BIOGRAPHICAL
MEMOIRS

Conrad Hal Waddington, 8 November 1905 - 26 September 1975

Alan Robertson, F. R. S.

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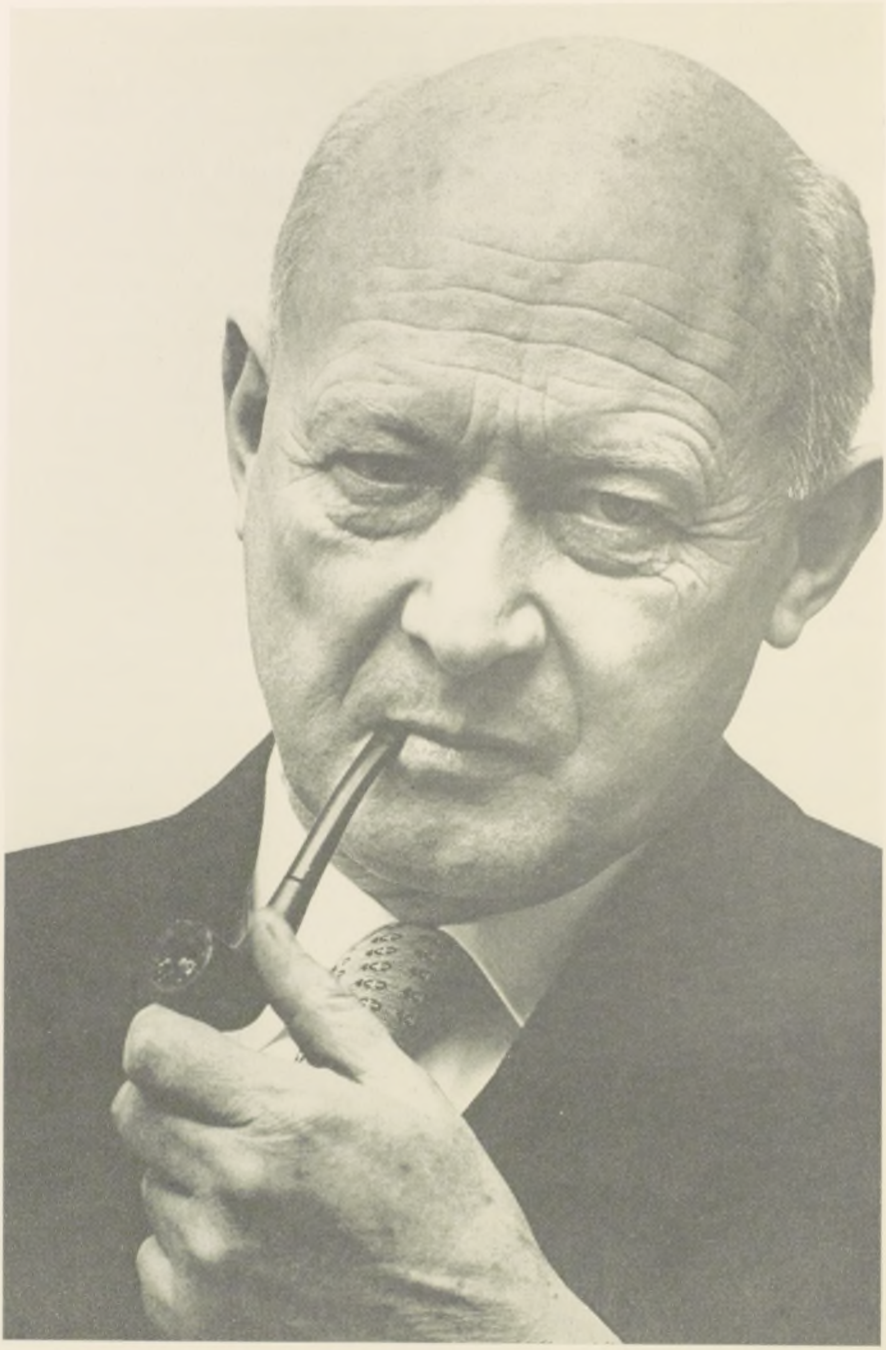

C.H.Waddington.

CONRAD HAL WADDINGTON

8 November 1905 — 26 September 1975

Elected F.R.S. 1947

By Alan Robertson, F.R.S.

Life

Conrad Hal Waddington was born in Evesham on 8 November 1905. His parents, Hal and Mary Ellen (Warner) Waddington, were of long-established Quaker families and were first cousins, as were Mary Ellen's parents. His surname traces to the Lancashire village of Waddington. He had one sister—Mrs Doris Christie. His father was a tea planter in South India and he spent his first 2½–3 years on a tea estate in the Wynaad district of the Western Ghats and then nearly two years in Coimbatore, both being in the Madras Presidency (now Tamil Nadu). In a brief autobiographical fragment he describes one of his few memories of India:

> 'One morning in the road outside our house I was scuffling my feet in the thick dust; as I remember it, it must have been at least six inches deep. I looked over my shoulder and there was a herd of young domesticated buffaloes coming fast towards me. I was terrified. I fled through the gate into the wide open garden, where the only cover was a rather straggly hedge in which I hid. It was made of some thick juicy plant, whose fleshy leaves were almost indistinguishable from the stem and when I broke one off and, without thinking, put it in my mouth as I watched with relief how the buffaloes went by without noticing me, the white acrid sap stung my tongue sharply, and I felt a renewal of terror that I was now poisoned and would surely die.'

He returned to England at the age of four (though his parents did not return permanently until 1928) to live with an aunt and uncle who had a son of his own age, on a farm in Sedgeberrow in the shadow of Bredon Hill. His uncle was farm manager for a bachelor gentleman farmer, always known as 'Squire Bowly', and the family lived with the squire in the farmhouse. His grandmother, who brought up his sister, lived in a house on the outskirts of Evesham where he went on school holidays.

> 'My grandmother belonged to the Society of Friends, or the Quakers as they are usually called, in fact all my family did, but in the village of

Sedgeberrow there had been no Quaker meeting house. My grandmother's views were not particularly strict as Quakers go, but of course on Sundays my sister and I were not allowed to do anything very frivolous. We had Sunday dinner in state in the large, cold, dank, drawing room, with the best crockery and linen, finishing up with dessert. After lunch we went on sitting in the drawing room, which was practically never used on any other day but this, and my sister and I had to do something suitable for Sunday; we might draw or press flowers, or sometimes my grandmother would open one of the cabinets and show her collection of curiosities and treasures. There was, I remember particularly, a set of beautifully carved, thin slivers of ivory made for playing the game of spillikins; and they passed muster as entertainment suitable for Sunday. Very often my grandmother read aloud to us, only serious books, of course, on Sunday.

