **15**, 114–131.
- 1938*c* Proprioception in insects. III. The function of the hair sensilla at the joints. *J. exp. Biol.* **15**, 467–473.
- 1938*d* (With G. FRAENKEL) Halteres of flies as gyroscopic organs of equilibrium. *Nature, Lond.* **141**, 919–921.
- 1939 The motor mechanism of the insect leg. *J. exp. Biol.* **16**, 220–231.
- 1940 The reflex mechanism of the insect leg. *J. exp. Biol.* **17**, 8–17.
- 1948 The gyroscopic mechanism of the halteres of Diptera. *Phil. Trans. R. Soc. Lond. B* **233**, 347–384.
- 1949 The excitation and contraction of the flight muscles of insects. *J. Physiol., Lond.* **108**, 226–232.
- 1950*a* The flight of insects. *Sch. Sci. Rev.* **31**, 364–369.
- 1950*b* The instrumentation of the living body. *Penguin Sci. News* **17**, 100–114.
- 1951 On the parallel between learning and evolution. *Behaviour* **3**, 174–215.
- 1952 (With V. J. WILSON) The response of a sense organ to a harmonic stimulus. *J. exp. Biol.* **29**, 220–234.
- 1953*a* The origin of life. *Symp. Soc. exp. Biol.* **7**, 1–21.
- 1953*b* Physiology of song in cicadas. *Nature, Lond.* **172**, 248–249.
- 1954*a* The evolution of living matter. *New Biol.* **16**, 54–67.
- 1954*b* The mechanism of the myogenic rhythm of certain insect striated muscles. *J. Physiol., Lond.* **124**, 269–291.
- 1954*c* A physiological analysis of cicada song. *J. exp. Biol.* **31**, 525–560.
- 1955*a* The function of the lyriform organs of Arachnids. *J. exp. Biol.* **32**, 270–278.
- 1955*b* The songs and habits of Ceylon cicadas, with a description of two new species. *Spolia zeylan.* **27**, 229–238.
- 1955*c* L'évolution de la matière vivante. In *Une discussion sur l'origine de la vie*. Paris: L'Union Rationaliste.
- 1956*a* Insect song. *Endeavour* **15**, 68–72.
- 1956*b* The physiology of insect song. *Acta physiol. pharmac. néerl.* **5**, 88–97.
- 1956*c* Proprioception in *Limulus*. *J. exp. Biol.* **33**, 658–667.
- 1956*d* The origin of life. Eaurpean Service Broadcast, B.B.C., 14 August.
- 1957*a* Myogenic rhythms. In *Recent advances in invertebrate physiology* (ed. B. T. Scheer), pp. 99–115. University of Oregon Publications.
- 1957*b* The structure and evolution of the organs of sound production in cicadas. *Proc. Linn. Soc. Lond.* **167**, 144–159.
- 1957*c* *Insect flight*. Cambridge University Press.
- 1958 Static sense of *Calliphora* and the physical stabilizing effect of the halteres. *Nature, Lond.* **181**, 1355–1356. (Answer to Dr G. Schneider.)
- 1959*a* (With F. W. DARWIN) The physiology of insect fibrillar muscle. I. Anatomy and innervation of the basalar muscle of lamellicorn beetles. *Proc. R. Soc. Lond. B* **151**, 194–203.
- 1959*b* (With K. E. MACHIN) The physiology of insect fibrillar muscle. II. Mechanical properties of a beetle flight muscle. *Proc. R. Soc. Lond. B* **151**, 204–225.
- 1960*a* (With K. E. MACHIN) The physiology of insect fibrillar muscle. III. The effect of sinusoidal change of length on a beetle flight muscle. *Proc. R. Soc. Lond. B* **152**, 311–330.
- 1960*b* Models of muscle. *Symp. Soc. exp. Biol.* **14**, 41–68.
- 1961*a* Proprioception in arthropods. In *The cell and the organism* (ed. J. A. Ramsay & V. B. Wigglesworth), pp. 256–282. Cambridge University Press.



- 1961b The function of the direct flight muscles in the bee. In *XI Int. Congr. Ent., Vienna, 1960*, vol. 1, p. 660 (with 16 mm film).
- 1961c The evolution of muscle. In *Problems of the evolution of function and enzymochemistry of excitation processes*, pp. 270–280. Moscow: Publ. U.S.S.R. Acad. Sci. [In Russian.]
