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Obituary Notice

MARJORY STEPHENSON, 1885–1948

The death of Marjory Stephenson on 12 December 1948 has robbed biochemistry of a vigorous and productive exponent, and microbiology of a valuable interpreter of the chemical way of thinking. She was born on 24 January 1885 at Burwell, twelve miles from Cambridge; her life centred on Cambridge; she knew the town well and was well known in it. After graduating from Newnham she had hoped to complete a medical course but found it necessary to study Domestic Science at the Gloucestershire Training College instead, and she taught for a time there and at King's College of Household Science, London. Her career as a biochemist started at University College, London, working with R. H. A. Plimmer. In later life she always spoke of him with gratitude for providing her with this opportunity. She there studied the lactase of intestinal mucosa and showed that this enzyme was inhibited by glucose but not by galactose (Stephenson, 1911). She turned next to the synthesis of esters of palmitic acid (Stephenson, 1913) and then worked on metabolism in experimental diabetes (Moorhouse, Paterson & Stephenson, 1915). This work was interrupted by the 1914–18 war, during which she served with the Red Cross in France and at Salonika. After the war she returned to Cambridge and worked in the department of Frederick Gowland Hopkins on the fat-soluble vitamins (Stephenson & Clark, 1920; Stephenson, 1920). Hopkins in his wisdom encouraged her to leave the fields of animal metabolism and vitamins and to initiate a comprehensive study of the biochemical activities of bacteria.

There are obvious differences in the characters of recruits to different sciences at different stages of development and the Cambridge Biochemical Laboratory, which was for many years the main centre of biochemical teaching in Britain, attracted in its early days people who were vigorous, self-confident and not always tactful. In this environment M. S. (to use the title by which she became known internationally) was very much at home. Hopkins had established a new department and a new attitude of mind in Cambridge and his personal gentleness served admirably to weld the members of the department into a co-operative group. This was no mean feat, for they were once described to Hopkins by an important official of the University as 'That wrecking crew of yours'. Hopkins's character moulded the scientific outlook of his department but he came to depend, to an extent that was not always fully recognized, on M. S. for advice and support with the social and strategic problems of the department. Biochemistry met with strong and skilful opposition from many of the old-established departments—an opposition that still confronts those establishing biochemical schools in such Universities as lack them—and this antagonism was reciprocated by the research workers in the young department.

MARJORY STEPHENSON (1885–1948)

Portrait by Mrs Campbell Dodgson; reproduced by permission of the Principal of Newnham College, Cambridge.

Some of the criticism had a superficial justice; the chemists said we lacked chemical skill, the biologists, biological knowledge. M. S. received, and returned with interest, criticism for her lack of fundamental bacteriological training. To her, in the first stages of her work, bacteria were simply tools and their taxonomy was of little importance. She recognized early that there could be greater metabolic differences between samples of the same culture at different phases of growth than between different species. The self-confidence that Pasteur had shown when, without medical training, he set about the construction of a bacteriological theory of disease, was an inspiration to her and she liked to quote his reply to someone who corrected him on a formal bacteriological point: 'If you only knew how little difference that makes to me.' As in Pasteur's case a new idea was of more importance than old knowledge and it is unlikely that her work would have been any more fruitful if she had had the training that many people looked on as essential.

Marjory Stephenson's new line of work at Cambridge was begun at a most exciting time: the Wieland-Thunberg theory of biological oxidations had been propounded; Hopkins had isolated what was thought to be an important hydrogen carrier, glutathione; and the Cambridge laboratory was turning to the study of intra-cellular enzymes with particular emphasis on oxidation mechanisms. This background had a profound and lasting effect on M. S.'s approach to bacterial metabolism.

Her first paper on bacteria, published in collaboration with Miss Whetham (Stephenson & Whetham, 1922), was concerned with fat formation by *Mycobact. phlei* and the effect of different media thereon. It was shown that acetate increased fat production more than any other substance tested. Methods were developed for the determination of both the respiratory quotient and the carbon balance-sheet during growth and it was found that, as the medium became exhausted, so the respiratory quotient fell and the stored fat disappeared (Stephenson & Whetham, 1923). These techniques were then applied to the study of the effect of oxygen on the metabolism of *Bact. coli communis* (Stephenson & Whetham, 1924).