'There was one that I read for myself—an old, I suppose mid-Victorian, book, a guide to what it called "indoor entertainments". Amongst other things it gave a lot of instruction for elegant chemical and physical experiments. My uncle, who was a bit of a naturalist, had already given me a taste for collecting odd things, like fossils. I used to spend hours hunting for them in the gravel used for paths in that neighbourhood; and I also collected snails, land snails and water snails from the river. I used to love rolling off my tongue, as a form of swank, their resounding Latin names like *Cyclostoma elegans* and *Planorbis cornuta*. Now with the aid of this book I started all sorts of experiments. One of the members of the Quaker meeting was an old gentleman, a Dr Doeg, who kept a chemist's shop in the town. He was a distant relation by marriage and I knew him as Grandpa Doeg. He dressed always in a black coat, and wore a black velvet smoking cap embroidered with gold thread. He was, I suppose, almost the last surviving real 100% scientist. By that I mean that he reckoned to deal with the whole of science. He would give one the name of a fossil, or show one microscopical preparations of bits of animals of plants; he made colour photographs by an early process which involved a lot of dyed starch grains; and he could explain about lenses and prisms and magnets. I would go to him and get pennyworth's of chemicals for the experiments in my book, in which they were referred to by their old 19th century names, like "muriate of potash", "oil of vitriol" or "saltpeter". All that was good for Sunday afternoons as well as weekdays.'

He and his cousin shared a governess at the farm until, when he was nine, he went to Aymestrey House Preparatory School in Malvern Link. At the start of World War I, he left his uncle's house and joined his sister with their grandmother in Evesham. From preparatory school, he got a scholarship to Clifton and then his home changed yet again when his grandmother moved to Weybridge to share a house with another of her sons and his family in 1919.

His sister describes his early intellectual development as follows:

'I should imagine a great influence on his seeking a scientific career was "Grandpa Doeg" at Evesham, of whom he speaks in his autobiography.

> My grandmother was also a notable naturalist and would have instilled "observation" into Con, as she did to me; she was also, for what we then thought of as "an old lady", always ready to learn and be interested in the doings of her small enquiring grandson. He was certainly encouraged and helped to have a miscellaneous collection of every sort of natural history, geological and archaeological object in what was known as "Con's museum" in one of the barns attached to our house, where he could also conduct his chemical experiments under the auspices of Grandpa Doeg. I think the headmaster of his prep school must also have seen his potentialities and encouraged him along the scientific path as I remember him more than once coming to see us during the school holidays and being proudly shown over "Con's museum" (which he did not do for many of his small pupils, I imagine). He took a scholarship to Clifton but I don't think specializations in subjects was made quite so early in those days, nor was one "streamed" on to one side or the other. But certainly during his Clifton days he was specializing in geology as a hobby and used to spend much of his holidays away with school parties on archaeological "digs" or collecting fossils at Lulworth.'

He therefore had very little conventional family life. Because of interruption in travel to and from India during World War I, he did not see his father between the ages of 5 and 15 and when his parents returned permanently from India around 1928 he was himself already married.

After Clifton, he went up to Sidney Sussex College, Cambridge, with a scholarship and took the Natural Sciences Tripos, with a First in Part II in geology in 1926. His career in Cambridge then becomes bewilderingly many-sided and he has left very little early record of it. Dr Barton Worthington, who was a close friend at this time, has sent me the following reminiscences:

> 'These early postgraduate years were a formative time of his career and had considerable impact on a number of his contemporaries. He was married in the same year as he graduated to "Lass" Lascelles who was some years older than himself and had strong artistic leanings. The association did not last many years but it resulted in a son and a wide broadening of interests. The Waddingtons lived in a house in Bateman Street, Cambridge, of which the spare room was occupied in succession by several contemporary postgraduate scientists, including myself, and during the evenings discussion used to cover not only science, but philosophy, modern art, music and the Dance. At this time Waddington devoted a good deal of attention to Morris dancing: he became an exponent of its techniques, squire of the Cambridge Morris Men, a group which tended to attract brains, rather than brawn, and he led dancing tours through the Cotswolds and other traditional centres. Indeed he collected one or two Morris dances and folk tunes which would otherwise have disappeared, and to see him dance one of these "The Nutting Girl" on a village green, accompanied by his wife on the accordion, could be a moving experience.

> 'A physical character of Waddington should not go without mention: he became remarkably bald at about the age of 21 and in the early part of his career this, coupled with his erudition, caused many people to think that he was much older than he actually was. Sometimes, when throwing out half-formed hypotheses or ideas he seemed surprised at being taken seriously.'

Of the first marriage, which ended in divorce in 1936, there was one child, Jake, now a professor of physics at the University of Minnesota. In the same year, Waddington married Justin Blanco White, an architect, who survives him. There are two daughters of the second marriage—Caroline, a social anthropologist working in Cambridge on the Buryats of Outer Mongolia, and Dusa, a mathematician at the University of Warwick.

He seems to have held simultaneously an 1851 studentship in palaeontology and an Arnold Gerstenberg studentship in philosophy for a thesis entitled 'The vitalist—mechanist controversy'. This award is made for the encouragement of the study of philosophy amongst natural scientists.

> 'I studied geology simply because it seemed that becoming an oil geologist would be a good way of earning a living. But I gradually got interested in evolution, chiefly because of an excellent tutor, Miss G. L. Elles. I then got interested in genetics, through friendship with Gregory, son of William Bateson, the introducer of genetics to Britain, and I did two years' research in systematics of fossil ammonites but decided I wanted to study "live" biology rather than fossils and never presented my thesis.'

He eventually got an Sc.D in 1938 on the basis of his publications. Gregory Bateson recalls Waddington's skill and nimbleness in clambering over the Dorset cliffs in search of ammonites. The intellectual outcome of these grants is somewhat surprising. The first is a paper in 1929 on the genetics of germination in stocks (*Matthiola*), clearly under the guidance of Miss E. R. Saunders, and a highly uncharacteristic (for Waddington) and very mathematical paper with Haldane published in 1931. His entry into embryology is amusingly described by Dame Honor Fell (he himself dates this as happening in 1930):

> 'Perhaps the manner in which he originally came to the Strangeways might be of interest. Somewhere in the early 1930s, one of my colleagues told me that she had met a young palaeontologist (with a scholarship in moral philosophy) who had been reading the works of Spemann. He wondered whether it would be possible to adapt our organ culture technique to the study of induction in warm-blooded animals. I thought it would be a long shot, but marvellous if it worked, so I said he could come along and try. This he did. I showed him the watch glass method that we were using at that time, he implanted his chick blastoderms and found that such preparations could be utilized very well for many types of embryological experiments including induction.'

About this time he started his fruitful collaboration with the Needhams on the chemical nature of the evocator, which I deal with in more detail later. His

position in Cambridge was always slightly insecure. Up till 1930 he had existed on a research fellowship. Having decided that his future lay in embryology he became a demonstrator in the Zoology Department and obtained a part-time grant from the Medical Research Council (M.R.C.) for his tissue culture work at the Strangeways. At about this time he spent 6 months with Spemann in Germany on a Rockefeller Travelling Fellowship. His part-time support from the M.R.C. continued but he eventually achieved some security when he was elected a Fellow of Christ's College in December 1933. He held a second Rockefeller Fellowship for a visit to the United States from June 1938 to April 1939, visiting successively the Carnegie Institute Laboratories at Cold Spring Harbor, Columbia University, and the California Institute of Technology in Pasadena.

