

SHORT ARTICLES AND REVIEWS

**THE GENESIS AND ACHIEVEMENT OF A LIMNOLOGIST:
GEORGE EVELYN HUTCHINSON, 1903-1991**

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One who more than anyone else gave form and coherence to the science to which *Freshwater Forum* is devoted died on 17 May 1991.

George Evelyn Hutchinson was born in Cambridge on 30 January 1903, into a distinguished academic family. His father, Arthur Hutchinson, FRS, was a mineralogist who became Master of Pembroke College. His mother, nee Evaline Demezy Shipley, could trace her ancestry back to an ancient Piedmontese family, the de Mezzi, which included several learned ecclesiastics, and her brother was the zoologist, Sir Arthur Shipley, FRS. The genetic makeup derived from this ancestry had an ideal environment in which to express itself. Cambridge, as well as providing intellectual stimulus, merged in those days with unspoilt countryside, abounding in ponds and waterways with kingfishers within the town limits. Already at the age of five, as recounted in his autobiographical *The Kindly Fruits of the Earth* (Hutchinson 1979), he kept small aquaria stocked with red watermites and other pond fauna which he had caught himself. Before he was eight he started collecting butterflies and moths and then, later on, fossils, receiving expert guidance from his father and friends of the family. The various university museums were a constant source of information and delight. His interests were not confined to natural history for he started writing a book on heraldry and explored the churches in the neighbourhood for brasses to rub. Wider appreciation of art was fostered by the Fitzwilliam Museum - "the most welcoming art gallery in the world". These leanings towards the humanities were solidly buttressed by being taught Latin and Greek at his preparatory school and he continued to use the former language with facility throughout his life. From 1917 to 1921 he was at Gresham's School, at Holt in the Norfolk countryside, where the education achieved a high intellectual level, albeit obscurantist, even for those days, on certain aspects of biology. The interests which he had already acquired developed at Gresham's and he published his first scientific paper, on the swimming ability of a tettigid grasshopper, in

1918. The teaching of chemistry was superb. Not only did it provide him with the knowledge to demonstrate, by testing for a sulphhydryl reaction, that the scrambled material served at school breakfast could not possibly contain any egg (this was war time) but, more importantly for his subsequent career, it led him to realise that organisms lived in chemical environments so that he would have to master chemistry adequately if he was going to be a good ecologist.

He went up to Emmanuel College, Cambridge, in 1921, graduating BA in 1924 and MA in 1928. His studies centred on zoology, in which he was awarded the prestigious Frank Smart Prize in Part II of the Tripos, but he took every opportunity of following up other interests - physiology, biochemistry, genetics, natural history (particularly of water bugs) and parapsychology, but not politics. At that time Cambridge could be described as the intellectual capital of the world and amongst those who influenced the undergraduate Hutchinson were E. D. Adrian, G. P. Bidder, H. Gilbert Carter, F. Gowland Hopkins, J. B. S. Haldane, R. Hill, J. Needham and R. C. Punnett.

After graduation he set out with a Rockefeller Higher Education Fellowship to work at the Stazione Zoologica in Naples. It was not the usual thing then to take a PhD and, in fact, although he eventually acquired several honorary doctorates, he never worked for a higher degree. His ostensible aim in Naples was to study the role of endocrines in invertebrates, a promising but then almost unknown field in which, although he did some interesting work in molluscan physiology, he did not get far. His absorbing interests at this time were art and folklore and he made a particular study of the miraculous liquefaction of the blood of Saint Januarius, which occasions one of the most celebrated festivals in Neapolitan life.

In 1926 he applied for and obtained the position of senior lecturer in zoology in the University of Witwatersrand, South Africa. The head of the department was notorious as a difficult man but Hutchinson, avid to see something of an entirely different fauna, was confident - pig-headedly so he himself admitted - of his ability to cope with this and did not learn until too late that his predecessor had been physically ejected from the zoological laboratories by the professor. The fauna, however, came up to expectations and he was soon at work studying *Peripatus*. The Cape flora, too, he found entrancing. Before long, deemed incompetent by his professor and relieved of his teaching duties, he turned his attention to limnological chemistry, which he was able to pursue thanks to the hospitality of a sympathetic professor of inorganic chemistry. With H. W. Harvey's *Biological Chemistry and Physics of Sea Water* (1928) and the *Standard Methods of Water Analysis* of the American Public Health Association (1923) as his guides he began