During this period her colleagues J. H. Quastel and Margaret D. Whetham were developing the resting-cell technique by which, in conjunction with the Thunberg methylene blue procedure, they had demonstrated the presence of dehydrogenases in bacteria and had shown that the succinic dehydrogenase was reversible. This made possible an investigation of anaerobic growth. It was known that *Bact. coli* could grow aerobically but not anaerobically with succinate, lactate, glycerol or acetate as the carbon source, and also that certain organisms, including *Bact. coli*, could reduce nitrate to nitrite. In collaboration with Quastel and Whetham, M. S. showed that washed suspensions of *Bact. coli* oxidized leuco-methylene blue in the absence of oxygen, provided that either nitrate or chlorate were present. The coupling of succinate oxidation with nitrate reduction was then demonstrated and also that this coupled oxido-reduction reaction would permit the anaerobic growth of *Bact. coli*: succinate was replaceable by lactate, glycerol or acetate; and fumarate, malate or aspartate could be substituted for nitrate as hydrogen acceptor. Chlorate,

whilst active as a hydrogen acceptor in cell-suspensions, could not be used as such in growth experiments owing to the toxicity of the chlorite formed as reduction product (Quastel, Stephenson & Whetham, 1925). These simple experiments served to emphasize the usefulness of washed suspension studies in the elucidation of problems of bacterial metabolism and at the same time made clear some of the principles underlying anaerobic growth. This line of work was continued with J. H. Quastel (Quastel & Stephenson, 1925) and later the effect of oxygen on the growth of obligate anaerobes was studied (Quastel & Stephenson, 1926).

Many years later, at the inaugural meeting of the Society for General Microbiology in February 1945, M. S. analysed the steps in the development of research in the field of bacterial metabolism, and pointed out that research took place at a series of levels. At the first level the worker was concerned with mixed cultures; at the second with pure cultures growing in complex media; at the third with pure cultures growing in chemically defined media; at the fourth with washed cell-suspensions from pure cultures; and finally at the fifth level with cell-free enzyme preparations. No one level was, by itself, adequate; and for an understanding of bacteria as they are found in Nature, research must occur at all levels. Till about 1927 she had worked at levels two and four, but in 1928 she developed a method for obtaining intra-cellular enzymes (Stephenson, 1928). Thick suspensions of *Bact. coli* were allowed to autolyse in phosphate buffer at pH 7·4, and lactic dehydrogenase was found in the cell-free autolysate. Unfortunately the technique had only a limited application and further progress had to wait until improved methods for breaking-up bacterial cells were developed, some ten years later. In the meantime, work was continued with washed suspensions, and in collaboration with R. P. Cook (Cook & Stephenson, 1928) she made a detailed study of the oxidation of various compounds by *Bact. coli* and *Bact. alkaligenes*. This yielded the surprising result that, whereas formate was oxidized quantitatively to carbon dioxide and water, glucose, lactate, pyruvate or acetate were, as judged by the oxygen consumed, only partially oxidized; at the same time the substrate disappeared completely. This phenomenon could not be related to the viability of the suspension. Subsequent work in other laboratories and with other organisms confirmed these observations and demonstrated that only part of the substrate was oxidized completely, the remainder being assimilated by the cell.

About 1930 the Cambridgeshire Ouse was polluted by waste from a sugar-beet factory to such an extent that an active fermentation could be observed in the river itself. This provided an opportunity for investigating the methane fermentation, using the polluted river water as an inoculum. These enrichment cultures, in addition to producing methane from formate, reduced sulphate to hydrogen sulphide and made methane from carbon dioxide and hydrogen. Stephenson & Stickland (1931 *a*) commented on these observations as follows: 'This led to the conception that carbon dioxide and sulphate were acting as hydrogen acceptors in a system where molecular hydrogen was the hydrogen donor and it seemed likely that bacteria were present in the mixed culture capable of activating hydrogen.' To test this hypothesis a washed suspension of

the enrichment culture was examined by the Thunberg method for its ability to activate hydrogen. It was found that, in the presence of hydrogen, a rapid reduction of methylene blue occurred. A coliform bacterium was isolated from the crude culture and was shown to contain the enzyme, which was named hydrogenase. This enzyme was found to be widely distributed amongst bacteria, and in view of this it was suggested, somewhat tentatively, that the production of hydrogen from formate, a reaction which L. H. Stickland (1929) had been investigating, involved two enzymes, formic dehydrogenase and hydrogenase.