Although his scientific life was very active it was only a part of his existence. His one sporting activity in Cambridge was running, where he was good enough to be considered for the university relay team. His physical dexterity has been mentioned by many people—as a Morris dancer in Cambridge, from Gregory Bateson for his climbing skill on the Dorset cliffs, and finally from his experimental collaborators in Cambridge and in Edinburgh for his skill as a micro-manipulator. But he was always interested in the arts and in philosophy. To quote his own words: 'More interested in poetry than in science as an undergraduate, I edited and printed a magazine of poetry that had the distinction of being the first vehicle in which Christopher Isherwood, the English novelist, appeared in print.' The one volume of this series that I have seen, with the title *Fanfreluche* (taken from Rabelais) includes a poem by himself which I have reprinted at the end of this memoir (see p. 614). His main interest was in the visual arts. In the foreword to his book on modern painting written in the late 1960s, he says:

> 'The thoughts I have had on these subjects have arisen in the course of a lifelong interest in paintings, beginning with my friendship, from about 1930 onwards, with the English *avant-garde* painters of that time: John and Myfanwy Piper were my closest friends, and through them, and the architect Justin Blanco White whom I married around that date, I came to know Henry Moore, Ben Nicholson, Barbara Hepworth, Ivon Hitchens, Sandy Calder, Moholy-Nagy, Gropius, and a few more—there were not so many of that kind at that time.'

I sometimes felt that Waddington subsequently looked back at the period in Cambridge in the 1930s as the most stimulating part of his life. He enjoyed college existence and while a Fellow of Christ's did his best to persuade the college to have a proposed new building designed by his friend Gropius. Life in Christ's is described in a fictional framework in several of C. P. Snow's novels (Snow having played a part in getting Waddington elected). His scientific work was very exciting although the search for the chemical nature of the evocator eventually petered out. But there were many stimulating friends whose activities had become a legend to the next generation of Cambridge scientists. The

closest of these to Waddington was probably Bernal who figures, thinly disguised, in Snow's first novel *The search*, which is more directly concerned with scientific research than his later books. One of Waddington's last public lectures was the Bernal Memorial Lecture to the Society with the title 'The New Atlantis revisited'. During this period, he was a member of the Theoretical Biology Club with, among others, the Needhams, Bernal, Woodger and Willmer. He also wrote several popular scientific articles, mainly for *Discovery*.

At about this period, he became a member of a scientific dining club called the Tots and Quots, which met in London. Its members included among others Blackett, Bernal, Zuckerman, Hogben and Pirie. In the meeting in June 1940, the discussion centred on the fact that probably less than half the scientists in the country were employed in war work and on possible remedies for this. Allen Lane, the publisher, was present as a guest and suggested that here was the basis of a very good book. The challenge was accepted, the text was produced in 11 days and the Penguin *Science in war* had been published when the Club next met a month later. Waddington's specific contribution was a short section on 'Meat at any price'. The book perhaps led in the end to a change in his career because he later quoted with approval from the section dealing with the scientific analysis of military operations: 'The scientific staffs of the services need to play a much larger part than they seem to do in the formulation and solution of strategical and tactical problems.' Blackett, after forming a research group in Anti-Aircraft Command, became Scientific Adviser to A.O.C./C., Coastal Command, R.A.F., and subsequently formed an Operational Research Section there. He left after less than a year to become Director of Naval Operational Research. Waddington joined O.R.S. Coastal Command in 1942, a group which contributed in the course of time five Fellows of the Society. He began as deputy to the officer in charge, Harold Larnder, and was responsible for the section dealing with photographic reconnaissance and with anti-shipping strikes. As the invasion of Europe approached and Larnder left to join the Allied Expeditionary Air Force early in 1944, Waddington became officer in charge of the section, a post he held until after the end of the war. The most critical period for this command had been during the Battle of the Bay in April to July 1943, and in 1944 its operations were dominated by the coming invasion. The coming into service of U-boats with a schnorkel which allowed them to surface without making a large radar target and of the type XX boats with an increased underwater performance fortunately came too late to influence events. Waddington wrote the Coastal Command chapter in *Operational research in the R.A.F.* which was not published till 1963, and his own monograph on *Operational research against the U-boat*, written in 1946, did not appear until 1973. While he was with the R.A.F., he also paid a visit to South East Asia Command with Bernal. This short period had a great effect on him. Discussing the successes of the section, he says: 'But most of this was done (by P. M. S. Blackett and others) while I was still very junior in the section—I can claim little credit for it but it profoundly influenced my outlook.' He wrote several popular articles stressing the value of such an approach in peace time.

As the war approached its end, he began to consider his own future career. His position in Cambridge teaching had never been very secure before the war and the prospects now seemed little better. But a new possibility appeared. In 1943, two American agriculturalists had visited Great Britain to advise on the development of agricultural research after the war. They suggested the setting up of a National Animal Breeding and Genetics Research Organization (N.A.B.G.R.O.) under the Agricultural Research Council (A.R.C.), and Waddington was offered the post of chief geneticist and deputy director which he accepted, with Professor R. G. White, then Professor of Agriculture at Bangor, as director.

Then, early in May 1945, there came out of the blue an offer of the chair of genetics at Edinburgh, whose previous occupant, F. A. E. Crew, was returning from the war with changed interests to a new chair of social medicine. There were then only three chairs of genetics in the country and this was obviously a most attractive offer. After some hesitation Waddington refused it, feeling too committed to the Agricultural Research Council. The matter was given a different twist after a chance visit by White to Edinburgh. There it was put to him that N.A.B.G.R.O. might find a permanent headquarters in Edinburgh (plans at the time were for Oxford) with Waddington combining the position of chief geneticist at N.A.B.G.R.O. with the chair of animal genetics in the University. After much discussion this was in the end agreed. This began one of his most fruitful periods, not so much in terms of his own output but of his influence both on his department and also on the development in Edinburgh of biology as a whole. He began to collect his staff through the bad winter of 1947 in a temporary laboratory in Hendon. His side of the new organization was built up much more rapidly than the more practical side under White, the latter being held back by the need to purchase farms for large animal experiments.

The Institute in Edinburgh, which had been used in part for housing an officer selection group during the war, was then almost empty. The only staff member who continued at the Institute long into the Waddington era was Dr Charlotte Auerbach who became a Fellow of the Society in 1957, Waddington himself having been elected in 1947. The laboratory was dominated by the new A.R.C. group who also took a major role in teaching while the university staff was slowly built up. There was not then an honours course in genetics (this was not started until 1957) but the revived department under its new head attracted many student visitors and a diploma in animal genetics was soon started. Two stimulating population genetics visitors from overseas came to the Institute for a stay of a year—Dr Sewall Wright from Chicago (now a Foreign Member of the Royal Society) and Dr I. M. Lerner from California. The latter wrote his well known *Population genetics and animal improvement* during his stay and the former, in giving a long course in biometrics, laid the foundations of his four-volume *Evolution and the genetics of populations* of which the last has still to appear.