- 1961d The flight of the bumblebee. *Nat. Hist.*, N.Y., August–September, pp. 21–29.
- 1962a (With K. E. MACHIN & M. TAMASIGE) The physiology of insect fibrillar muscle. IV. The effect of temperature on a beetle flight muscle. *Proc. R. Soc. Lond. B* **155**, 493–499.
- 1962b A preliminary classification of cicada songs. In *XI Int. Congr. Ent., Vienna, 1960*, vol. 2 (with tape).
- 1962c Prologue: the input element. *Symp. Soc. exp. Biol.* **16**, 1–11.
- 1962d Possible changes in the teaching of zoology at universities. *J. Inst. Biol.* **9**, 77–78.
- 1963a Proprioceptive background to mechanisms of orientation. *Ergebn. Biol.* **26**, 1–10.
- 1963b *The two biologies*. Inaugural lecture, 24 October. Oxford.
- 1963c Biology at Oxford. *Sch. Sci. Rev.* **154**, 1–2.
- 1963d Physiologie du muscle de vol chez les insectes. *Actualités neurophysiol.* (5th series), pp. 123–136.
- 1964a (With D. LESTON) Acoustical behaviour of Hemiptera. In *Acoustic behaviour of animals* (ed. R.-G. Busnel), pp. 391–411. Elsevier.
- 1964b (With D. LESTON) Addendum of chapter 14 [1964a]. In *Acoustic behaviour of animals* (ed. R.-G. Busnel). pp. 798–799. Elsevier.
- 1964c Input and output elements of behavioral models. In *Neural theory and modelling* (ed. R. F. Reiss), pp. 31–42. Stanford University Press.
- 1964d (With B. R. JEWELL & J. C. RÜEGG) Oscillatory contraction of insect fibrillar muscle after glycerol extraction. *J. Physiol., Lond.* **173**, 6–8.
- 1964e (With B. R. JEWELL & J. C. RÜEGG) Langdauernde Oscillation der fibrillären Flugmuskeln von Insekten nach Extraction mit Wasser-Glycerin. *Pflügers Arch. ges. Physiol.* **281**, 47–48.
- 1964f The evolution of muscle. In *Essays on physiological evolution* (ed. J. W. S. Pringle), pp. 243–252. Pergamon Press. [Translation from Russian of 1961c.]
- 1964g Can there be a scientific study of man and society? Special Lecture, Oxford, 13 October.
- 1965a (With S. B. BARBER) The functional organisation of the flight system in Belostomatid bugs (Heteroptera). In *Proc. XII Int. Congr. Ent., 1964*, pp. 185–186.
- 1965b Locomotion: flight. In *The physiology of insects* (ed. M. Rockstein), vol. 2, pp. 283–329. Academic Press.
- 1965c (With D. LESTON & D. C. S. WHITE) Muscular activity during preparation for flight in a beetle. *J. exp. Biol.* **42**, 409–414.
- 1965d Biological responsibility in a technological society. *Biology hum. Affairs* **30**, no. 3.
- 1965e Research on muscular contraction at the Department of Zoology, Oxford. (Scientific Memo no. 34 of Information Exchange Group no. 4.)
- 1965f (editor) *Essays on physiological evolution*. Pergamon Press. (Based on a book published in Moscow in 1961 in memory of K. S. Koshtoyants.)
- 1966a (With S. B. BARBER) Functional aspects of flight in belostomatid bugs (Heteroptera). *Proc. R. Soc. Lond. B* **164**, 21–39.
- 1966b The treasure-house of nature. *Adv. Sci.* **23**, 297–304. (Presidential address to section D of the British Association, Nottingham, September.)
- 1967a The contractile mechanism of insect fibrillar muscle. In *Progress in biophysics and molecular biology* (ed. J. A. V. Butler & H. E. Huxley), vol. 17, pp. 3–60. Pergamon Press.
- 1967b (With K. MARUYAMA) The effect of ADP on the ATPase activity of insect actomyosin at low ionic strength. *Archs Biochem. Biophys.* **120**, 225–226.
- 1967c Evidence from insect fibrillar muscle about the elementary contractile process. *J. gen. Physiol.* **50**, 139–156.
- 1968a Richard Julius Pumphrey. *Biogr. Mem. Fell. R. Soc. Lond.* **14**, 435–442.