The reduction of sulphate to hydrogen sulphide by hydrogen was next investigated (Stephenson & Stickland, 1931*b*) and a bacterium closely related to *Desulphovibrio desulphuricans* was isolated in pure culture. The bacterium possessed a powerful hydrogenase and could grow on sulphate and hydrogen with carbon dioxide as carbon source; sulphite or thiosulphate could replace sulphate as hydrogen acceptor. This work provided the first indication that this group of organisms could live autotrophically.

Finally the methane organisms were examined (Stephenson & Stickland, 1933*a*). Enrichment cultures were readily maintained on formate and produced methane according to the following equation:

$$4HCOOH \rightarrow CH_4 + 3CO_2 + 2H_2O.$$

A pure culture was isolated by the single-cell method, since conventional plating techniques consistently failed, and the organisms so obtained were found to possess hydrogenase. A number of one-carbon compounds, including formate, formaldehyde (added as hexamethylenetetramine), methanol, carbon monoxide and carbon dioxide, were reduced to methane in the presence of hydrogen by this organism; in addition sulphate was reduced to hydrogen sulphide. Though possessing some of the characteristics of the methane bacteria subsequently isolated by Barker and by Schnellen, this organism was unique in its ability to reduce methanol, formaldehyde and formate to methane, and to-day it seems probable that in spite of all efforts to purify it the culture was contaminated with a sulphate-reducer (the reduction of sulphate to hydrogen sulphide supports this view). The sulphate-reducer would produce carbon dioxide from the above substrates, which carbon dioxide would then be reduced to methane by the methane bacteria.

At this point the work along these lines was dropped and a re-investigation of the production of hydrogen from formate was begun (Stephenson & Stickland, 1932). L. H. Stickland (1929) had shown that washed suspensions of *Bact. coli* grown on a tryptic digest of casein medium, possessed a powerful formic dehydrogenase, but would produce hydrogen from formate only after a prolonged incubation with the substrate; it seemed as though hydrogen production were associated with the growth of the organism. The appearance of Karström's paper (1930) on adaptive enzymes prompted the suggestion that the production of hydrogen and carbon dioxide from formate might be an adaptive phenomenon; accordingly *Bact. coli* was grown on media containing formate and it was found that washed suspensions of these 'adapted' cells decomposed formate to hydrogen and carbon dioxide. Enzymes producing

hydrogen were called hydrogenlyases, and the formic enzyme, formic hydrogenlyase, to distinguish it from glucose hydrogenlyase, an enzyme considered to produce hydrogen specifically from glucose; two distinct enzymes were postulated on the grounds that the substrate affinity curve and the pH curve for the two processes differed from one another. This view met with considerable opposition and it now appears unlikely that there are, in fact, two hydrogenlyases in *Bact. coli*. In an earlier paper Stephenson & Stickland had suggested that the production of hydrogen from formate might be explained in terms of a coupled reaction between formic dehydrogenase and hydrogenase:

$$\mathrm{HCOOH} \overset{\text{formic dehydrogenase}}{\rightleftharpoons} 2\mathrm{H}^{\cdot} + \mathrm{CO_2} + 2e$$

$$2\mathrm{H}^{\cdot} + 2e \overset{\text{hydrogenase}}{\rightleftharpoons} \mathrm{H_2}$$

If this were true, it was clear that all organisms producing hydrogen from formate must contain both hydrogenase and formic dehydrogenase. This was not the case; four strains of *Bact. lactis aerogenes* were found which made hydrogen from formate yet contained no hydrogenase, and it was concluded that formic hydrogenlyase was in fact a separate enzyme. The adaptive nature of formic hydrogenlyase was established by Stephenson & Stickland (1933*b*), for the enzyme was produced only when the medium contained formate and under conditions of partial anaerobiosis; further, enzyme production seemed to be independent of growth.