The simultaneous arrival from England of several staff families led Waddington to suggest to the A.R.C. a communal solution to the problem of finding accommodation. In consequence, the Council decided to rent Mortonhall

House, a large country house in the outskirts of Edinburgh. About ten families moved in in the middle of 1947 with singles accommodated in the attic. A domestic staff of three looked after the house and the cooking. The adult inmates ate together at one large table. As the house was about three miles from the laboratory and over a mile from public transport, communal transport had to be provided.

As a solution to the immediate problem this was satisfactory but as an experiment in communal living in the long term it was not. Waddington probably had a Cambridge college in mind in setting up this structure but there were critical factors which complicated matters. Even in Cambridge, high-table life is not all harmony, as the readers of Waddington's friend and fellow don, C. P. Snow, will know. Here we had a group with the same hierarchy at work as at home and the added problem of wives staying behind during the day, with very different ideas as to how children should be brought up. Distance from public transport made it difficult to keep staff. After two or three years, families began slowly to move away and the house was closed after six years. It provided many anecdotes, usually of a rather wry kind, and a novel.

The Institute grew in staff and in laboratory space until it became certainly the largest genetics department in the United Kingdom and one of the largest in the world. It was heterogeneous in structure. There were at different times not only the A.R.C. group and the university staff but also a Mutagenesis Research Unit of the Medical Research Council under Dr Auerbach, a protozoan genetics group under Professor G. H. Beale, holding a Royal Society Research Professorship, and a research group under Waddington's honorary direction headed by Dr T. C. Carter working on radiation mutagenesis in small mammals. This latter was formally a part of the M.R.C. Radiobiological Research Unit and moved to Harwell in 1954 when facilities were built for it there. These separate units occupied a series of small buildings around the main Institute, the mouse mutagenesis unit in an old A.R.P. report centre. When I became a Fellow of the Society, our local wit said: 'Now they'll build *you* a hut in the garden to live in.'

But one development did not go as expected. Waddington had been deputy director of N.A.B.G.R.O. which had developed physically in two separate sections, the genetics group in the Institute and a more applied group under White in a building about a mile away. Waddington had hoped that, when White retired, he would be made director but the A.R.C. decided to make the split permanent. All members of the genetics section remained in the Institute as an A.R.C. Unit of Animal Genetics with Waddington as Honorary Director and the applied section became the Animal Breeding Research Organization, now housed in a new building on the university site almost next door to the Institute.

In 1955, there occurred his fiftieth birthday party which marks in a way the peak of the Institute's existence under his leadership. This party was arranged with great effort, with a series of genetic ditties composed by Barnet Woolf and sung by a male voice choir conducted by Selman. They included a song *Magic words* to the tune *Mush mushalorum* with the verse:

If you want the correct explanation
Why embryos grow into men
The Alsatian begets an Alsatian
A hen's egg gives rise to a hen
Why insects result from pupation
Why poppies grow out of a seed
Then just murmur 'canalization'
For that is the word that you need.

Chorus Then three cheers for canalization
Oh, come on now, hip hip hooray
A stiff dose of canalization
Will drive all your troubles away.

There was an epigenetic landscape constructed as a pinball machine, with the ball mostly travelling down the main valley to produce normal phenotypes but on occasions being diverted into a secondary valley and producing a mutant. Waddington was suddenly introduced into the party (to his great amazement—he had been out to dinner and was coaxed back to the laboratory, as he thought, 'to see some scientific films') when it was well under way. It was the peak of his time at the Institute for two related reasons; first, because after this, he began to spend less and less time in Edinburgh and secondly because the Institute became more and more compartmentalized. One of the reasons for this was the building of the Epigenetics Laboratory.

Waddington had proposed both to the M.R.C. and the A.R.C. that a new laboratory should be set up for the study of 'epigenetics'—a word he himself had first used to describe the causal analysis of development, one of the fundamental ideas of his book *Organisers and genes*. He argued that the classical approach to disease had lost relevance with the conquering of infectious diseases and that the future lay in the study of subtler problems in the development of 'normal' individuals. The M.R.C. then agreed to finance an Epigenetics Research Group with Waddington as Honorary Director. He got further support for a building from the Wellcome Foundation and from the Distillers Company and this was opened in 1965. This bold concept did not develop, in retrospect, in the way he would have hoped. One reason is historical. Just after the lab was started there was a tremendous flowering of molecular biology arising from the discovery of DNA and RNA hybridization techniques. So most of the newly acquired laboratory space, salaries and technical assistance went to work in this field, which had no immediate relevance to problems of development, rather than on the kind of work that Waddington had originally envisaged. A notable exception which fitted into Waddington's original concept was the work on the development of the avian lens in the group led by Mrs Ruth Clayton. The laboratory became well known for the DNA–RNA investigations which earned a world reputation for at least two of the leading workers.

In 1968, Dr D. S. Falconer who had been a member of the A.R.C. staff was awarded a personal chair by the University and took over responsibility for genetics teaching and for the administration of the genetics laboratory (the Epigenetics building had a separate deputy director in Dr Max Birnstiel). In 1970, Waddington accepted an invitation from the State University of New York to spend two years in Buffalo in an Albert Einstein Chair in Science. These chairs had been established by the state legislature of New York to attract eminent scholars to colleges of the State University for periods of up to two years. His visit to Buffalo was not a complete success, owing in part to a change in Vice-Chancellor at the University between the initial invitation and his eventual appearance in Buffalo. As a result, he found himself rather isolated within the University. This was also a time of severe student unrest in American universities. Shortly before his return to Edinburgh, he had his first indications of heart trouble.

After his return, his contacts with the Institute were reduced. In Buffalo, he had been responsible for starting a course on 'The man-made future' and this became his main interest in his final years. Mr Robert Underwood, who had gone to Buffalo to help with the course, formed the nucleus of his staff in Edinburgh, backed initially with a small amount of financial support attached to the chair of genetics, but from 1974 financed by a grant of £15 000 from the Leverhulme Foundation. The school was concerned first of all with the setting up of a small library and then with running several courses of lectures. But Waddington's death cut short its development and it did not survive in its original form.

His interests in this direction had perhaps been stimulated by his part in setting up the International Biological Programme (I.B.P.) which I deal with at greater length later. He had been involved in the Pugwash Conferences as chairman of a small committee responsible for the organization of some of the sessions of the London Conference in 1962. In 1963, he became a member of the British Pugwash Group but attended no more of the international conferences. He was also invited to the second Delos Symposium, organized by Constantinos Doxiadis in Greece in 1964, and attended several of these meetings—informal gatherings covering a wide range of disciplines but concerned with the general area of 'the crisis in human settlements'. He contributed several articles to the related journal *Ekistics*.