- 1968b (With K. MARUYAMA & R. T. TREGGAR) The calcium sensitivity of ATPase activity of myofibrils and actomyosins from insect flight and leg muscles. *Proc. R. Soc. Lond. B* **169**, 229–240.
- 1968c Comparative physiology of the flight motor. *Adv. Insect Physiol.* **5**, 163–227.
- 1968d Mechano-chemical transformation in striated muscle. *Symp. Soc. exp. Biol.* **22**, 67–78.
- 1969 (With R. T. TREGGAR) Mechanical properties of insect fibrillar muscle at large amplitudes of oscillation. *Proc. R. Soc. Lond. B* **174**, 33–50.
- 1970 Biology as a human science. *Biologist* **17**, 204–207.

- 1972a A vision of man (12th Darwin Lecture). *Biologist* **19**, 223–237.
- 1972b Arthropod muscle. In *The structure and function of muscle* (ed. G. H. Bourne), pp. 491–541. Academic Press.
- 1972c (editor) *Biology and the human sciences* (The Herbert Spencer Lectures, 1970). Oxford: Clarendon Press.
- 1972d 3rd Session of Oxford discussions on higher education. *Minerva* **10**, 303–308.
- 1974a Locomotion: flight. In *The physiology of insects*, 2nd ed. (ed. M. Rockstein), vol. 3, pp. 433–476. Academic Press.
- 1974b The resting elasticity of insect flight muscle. *Symp. biol. hung.* **17**, 67–78.
- 1974c Singing muscles in a katydid. *Nature, Lond.* **250**, 442.
- 1975a *Insect flight*. Oxford Biology Reader no. 52. Oxford University Press.
- 1975b Insect fibrillar muscle and the problem of contractility. In *Comparative physiology—functional aspects of structural materials* (ed. L. Bolis, H. P. Maddrell & K. Schmidt-Nielsen), pp. 139–152. North-Holland.
- 1975c Effects of World War II on the development of knowledge in the biological sciences. *Proc. R. Soc. Lond. A* **342**, 537–548.
- 1976a Obituary. The research work of Torkel Weiss-Fogh. *Trends Biochem. Sci.* **1**, 38–39.
- 1976b The muscles and sense organs involved in insect flight. *Symp. R. Ent. Soc.* **7**, 3–15.
- 1976c *The flight of the bee*. Central Association of Beekeepers, 8 Gloucester Gardens, Ilford, Essex, England. (Gooding Lecture.)
- 1976d The mechanism of knowledge: limits to prediction. In *Proc. 5th Int. Conf. Unity Sci., Washington, D.C.*, vol. 2, pp. 961–980. New York: International Cultural Foundation.
- 1977a The mechanical characteristics of insect fibrillar muscle. In *Insect flight muscle* (ed. R. T. Tregear), pp. 177–196. North-Holland.
- 1977b The availability of insect fibrillar muscle. In *Insect flight muscle* (ed. R. T. Tregear), pp. 337–344. North Holland.
- 1977c Hard reason and deep humanity. *Nature, Lond.* **265**, 477. (Review of book by V. B. Wigglesworth.)
- 1978 Croonian Lecture, 1977. Stretch activation of muscle: function and mechanism. *Proc. R. Soc. Lond. B* **201**, 107–130.
- 1979 Le vol des insectes. *Probio-Revue*, vol. 2, pp. 283–298. Association Francophone des Professeurs de Biologie de Belgique.
- 1980 Science of a pest: research on the African armyworm at the International Center of Insect Physiology and Ecology, Nairobi. In *Insect biology in the future* (ed. M. Locke & D. S. Smith), pp. 925–945. Academic Press.
- 1981a A review of arthropod muscle. In *Development and specialisation of muscle* (ed. D. F. Goldspink), pp. 91–105. Cambridge University Press.
- 1981b (With B. BULLARD & G. SAINSBURY) Localization of a new protein in the Z-discs of insect flight and vertebrate striated muscle. *J. Physiol., Lond.* **317**, 19–20.
- 1981c Review of *Reflections on muscle* by Sir Andrew Huxley. *J. Muscle Res. Cell Motil.* **2**, 469–470.
- 1981d The evolution of fibrillar muscle in insects. (Bidder Lecture, 1980.) *J. exp. Biol.* **94**, 1–14.
- 1982a Le vol des insectes. *La Recherche*, no. 130, Février, pp. 158–168.
- 1982b Chairman of symposium *Population and values*. International Conference on the Unity of the Sciences, Miami Beach, November 1980.