This work on adaptive enzymes turned M. S. to the study of the factors involved in enzyme formation, but hydrogen metabolism was not dropped. D. D. Woods (1936) showed that formic hydrogenlyase was reversible and Woods & Clifton (1937) studied hydrogen formation from amino-acids and demonstrated that formate was not an intermediary. In 1937 M. S. reviewed the position of formic hydrogenlyase (Stephenson, 1937) and passed her final judgment on hydrogen metabolism in her contribution to the volume dedicated to A. J. Kluyver (Stephenson, 1948).

The formation of galactozymase in the presence of the substrate by *Saccharomyces cerevisiae* was investigated by Stephenson & Yudkin (1936) and in *Bact. coli* by Stephenson & Gale (1937*a*).

M. S. had always been interested in the amino-acid metabolism of bacteria, and under her guidance L. H. Stickland, and later D. D. Woods, elucidated the metabolism of *Cl. sporogenes*. It had been widely held that glucose exercised a 'sparing' action on amino-acids; this she disbelieved, and with E. F. Gale undertook the study of the enzymes oxidizing amino-acids (Stephenson & Gale, 1937*b*). The method of attack was to examine the effect of different media and conditions of growth on the formation of the alanine, glycine and glutamic deaminases. In all cases the presence of glucose in the medium inhibited the formation of the enzyme. This inhibition was due neither to the anaerobic conditions set up by the resulting fermentation nor to the increase in hydrogen ion concentration. The enzymes, once formed, were not markedly affected by glucose.

The serine deaminase was next investigated (Gale & Stephenson, 1938). The

enzyme resembled those previously studied in that its formation was inhibited by glucose, but it differed in that the deamination occurred both aerobically and anaerobically, and was much more rapid than those previously studied. The enzyme was not stable; a suspension allowed to stand even at 0° lost its activity. This inactivation could be prevented by the addition of extracts of *Bact. coli*, or by such reducing systems as hydrogen, formate, glutathione, all of which required phosphate for maximum activity. Reactivation after decay had taken place could only be brought about if the decay took place at 0°, and systems similar to those preventing decay also restored activity.

In collaboration with A. R. Trim (Stephenson & Trim, 1938), the deamination of adenylic acid, adenosine and adenine was investigated. Adenylic acid was both deaminated and dephosphorylated; adenosine was rapidly deaminated whereas adenine was attacked but slowly, this last reaction being stimulated by adenosine.

Meanwhile V. H. Booth and D. E. Green had made their wet-crushing mill which made possible the preparation of cell-free enzymes from bacteria. With this new tool M. S., with E. F. Gale and J. L. Still, made cell-free preparations of a number of enzymes from *Bact. coli* (cf. Gale & Stephenson, 1938; Stephenson, Gale & Still, 1939).

When the second world war started, the possibility of a rubber shortage and the probable extension of the synthetic rubber industry stimulated M. S. to study the mechanism of the butanol fermentation, with a view to increasing the yield of solvents. This fermentation had never been examined by the use of washed cell-suspensions. Great difficulty was experienced in the preparation of active suspensions, for the enzymes involved were very labile. The inclusion of both glucose and yeast autolysate in the suspending medium, and careful attention to anaerobiosis throughout the preparation of suspensions finally gave active preparations. This work was done with R. Davies as her co-worker (Davies & Stephenson, 1941).

The microbiological assay of vitamins of the B group next engaged her attention, and although M. S. published nothing on this, she took an active part in the large-scale trials of the various methods, thought necessary as a result of the divergent values for the same materials reported by different laboratories. She did not enjoy this work, though the full-cream dried milk left over from the experiments was some compensation.

When the war ended, M. S. became interested in the synthesis of acetylcholine by micro-organisms. There were reports in the literature of the production of acetylcholine during the sauerkraut fermentation; this was confirmed (Stephenson & Rowatt, 1947), and the responsible organism isolated from sauerkraut. The presence of choline in the medium was obligatory for the synthesis and, following up F. Lipmann's observations on acetylation by the liver, it was demonstrated that pantothenic acid also was a component of the system.