His interests in this direction came to a focus with an invitation from Dr Alexander King, writing on behalf of Dr Aurelio Paccei, to a meeting in Rome, with the financial backing of the Agnelli Foundation. 'It is increasingly evident, that in the future, many problems of essential importance to the social and economic development of the nations are of such character and complexity that they are unlikely to yield to the traditional methods of science.' The background paper for the meeting was written by Dr Erich Jantsch. From this initiative came the Club of Rome, of which Waddington was therefore a founder member. He attended the first meeting in Rome as well as the second, a year later, in Austria. As far as I can gather, he did not attend any subsequent meetings,

because of his stay in Buffalo and of his reluctance to travel after his first heart attack. From his correspondence, I detect that he felt that the club had subsequently become too associated with the kind of world model-building typified by the book *Limits to growth*. His last, posthumous, book *Tools for thought* deals in a general way with methods for the analysis of complex systems. It was published too late for detailed comment in this memoir.

Waddington played a major rôle in the expansion of the biological faculty of the University of Edinburgh, one important step being the appointment of Dr M. M. Swann (now Sir Michael Swann, Chairman of the British Broadcasting Corporation) as professor of zoology. During the next 20 years, this part of the University expanded enormously with the appointment of a second professor of zoology, the creation of a molecular biology department under Professor M. R. Pollock and the move of the botany department from its physical isolation from the rest of the University in the Botanic Gardens to a new building on the King's Buildings site.

He was always keen to present this growth in terms of the number of Fellows of the Royal Society in biology in Edinburgh and in particular those working in the Institute. For several years, the latter total was five (Waddington, Auerbach, Beale, Robertson and Falconer—probably more than for any department in any science outside Oxford and Cambridge) and was nearly six because Dr Anne McLaren left to take up a chair in London only months before she was elected. Staff members who became Fellows after they had moved elsewhere were Professor H. G. Callan and Dr Mary Lyon.

He served on two important Government committees. The first under the chairmanship of Sir Harold Himsworth was appointed in April 1955 by the Medical Research Council 'to review the existing scientific evidence on the medical aspects of nuclear and allied radiations, including the genetic aspects'. Its report, in June 1956, was a major contribution to the discussion, both national and international, which led in the end to the Nuclear Test Ban Treaty. Having been a member of the Minister for Science's Advisory Council on Scientific Policy, he and Lord Todd were the only two scientists appointed to the Trend Committee, set up in 1962 to consider the structure and financing of civil scientific research. It reported in 1963 and subsequent Government action in the Science and Technology Act, 1965, produced a major change in the structure of official support for scientific research. The previous Department for Scientific and Industrial Research was separated into three: the Science Research Council, the Natural Environment Research Council (covering both ecology and the earth sciences), and finally some of the more applied engineering research institutes were put under the direct control of the Ministry of Technology. Subsequent action based on the Rothschild report has left this structure essentially unchanged but has given the relevant ministries more control of the scientific work done in their respective fields, by allowing them to finance a part directly on a contractual basis. Waddington also served for a long while as a member of the Animals Research Committee of the Agricultural Research Council. He was a member of the Council of the Royal Society from 1960 to 1962.

He was awarded the C.B.E. in 1958 and was elected a Fellow of the Royal Society of Edinburgh in 1948, became a foreign member of the American Academy of Arts and Sciences in 1959 and of the Finnish Academy in 1957. In 1974 he was elected a Fellow of the Deutsche Akademie der Naturforscher Leopoldina, a scientific academy with an uninterrupted history since 1677. He was awarded the honorary degree of D.Sc. by the Universities of Montreal, 1958, Trinity College, Dublin, 1965, Prague, 1966, Geneva, 1968, and that of LL.D. in 1966 in Aberdeen. He was the main mover in starting the journal *Genetical Research*, published by the Cambridge University Press, and served as chairman of the editorial board for the remainder of his life. He was also for a period on the editorial board of the *Journal of Embryology and Experimental Morphology* and of the *Journal of Theoretical Biology*.

He seemed much slowed down after his return to Edinburgh from Buffalo in 1973. He had a further and fatal heart attack outside his house on 26 September 1975, two months short of his seventieth birthday.

I.U.B.S. and the International Biological Programme

After the great success of the International Geophysical Year in 1957–58 various biologists were stimulated to think of some similar international effort. The seed was sown at a meeting in Cambridge in 1959, the main mover being Sir Rudolph Peters, at that time President of the International Council of Scientific Unions. But the future was not very clear even two years later when Waddington became involved and essentially guided the fortunes of the International Biological Programme (I.B.P.) until an executive secretary was appointed in E. B. Worthington. Sir Rudolph says: 'I think that I.B.P. would have failed without the help of Waddington.'

Waddington has himself described the origin and early history of I.B.P. at some length and it will, I think, suffice if I summarize this by a series of quotations from him.

> 'I first came into any close contact with the I.B.P. at the General Assembly of the International Union of Biological Sciences (I.U.B.S.) held in Amsterdam in July 1961. When I was sent by the Royal Society as one of the British delegates to this Assembly, I knew very little about the I.U.B.S. or its work. It was a great surprise to me when towards the end of the meeting I was approached by Paul Weiss on behalf of the Nomination Committee and asked to allow my name to be put forward as the next President of the Union. I was rather reluctant to accept this, but eventually did so. One of the reasons why I was willing to contemplate taking on the job was that my interest had been aroused in the potentialities implied in the proposal to start an International Biological Programme. . . .
>
> 'At Amsterdam a morning was devoted to a symposium by four invited speakers on possible topics for the I.B.P. I was one of those invited to contribute. From what I had learned in the past, I had formed the impression that up to that time the whole enterprise was extremely dubious.

There was talk of organizing something on a large world-wide scale, comparable to the I.G.Y., but the people putting forward the ideas seemed to have no firm grasp of how it should be financed or organized. Moreover, each sponsor seemed to think that the programme should be devoted to his own speciality. . . . My private opinion was that it would probably be most satisfactory to kill the whole thing before it went any further, if this could still be done. However, it seemed rather likely that matters had already gone too far for this to be practical. If, on the other hand, it would proceed, I felt that the only possible line would be to formulate a programme around something which was undubitably of major social and economic importance for mankind as a whole.

'It seemed pretty obvious that the kind of biology in which I was professionally engaged—genetics, epigenetics and so on—did not need, and was not suitable for, any internationally organized cooperative attack of the kind contemplated in an I.B.P. I therefore felt I had no personal interests at stake, and could attempt to form a judgment from a relatively neutral point of view as to what was the most important contribution biology could make to man. The most attractive field, I thought, was something to do with the way in which solar energy is processed by the biological world into the formation of complex molecules which man can use, as food or otherwise. I gave my contribution to the Amsterdam symposium along these lines.'

He then goes on to describe his problems in turning this general idea into an organized research programme supported by the biological establishment.