investigations of the pans, shallow depressions intermittently filled with water, which are characteristic of the southeastern Transvaal. Here he found his life's work - "all the ways of looking at nature that I had acquired in a random, disorganized way could be focussed together on lakes as microcosms. I had, in fact, become a limnologist." (Hutchinson 1979, p. 208). Hydrobiology satisfied both his naturalist and physiologist instincts. However, it was only the concept that was satisfying; his opinion, confided at this time to his parents, that this branch of biology "has been the dumping ground for inferior off-scourings of the profession of zoologists" he later admitted to be arrogant and unfair but it expressed his dissatisfaction with the existing state of the science.

Hutchinson resigned from his post in the University of Witwatersrand in 1927, precipitating an enquiry which found in his favour, and soon afterwards was appointed, without an interview, to an instructorship at Yale University. Evidently in those days authorities in American universities could be impressed by the enterprise shown in the dispatching of a transatlantic cable from the Southern Hemisphere. In Hutchinson's early years at Yale the chairman of the Department of Zoology was R. G. Harrison, a distinguished developmental biologist whom he came to admire immensely. There had been no particular emphasis on aquatic ecology in the department and for a long time Hutchinson had the unsuitable assignment of teaching embryology, but a course on oceanography was initiated in 1929 and a year later he was asked to give one on freshwater biology. At that time American limnology was dominated by the Wisconsin school led by E. A. Birge and C. Juday. At their Trout Lake Laboratory he was given first-class instruction in limnological techniques but his feeling of dissatisfaction, that there was no general framework into which the mass of data which had been accumulated could be fitted, was not dispelled. For some years he was occupied by working up his African studies and a substantial proportion of his publications was concerned with the taxonomy and zoo-geography of the aquatic Hemiptera. A venture into more physiologically based limnology was an experimental study of the effects of magnesium salts on Cladocera which showed that the supposed effects of magnesium in limiting distribution of these animals did not exist. In 1932 he went as biologist on the Yale expedition to the western end of the Tibetan Plateau. This enlarged his limnological experience and led to a series of papers on high altitude lakes in Ladakh, some of which were on Hemiptera and others concerned with limnological physics and chemistry.

Hutchinson did not fail to observe and ponder the patterns of human life which he encountered in India and Tibet and he evidently found the expedition deeply emotive as well as scientifically valuable. His essay in

autobiography (Hutchinson 1979) ends at this point with a recollection that recurred insistently to him of a Kashmiri boy aged about six who, when he was trying to find a certain monastery, understood immediately that they could not communicate by speech and, taking him by the hand, led him to it, staying with him until dusk. It was on the return voyage from India that he met his first wife, Margaret, whom he married in 1933.

Under Hutchinson's direction Linsley Pond, a lake of 9.4 hectares in Connecticut, became the main object of the Yale department's limnological studies, which were directed to understanding its functioning - metabolism was the word he used - as a whole (Brooks & Deevey 1963). The first visit was made on a chilly March day in 1935 and Riley (1971) recalled a hazardous reconnaissance in a leaky rubber boat which had seen hard service on the Tibetan trip. On a later occasion Hutchinson went out on ice which Riley refused to trust and successfully obtained samples. Fundamental work on mechanisms of heating, mixing and chemical events during stagnation was carried out. Movements of nutrients and other substances were estimated quantitatively using eddy diffusion coefficients calculated from vertical temperature gradients. The distribution of phosphate was studied in particular and it was shown that the pattern was complicated by non-turbulent processes, phosphate escaping from the bottom deposit under reducing conditions during stagnation and being transported rapidly from the littoral regions to the central part of the lake by horizontal circulation (Hutchinson 1941). This paralleled work being carried out in England and Germany at about the same time but subsequent direct measurement of horizontal movement by injection of radiophosphorus (Hutchinson & Bowen 1950) seems to have been the first use of isotopic tracers in *in situ* limnological research. Realizing the possible importance of organic factors in determining the occurrence of organisms in freshwater, Hutchinson (1943) determined thiamin concentrations in Linsley Pond and other vitamins and organic factors in fresh waters were studied by his students. Following up his own work on cladocerans and that of VV. H. Pearsall in the English Lake District on phytoplankton, he examined the relationships between the periodicities of various species and chemical changes in the water (Hutchinson 1944), confirming some of Pearsall's conclusions but obtaining contrary results in other cases. Now that it is more fully realized that it is the turn-over rates of nutrients rather than their actual concentrations that are ecologically important, such discrepancies are not surprising. Lake sediments appeared important not only in exchange of materials with the water in the short term but as repositories of remains which might yield information about conditions in the past. This idea was suggested to Hutchinson by a report from Austria of fossil chironomids, which might be indicative of different lake types, in lake sediments