Her last piece of work, not yet published, was concerned with nucleic acid metabolism; soon after she had begun this problem she wrote...'I have got onto the most interesting piece of research I have ever done and where it's going to turn next I just don't know.'

Her research work may be summarized as the application to bacteria of Hopkins's concept of dynamic biochemistry; her tools were washed cell-suspensions and, where possible, cell-free extracts. She was not particularly interested in complex reactions, at least until her last years, and in general she attempted to study single enzymes. Her approach was simple: to demonstrate the reaction with washed cell-suspensions; to study the kinetics of the system and the factors controlling the formation of the enzyme; and finally, in order to learn more about the mechanism, to try to prepare an active cell-free extract. This was the method developed by her and now used wherever bacterial metabolism is studied.

She spread her gospel in a number of ways, not the least of which was her course given to the Part II Tripos class in biochemistry at Cambridge. It is a testament to her activities that bacterial metabolism flourished in Cambridge to such an extent that it was recognized by the University as a discipline in its own right, and she herself was made University Reader in Chemical Microbiology in 1947.

She approached bacteriology without, in the first instance, any regard for its practical applications and the support for her work by the Medical Research Council from 1922 and her establishment on its Staff in 1929 were instances of the breadth of view of that body. In the first edition of *Bacterial Metabolism* (1930) it is clear that the paucity of references to pathogenic bacteria is due rather to absence of information on these organisms than to avoidance of them by the authoress. She took the view that her business was to deal with bacteria 'as living organisms apart from their role as disease germs', but, as her second edition (1939) records, disease germs had in the meantime disclosed characters which made them eminently suitable for study as living organisms. Thus, as time went on her interests tended to embrace medical bacteriology to an ever-increasing extent, and though she herself did little work with pathogenic bacteria, she certainly had an influence in creating that wider outlook which is notable in present-day teaching in medical bacteriology.

In harmony with her views of the wide discipline of microbiology as a whole, M. S. took an active part in founding the Society for General Microbiology, and attending numerous preparatory committee meetings between November 1943 and February 1945, when the Society was formally inaugurated. She was an Original Member, served on the Committee of the Society from its foundation, and was unanimously elected as the Society's second President in September 1947, which office she held at the time of her death. She attended her last Committee meeting only a few weeks before she died.

The monograph, *Bacterial Metabolism* (1930, 1939, 1949), enabled M. S. to reach a wider public, and in this she was aided by a lucid and forceful style; it is a very personal book. The subject is presented in terms of enzyme mechanisms and she has little to say on those aspects which at the time of writing were not amenable to this treatment. It is interesting to compare the three editions of *Bacterial Metabolism* with this in mind, and to observe the succession of problems which have been answered in these terms. The book has been criticized on the grounds that it represents bacteria as 'little bags of enzymes'. In reply

it may be asked, how else can bacterial metabolism be described save in terms of the actions of enzymes? *Bacterial Metabolism* rendered a very great service by introducing to a wide public a new approach in the study of bacteria. In addition to this book she wrote the articles on Bacterial Chemistry in the first four volumes of the *Annual Review of Biochemistry*, thereby helping to keep biochemists in touch with what she considered to be the important advances in her own subject. The article of which she was proudest, and over the writing of which she took great pains, was her obituary of Hopkins for the *Biochemical Journal*; when she had finished it she exclaimed 'I feel I know Hoppy now', and he was, of course, her hero.

Marjory Stephenson's scientific outlook was strictly empirical. In her own field she kept her attention firmly on the actual observations and was less interested in the theories that flowed from them. This made her impatient with arguments that depended on the fitting of equations to observed curves; she used mathematics as a tool rather than as a guide. A quotation from the second edition of *Bacterial Metabolism* illustrates her attitude:

> In the problem of bacterial growth advances have been made along new lines. Happily this subject now attracts mathematicians and statisticians less than formerly but has passed into the hands of biochemists interested in problems of nutrition; this has led to results of both theoretical and practical importance and has revealed *inter alia* that the complex and peculiar media employed by bacteriologists in the cultivation of 'difficult' pathogens are rendered necessary owing to the inability of many parasitic organisms to synthesise for themselves certain molecules essential for growth.