'The committee finally came up with a structure for the organization of I.B.P. which is essentially what has been preserved throughout the programme, namely, a set of seven sections or subcommittees: three on biological productivity in terrestrial communities (of these three, one on general productivity, the second on the metabolic processes—mainly biosynthesis and nitrogen fixation—on which this productivity depends, and a third on the conservation of threatened communities); then a fourth on productivity in fresh water; a fifth on productivity in marine communities; a sixth on human adaptability (physiological and genetic); and a seventh on public relations and training.

But the whole scheme had still to be sold to the biological world.

'The really difficult biological communities were those in Britain and particularly those in America, which had very strong divisions under the dominance of physiology, biochemistry and molecular biology. In Britain the dominant medico-physiological establishment filled more or less *ex officio* the main official positions in the Royal Society, and were sceptical and indifferent, though not definitely antagonistic. The intellectual leaders in molecular biology and genetics were just simply uninterested, but again not really effectively hostile. The only strong British group in the ecological-natural history field was centred round the Nature Conservancy which had

> its own subcommittee (the third) in the programme and which was even prepared to think they might in future take productivity more seriously than they had done in the past. Meeting the Royal Society I.B.P. committee in its early days, I often felt that I was being called upon to invent a new discipline of production ecology off the cuff; but the Royal Society officials —the Executive Secretary, David Martin, and his assistant, Ronald Keay, whose professional fields were science policy—immediately saw the socio-economic importance of I.B.P. and gave it every assistance.
>
> 'The toughest biological community into which to launch the scheme was that of the United States. The American biological world was not dominated—establishment-wise—by medical physiologists and biochemists to the same extent as the British; but the analytical school of molecular biologists and microbiological geneticists had a far higher status than in Britain and much less hesitation in asserting, in the hearing of government or the Academy, that any organism bigger than *E. coli* serves only to confuse the issue.'

Waddington managed slowly to bring some of his more influential friends amongst the American biologists on to his side but he writes that 'it was not till about 1966 that the real importance of I.B.P. got across to the Americans'.

His other problem was to find suitable staff and in particular a suitable senior executive. He had had the blessing of the Director of the Nature Conservancy, Max Nicholson, and the latter was eventually persuaded to let his Deputy Director, Dr E. Barton Worthington, go over to I.B.P. to act as its Scientific Director. This appointment was finally ratified in July 1964.

Epigenetics

I have already mentioned Waddington's successful attempts at the Strangeways Laboratory to study induction in the chick embryo. The concept of 'embryonic induction' comes from a long period of work by Spemann on amphibian development, culminating in an experiment with Mangold in 1924 in which they showed that transplantation of sections of the blastopore region of the embryo to other regions drastically altered the developmental fate of the latter. In normal development, the cells in the blastopore region (sometimes called the 'grey crescent') are folded into the interior of the egg and come to lie underneath a large part of the animal half. The part of the exterior thus underlain develops into the main ectodermal organs of the dorsal axis or backbone—namely, the brain and neural tube. The transplantation experiments showed that the blastopore region had the property of altering the developmental fate of cells which were placed in contact with it, irrespective of their normal fate.

> 'There it does not join in the development of its surroundings, but sticks to its own direction of development. Indeed it does more than this. It induces or even organizes its surroundings, and builds from its own substance and from that of its surroundings a small secondary embryo, which can reach a high degree of perfection' (Spemann and Mangold).

Further work showed that this process of 'embryonic induction' is very common in embryonic development.

> 'In vertebrates such as newts, birds and mammals, very many types of induction have been described. For instance, shortly after the crescent cells have induced the formation of the brain and nervous system, about the time of gastrulation, these organs begin to induce other things in their turn. The very front tip of the brain induces the formation of the nose organs; slightly behind this, two outgrowths from the brain, which later develop into the eyes, induce the overlaying skin to form the lenses; still further posteriorly, behind-brain induces the ears; and so on.'

At the conceptual level, Waddington always insisted on the distinction between 'induction' and 'individuation'.

> 'In a living embryo the crescent cells do not merely switch the neighbouring cells into a new line of synthesis so that they produce the proteins characteristic of nerve cells. The induction gives rise to a well organized brain and the nervous system, with an elaborate morphological structure and pattern. This, of course, involves a much higher level of complexity of biological organization than a mere collection of cells containing specific nerve proteins. The original German words seem to imply that induction always involves the complex levels of organization, since the word chosen to refer to what we have called the crescent cells was the "organization centre" or, for short, "the organizer". Now this really confuses two issues. It is perfectly possible to switch a mass of embryonic cells from becoming a disorderly group of skin cells into becoming an equally disorderly collection of nerve cells, with no or minimal organization. This is, in some sense, an "induction". But something that brings this about is scarcely entitled to be called an organizer. It is better to refer to it instead as an "evocator". When morphological organization occurs as well, as it often does, then we are obviously dealing with something more, and we require another word to refer to it. Since "organization" has already been used in a loose sense to refer to the whole process, it is better to use for this purpose the word "individuation". It is still reasonable to go on using the expression "embryonic induction" when we want to refer to the whole process, without specifying precisely any particular aspect of it.
>
> 'There is another important aspect to induction for which we also require a word. The induction of a particular organ can only be carried out on the cells from a particular part of an embryo at a particular stage in their development. For instance, the cells of an early amphibian embryo do not being to respond to the evocators of nervous tissue until about the time of gastrulation, and they lose this responsiveness again fairly soon after gastrulation ends. The word "competent" is used to describe their state during the period when they can respond; or we can speak of them at that time as "competent with respect to neural induction". A little later they will become competent with respect to other types of induction, for instance that

of a lens. Interpreted in genetic terms this must mean that there is only a certain period during which the particular genes for these types of tissues are susceptible to being switched on or off.'

Waddington made experimental contributions in two directions. The first concerns the new techniques that he devised for the study of the avian egg which he himself used to show induction in the chick.

'The study of the epigenetic processes involved in avian development was held up by technical difficulties greater than those offered by the amphibia. There were not only the usual obstacles of small size, but the embryo is located under a hard shell and viscous albumen, and on top of a fluid "yolk". . . . New possibilities were opened up when the technique of tissue culture was adapted to the task of keeping alive the entire blastoderm after removing it from the egg and cleaning it of the adhering albumen and yolk. In such blastoderms, the three germ-layers can be separated from one another, at least in certain regions, and fragments can be grafted into abnormal places where their influence on the surrounding tissues can be studied (Waddington, 1932).'

Using the new techniques, he showed that induction also occurred in the avian embryo.

'The final proof of the reality of induction had to be obtained by a different method. This was done by taking two blastoderms, removing the endoderm from each of them, then placing them with their mesoderm faces together, and with the two primitive streaks not on top of one another. When the whole of such a combination is grown *in vitro*, as many as four embryonic axes may appear; one from each of the original primitive streaks and two more, one induced by each streak in the other epiblast against which it lies. The neural grooves are still firmly attached to the epiblast from which they arose, and it can be quite definitely seen that the secondary ones have been induced and were not formed from the original streaks. The origin of the mesodermal parts of the embryonic axes is not so certain, and one must guess that they are formed partly from the original streak and partly by induction.'