(Brooks & Deevey 1963). Again, parallel work was being pursued in England by C. H. Mortimer, W. Pennington and W. H. Pearsall but it seems that this immensely productive idea of using stratigraphical sequences in lake deposits as clues to ecological history arose independently on the two sides of the Atlantic.

Hutchinson is revered not only by limnologists but by population ecologists. This interest was aroused by the work of Volterra - which, incidentally, had its origins in a fisheries problem - on population mechanics. Hutchinson (1948) examined the crucially important consequences on predator-prey oscillations of changing the time-lag in the feed-back process described by the Lotka-Volterra model. With his students he investigated competition in animal populations, some of them terrestrial, and brought his conclusions together in *An Introduction to Population Ecology* (Hutchinson 1978). For limnologists his best known essay in this field was the paper entitled *The Paradox of the Plankton* (Hutchinson 1961). Volterra had predicted that two species feeding in unrestricted competition on precisely the same food under the same conditions could not co-exist indefinitely as equilibrium populations. The plankton presents a contrary state, having a number of species co-existing in an apparently isotropic and unstructured environment in which competition for the same essential nutrients is particularly acute. Hutchinson's conclusion was that the plankton must be a non-equilibrium system because the time for virtually complete competitive replacement of one species by another is of the same order as the time taken for a significant change in the environment. If he had moved down the size scale from net-plankton to organisms two orders of magnitude smaller, from the domain of turbulence to that of viscous flow, he would have discovered an equilibrium community behaving in accordance with Volterra's predictions. Hutchinson, of course, did his most creative work when aquatic microbiology was in a rudimentary state; bacteria played only incidental roles in his concept of lake ecosystem and picoplankton were scarcely recognized at that time.

For Hutchinson learning was a seamless whole and, as Riley (1971) wrote, he had "a feeling that science is an artistic achievement, to be relished as such." He was accordingly somewhat upset on arrival at Yale to find that scientists were regarded as contaminant and dangerous by the arts establishment and that botanists and zoologists scarcely spoke to each other. Throughout his life he wrote copiously on art and folklore and his scientific publications were enriched with erudite quotations - never translated because he expected his readers to be reasonably educated. Sometimes his liking for mixing the two cultures invited criticism, as when in a major invited address, entitled *The Enchanted Voyage* (Hutchinson 1955), to the Oceanographic Convocation held at

Woods Hole in 1954, he devoted his time entirely to an entertaining, but profitless from the narrowly scientific point of view, account of some rather obscure symbolic and allegorical aspects of the sea. More often the Hutchinsonian blend of classical learning and science was immensely satisfying and illuminating. An example of this is the collaborative investigation entitled *Ianula: an account of the history and development of the Lago di Monterosi, Latium, Italy*. This small crater lake was primarily selected as one in which maturation of the lake itself might be investigated by palaeolimnological methods which hitherto had been applied only in regions where glaciation had been a profoundly modifying external influence. A bonus was that Hutchinson's knowledge and contacts provided informed reconstruction of human activities in the lake's catchment area from Etruscan and Roman times to the mediaeval period and later. The result was a picture of the history of the lake, from its shallow, fairly productive beginning in pre-classical times, through an abrupt transition in chemistry and biology to a eutrophic state which coincided with the building of the Via Cassia around 170 B.C., after which it reverted to its present mesotrophic condition. No evidence of inevitable development from oligotrophic to eutrophic as postulated by limnological theory was found and the major event in the lake's history was increased run-off from the catchment area with massive inputs of nutrients, particularly calcium, caused by Roman road-building (Hutchinson 1970).