The point also figures in some of her, lamentably infrequent, contributions to *Brighter Biochemistry* (a laboratory journal published in Cambridge). Her arguments, written or verbal, depended on the assumption that a bacterium does not bring about actions by accident but is adapted for survival in some of the environments it may meet in Nature and that it is unlikely to retain a given capacity, against the flood of mutations and variations, unless it has survival value on occasion. M. S. was safeguarded from being led by physiology into simple teleology by this awareness of selection and of the probability that many enzymes do not bring about the same action in Nature that is studied in the laboratory. Enzyme specificity is never complete and in the economy of the bacterium an enzyme may be occupied with a different substrate or with catalysing an action in the reverse direction. In the environment supplied by Hopkins's dynamic approach to biochemistry her physiological interest led her naturally to the study of adaptive enzymes and she liked to emphasize that they were a feature of microbial rather than vertebrate economy, because the former was suited to a variable and varying environment, whereas the latter maintains a relatively constant internal environment for its enzymes.

Marjory Stephenson adopted much the same attitude towards people as she adopted towards science. She was concerned with what they were actually doing and with their motives rather than with what they said they were doing and why. This pursuit of personal information and discussion of motive, especially when undertaken by someone with her infectious gaiety, could become formally indistinguishable from gossip and the pejorative word was

sometimes used by those whose activities were being analysed. The analysis of motive was however a necessary means towards the end of planning an environment in which research workers could flourish. She knew that it was only when one had begun to understand the motives that had led a person into research that one could give any useful advice if he seemed not to be making a success of it. She was unsparing in her condemnation of secretiveness, personal vanity and competitiveness in scientists and for this reason jeered at most of the medals and awards that scientists on occasion confer on one another. Although she realized that it was probably unavoidable, she looked on many of the consequences springing from the existence of bodies of limited membership, such as the Royal Society, as unfortunate. Each year when a new list of Fellows was published she would remark '...that means a few more scientists can settle down to their work instead of fussing about their reputations'. In this context another comment of hers should be preserved: 'These young men fuss about their reputations as if they were ageing virgins in a Victorian novel.' The various disabilities to which women scientists are subjected were, in her opinion, almost compensated for by their freedom, between the ages of 35 and 50, from this anxiety. As a feminist she was pleased when the old anomalous rule that women could not be Fellows of the Royal Society was abolished and she was human enough to be gratified that she was one of the first to be admitted. Her pleasure was however marred by the realization that she might be accused of inconsistency on what had been almost a matter of principle.

Outside the laboratory M. S. had many interests. She was widely travelled and widely read and it would have been difficult to find a conversational theme that would not have interested her. She was a fellow of Newnham College and spent a considerable amount of time working and thinking for the College and acting on those committees to which she could contribute. Politics interested her greatly. As might be expected in a person of her independence of mind, she did not adhere docilely to any party but supported particular activities of whatever party was being most useful at the time. Her main political activity was in the period 1931–1937 when she gave valuable help with advice, money and hospitality to those anti-war movements that looked on war as a manifestation of economic and political imbalance. She was satisfied that if politics were the cause of war the cure must be political too. At the time of her death she was a vice-president of the Association of Scientific Workers and had on many occasions been a source of strength to it; she was, for example, a guarantor during the period when its finances were rather insecure.

Gardening always interested her; at the house in which most of her life in Cambridge was spent the opportunity was poor, but when she moved to more open surroundings her garden gave her intense satisfaction. She believed strongly in its psychotherapeutic value and attributed the relatively low crime and suicide rates in Britain to our national preoccupation with gardening. She often suggested that if those scientists whose behaviour did not come up to her standards would only undertake the care of a garden they would be much improved. From time to time she painted, but apparently with less

satisfaction, for she was always unwilling to show her pictures to those who might be critical.

It is difficult to imagine what a protracted old age might have been like; she had so many interests—and would probably have developed more—that it would not have been notably peaceful. 'Middle aged' was a term that she used contemptuously of some of her contemporaries and juniors. She herself escaped it and passed quickly from youth to old age after her first operation for cancer. Soon after this operation she knew that death could not be long postponed but had the wisdom and courage to remain gay, argumentative and active to within a few weeks of her death.

S. R. Elsden
N. W. Pirie

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