He also developed methods for use with mammalian embryos (rabbit), similarly keeping them alive and developing in an artificial environment. His work on avian development was eventually summarized in his book *Epigenetics of birds* published in 1952.

His other main line of work concerns the search for the chemical nature of the 'evocator'. For this work, done in collaboration with the Needhams, he received the first Albert Brachet prize in 1936, awarded by the Royal Academy of Belgium for the best published work on embryology in the year. This work led through many twists and turns and eventually became disembodied like a will o' the wisp. It was early discovered (amongst others by Waddington himself) that induction could be brought about by grafts of dead organizer. Further, many adult tissues,

which would not bring about induction while alive, would act as evocators when killed.

> 'This appeared at first sight greatly to facilitate the attempts which several groups of workers were making to extract and identify the evocator substance; instead of starting with dead organizer material, which can only be obtained by dissection of the small gastrula, one could start with large masses of liver and test the activity of various fractions. But the different groups of investigators came to quite different conclusions as to which fractions were the most active. Spemann and his collaborators at first identified the evocator with glycogen; Fischer argued that evocation could be brought about by the stimulation of various acids, among which he mentioned the nucleic acids; Needham and Waddington traced the activity to the fraction of the extract which contained the sterol-like substances, and Waddington demonstrated a high degree of activity in certain synthetic substances of the same nature; while Barth suggested that the evocator substance was cephalin. Obviously not all of these conclusions could be true; and although some of the claims were mistakes based on the presence of impurities, the situation appeared to be one of complete confusion. It only began to clear up when it was shown that evocation could be produced by chemicals which quite certainly are not the evocator which occurs in the naturally developing embryo.'

Finally, Okada showed that induction could be brought about by mechanical irritants such as siliceous earth and Holtfreter did the same by killing a certain number of cells with a glass needle. Waddington, Needham & Brachet (1936) had shown that if small pieces of ectoderm were isolated in salt solution containing methylene blue and were then implanted into a young gastrula, they could induce neuralization of the competent ectoderm against which they lay. And so the search gradually petered out at about the same time as the outbreak of World War II. Looking back in 1966, Waddington summarized the state of affairs at that time.

> 'We must in fact be dealing with a situation that has many similarities with that which has been discovered more recently in induced enzyme synthesis in bacteria. There, as we have seen, the cells contain regulator substances which can, on the one hand, act specifically to repress or derepress particular genes, while, on the other hand, their ability to do this is affected by their interaction with relatively unspecific inducer molecules in the medium. In embryonic induction the cells must also contain some regulator substances capable of specifically activating or derepressing certain genes; and again the effectiveness of these regulator substances must be altered by less specific changes in the metabolism of cells, which can be brought about in many different ways. In the early studies on amphibian neuron induction, the gene-controlling or "genotropic" regulating substance was referred to as the "masked evocator" and it was supposed

that this was without effect until some change in cellular metabolism, such as that which occurs at the blastopore region, brought it into play.

'We know even less about the chemical nature of the masked evocator regulator substance in embryonic cells than we do about the regulator substances in bacterial enzyme induction. In the latter, as we have seen, the regulator may probably be an allosteric protein with two active sites in the molecule, one specific for a particular gene and the other capable of acting with the less specific inducer molecules. In embryonic cells the regulatory substances capable of acting specifically on particular genes may also be proteins. However, we are still very far from having identified them; and one must remember that the situation in the cells of the higher organisms is certainly much more complicated than that in the simple cells of bacteria. . . . Studies are still being very actively made to try to get nearer to the crucial points in the embryonic switch mechanisms at which particular genes or groups of genes are brought into activity. Many of the substances that were first shown to be very active in bringing about induction have their first effects on the cytoplasm, and certainly do not directly impinge on the genes. Some of the "metabolic" treatments probably have their first effect on the yolk granules, others on the external membrane of the cells. . . .

'The general picture that emerges from all this is that the embryonic cell is rather like a room where a cocktail party is going on with the radio set with press button tuning in the centre of it. The switching on of a particular battery of genes, controlling the synthesis, say, of nerve proteins, corresponds to pressing one particular button which brings in a programme precisely from one station. But you may succeed in getting this button pressed by jogging the elbow of somebody at the other side of the room, who stumbles against the next man, and so on down the line until somebody finally falls against the radio set, and this may be sufficient to click on whichever of the tuning buttons is most insecure. (Changes in the competence of the cells would correspond to changes in the ease with which the tuning relays could be tripped.) Similarly many influences impinging on competent embryonic cells may produce inductions, without revealing anything essential about the fundamental mechanisms controlling the underlying gene activities.'

He then turned his attention from the experimental modification of development to its disturbance by genetic means. In this he seems to have been stimulated by the great American *Drosophila* geneticist T. H. Morgan who had begun his life as an embryologist and who indeed in 1934 wrote a book entitled *Embryology and genetics*. 'He firmly advocated the point—and should have fully established it, if people had been ready to listen to him—that the fundamental agents that bring about embryonic development are the genes, and that the only satisfactory theory of embryology must be a theory of how the activities of genes are controlled.' Though this is Waddington talking about Morgan, it very aptly sums up his own view of the interrelationship between the two disciplines

and, indeed, he took up the theme himself in his book *Organisers and genes* which he published in 1940. Although centred round discussion of the phenomenon of embryonic induction, its scope is much wider.

> 'I have not, however, attempted any extended discussion of the relation between the inductive mechanism of vertebrates and the causal processes which have been discovered in embryological investigations of invertebrates. I have instead devoted some space to pointing out the similarities between the concepts derived from the consideration of the organiser and those which arise in connection with the developmental effects of genes. The two sets of phenomena have of course been investigated in different organisms but the principle of genetics are so uniform throughout the animal kingdom that it may not be too much to hope that processes occurring in one group may provide a valuable guide to those in another.'

The book also includes his first use of the word 'epigenetics' to describe the causal analysis of the processes of development and his famous 'epigenetic landscape', a visual analogy of the stable pathways of development (for which he eventually coined the word 'chreod') here makes its first appearance.

He therefore turned to *Drosophila* in which a great many morphological mutants were by that time known.

> 'In using the data of genetics to throw light on the general character of developmental processes we are not concerned with the way in which any particular gene obtains its effect. Here we want to start from the other end, taking an organ or tissue and seeing how genetics would lead us to envisage its development. It will be convenient before discussing particular cases to summarize the general principles which we shall in fact find to emerge. The most important of these are:
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> '(i) The development of an organ or complex substance takes place in a series of steps, each of which is affected by genes.
>
> '(ii) At each step there are several genes acting, and the actual development which occurs is the result of a balance between the opposing gene-instigated tendencies.
>
> '(iii) At certain stages in the development of an organ, the system is in a more than usually unstable condition, and the slightest disturbances at such times may produce large effects on later events. Such times have been called "epigenetic crises".
>
> '(iv) An organ or tissue is formed by a sequence of changes which can be called the "epigenetic path" leading to it. In a normal egg which contains the genes usually found in the wild individuals of the species, these paths are rather definitely distinct from one another, so that a developing mass of tissue turns either into a leg or into a wing, say, but it is difficult to persuade it to become something intermediate. And also each path is "canalized", or protected by threshold reactions so that if the development is mildly disturbed it nevertheless tends to regulate back to the normal end-result.'