Hutchinson's contribution to science extends far beyond the body of fact which he added (Edmondson 1971). His approach to ecology, particularly in its dynamic aspects of population ecology and mineral cycling, have permeated throughout this science. His view, expressed in 1943, that the most practical lasting benefit of science would be to teach man how to avoid the destruction of his own environment, may be commonplace now but was scarcely articulated then. Also important was the inspiration which he gave to his students although this was instilled unselfconsciously by example rather than didactically. A list of the doctoral dissertations completed under his direction is given in the special issue of *Limnology and Oceanography* (1971, vol. 16 no. 2) which marked his retirement as Sterling Professor of Zoology at Yale. It is illustrated with a phylogenetic tree of his intellectual descendants, the main branches of which are labelled with the names of his own students, most of them now distinguished in the aquatic sciences in their own right. They in turn transmitted the Hutchinsonian outlook to their students so that the tree has a multitude of twigs. The variety of research topics which he supervised can only be indicated by a few examples. G. A. Riley, his first student and now an eminent oceanographer, worked on the copper cycle in Connecticut lakes; E. S. Deevey, known for his

palaeolimnological work, on typological succession; W. T. Edmondson began his important studies on the population dynamics of rotifers with an investigation of the ecology of sessile forms; L. B. Slobodkin, population ecologist, started with work on *Daphnia*; J. R. Vallentyne examined organic pigments in lake sediments, providing a useful new approach for palaeolimnologists; T. F. Goreau, who died tragically early, began his seminal work on the biology and histochemistry of corals. These and other students, migrating the length and breadth of North America and overseas, gave Hutchinson's influence a wide geographical distribution (Kohn 1971). In a still wider arena he was President of the Limnological Society of America in 1947-48, the crucial year in which it was decided to expand it into the American Society of Limnology and Oceanography. These two sciences have much in common and much to give each other and it is characteristic that Hutchinson saw this and brought them together. Always he strove to obtain recognition for the work of others which he thought important. Through Russian colleagues at Yale he learnt of the work of V. I. Vernadsky on biogeochemistry and did much to make it better known in English-speaking countries. R. Lindeman's eventually famous paper on trophic-dynamic aspects of ecology met with great opposition from some plant ecologists with deep suspicions of theoretical formulations. Hutchinson campaigned for its publication and it was finally accepted and went to press as its young author was dying of hepatitis.

His great work *A Treatise on Limnology* carried Hutchinson's influence world-wide and ensured its endurance. Volume 1, *Geography, Physics and Chemistry*, appeared in 1957, Volume 2, *Introduction to Lake Biology and the Limnoplankton* in 1967, and Volume 3, *Limnological Botany* in 1975. What has to be the final volume, on benthic animals, was prepared with the assistance of Dr Yvette Edmondson and will be published posthumously. The wealth and breadth of information, given meaning by unifying ideas, contained in these volumes is astounding. They are likely to be standard reference works for a long time to come.

Hutchinson was a shy man, not given to self-advertisement, but his worth became widely recognized and many honours came his way. These honours took many forms and not least was the naming after him of a lake in Ontario. Many species bear his name and there is a picture showing him collecting from an imaginary habitat in which 22 of them are represented (Vallentyne 1971). The American Society of Limnology and Oceanography's highest award was established in his honour in 1982. He had received the Naumann Medal of the International Association of Theoretical and Applied Limnology in 1959 and was President of this Association from 1962 to 1968. He also received the Eminent Ecologist Award of the Ecological Society of America and the

Tyler Prize for Environmental Achievement. He was a member of the National Academy of Sciences of the USA. Having become an American citizen in 1941 - he did, however, retain a very distinctive English accent to the end - he was not eligible for the Fellowship of the Royal Society but in 1983 achieved the more exclusive distinction of being elected a Foreign Member. His native land claimed him back in the end; after the death of his second wife, Anne, in December 1990 he returned to be with his family and died in London.

In her *In Memoriam*, in *Limnology and Oceanography*, Yvette Edmondson summed up his place in twentieth century science in words which cannot be bettered:

"The era that ended with G. E. Hutchinson's death was not only that of a thoughtful man and the growth of a science imprinted by his thinking. Even more sadly, we may be seeing the end of an intellectual climate in which the sparkling mind of one individual can so illuminate a science. Science by committee casts a very different light".
(Edmondson 1991)

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