He first investigated the development of the wing in *Drosophila*, which had already been considered from this point of view by Goldschmidt. Waddington analysed the process by considering the abnormalities produced by about 30 different wing mutants. He and his student Lees considered the effects of environmental interference with development, such as pricking the wing with a needle or subjecting the pupa to temperature shocks, to produce 'phenocopies'—which eventually led to his experimental work on genetic assimilation some 15 years later. Together with Lees he also published a genetic analysis of a developmental sequence using a series of mutants affecting the formation of bristles (macrochaetae) and with Pilkington he studied four eye mutants.

When he restarted work on development in Edinburgh, he and his students followed several different lines, often related to parts of his earlier work.

He continued to study amphibian and avian development but now mainly using new biochemical techniques which became available with the rapid increase at the time in our understanding of the chemical basis of the gene and of protein synthesis. He was the first to use tracers in the study of development. He was particularly interested in variation in biochemical activity between different parts of the embryo (in order to analyse problems of differentiation at the biochemical level), using labelled amino acids to study protein synthesis as well as the diffusion of labelled material from graft to host in graft induction (with Sirlin). The work was extended to an examination of the population of RNA molecules in different tissues of the developing embryo but this proved very tedious because of the necessity of tissue dissection.

He also looked at various methods of disturbing the process of development, both physical and chemical. These included the reaggregation of both amphibian and *Drosophila* embryos after disintegration with ultrasonics or with EDTA and bicarbonate buffers. The work on amino-acid uptake was then extended to study a series of antimetabolites such as amino-acid-(ethionine and parafluorophenylalanine) and purine analogues (8-azoguanine and azohypoxanthine) using both amphibian and chick embryos. He continued his work on genetically modified development in *Drosophila* using sex-linked lethals (Ede, Shatoury) and Counce studied female steriles, such as fu and d-or in which the sterility results from a failure of ooplasm in mature females to support embryonic development. He also studied various homoeotic mutants, such as aristapedia and bithorax.

Together with Perry, he used electron microscopy to examine comparative ultrastructure of various stages of development, such as that of oocyte and eye development in *Drosophila*. He and others examined different stages of amphibian development, with particular reference to the processes leading to cell movement and physical deformation in the embryo. With Selman, he investigated the mechanism of cell division during cleavage of the amphibian egg, with particular emphasis on the movement of the cells of the cortex and with the synthesis of the new cortex. It was found that the new unpigmented cortex is formed as a sheet of gel which grows downwards through the cytoplasm from the vegetal surface and contracts at the same time. Using the principle of the moving

iron ammeter, it proved possible to measure the magnitude of various forces operating during neurulation in amphibian embryos, here taking up a line on which he had originally published in 1939.

But his most important contributions in later years were at a conceptual level. They culminated in a series of four meetings which he organized in successive years in the late sixties at the Villa Serbelloni in Bellagio on Lake Como. They were supported by I.U.B.S., of which he was President at the time, and the Villa was put at his disposal by the Rockefeller Foundation. Each was subsequently summarized in a book edited by Waddington under the general title *Towards a theoretical biology*. There were generally 15–20 participants, chosen because of the widths of their interests and including several younger workers interested in extending mathematical concepts to biological problems.

> 'The intention was that the discussions would be concerned, not with the theory of particular biological processes, such as membrane permeability, genetics, neural activity, but rather with an attempt to discover and formulate general concepts and logical relations characteristic of living as contrasted with inorganic systems; and further with a consideration of the implications that these might have for general philosophy.'

They were perhaps noteworthy for the introduction of René Thom's catastrophe theory into a biological context and, indeed, Waddington subsequently wrote a foreword for Thom's book *Stabilité structurelle et morphogenèse*.

Waddington contributed much, both in discussion and in writing, to these meetings and the third volume contains an excellent summing up of his later views under the title *Concepts in the theory of growth, development, differentiation and morphogenesis*. Here he discusses again many of the topics he had discussed in such a stimulating manner in his earlier book *New patterns in genetics and development*.

His books on development, a discipline in which he is responsible for a great deal of accepted terminology, were a most important contribution beginning with an elementary book *How animals develop* in 1935. His interest in the integration of concepts in genetics and development lead to *Organisers and genes* and to *An introduction to modern genetics*. After the war, he published two major textbooks, first *The epigenetics of birds*, a subject to which he had himself made major contributions, and then in 1956 *Principles of embryology* aimed at final-year students of embryology and genetics and at research workers in other branches of biology. In 1961, when he held a visiting fellowship at the Institute for Advanced Studies at the Wesleyan University, Middletown, Connecticut, he wrote *New patterns in genetics and development*, a discussion of 'the impact of the recent great advances in genetics on our understanding of the development of multicellular organisms'. On the whole, his books are too stimulating, too wide-ranging and too speculative to be ideal textbooks though, on the occasion he did deliberately set out to write an elementary text, as with the paperback *Principles of development and differentiation*, published in 1966, he succeeded admirably. His final publication in this field was the two-volume *Developmental systems:*

insects which he edited with Dr S. J. Counce and to which he contributed a section on 'The morphogenesis of patterns in *Drosophila*'.

Evolutionary studies

His final view on the relevance of his work on natural selection and evolution is best summarized by a long quotation from *The evolution of an evolutionist*.

> 'I began to work as a palaeontologist, studying the evolution of certain groups of fossils. And I chose, as my main interest, a group which forces on one's attention the Whiteheadian point that the organisms undergoing the process of evolution are themselves processes. The Ammonites were cephalopods, related to squids and the Nautilus, which laid down spiral shells. The animal occupied only the latest-formed part of the shell and from time to time moved forward a little, leaving behind it the part it had previously inhabited. Thus, following the whorls of the spiral shell outwards, from the centre to the periphery, one has a record of the whole life-history of the animal; it never appears just as an adult whose juvenile stages have vanished. The whole developmental process is preserved so that one cannot avoid examining it. And the process is, of course, complex, with many facets. On the surface of the shell there are "ornaments"—ribs, knobs, tubercles, etc.—which change as development proceeds; the cross-sectional shape of the tube may change and so may the closeness with which it is coiled; and behind each living-chamber a partition is laid down which meets the outer shell in a complex "suture" which is one of the most characteristic features of a species.
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> 'In most types of animals in which the adult form of the individual replaces the young stages, the only way to study the developmental history is to collect a large population containing juvenile as well as adult stages. Age can usually not be determined directly, but one can take some measure of size as an indication of it. The figures show a draft I made, around 1927, in the variation in ratio of breadth to length in a collection of fossil cells (a brachiopod, *Terebratula*). [The figures have been omitted here. A. R.]
>
> 'These early exercises left me with a deeply ingrained conviction that the evolution of organisms must really be regarded as the evolution of developmental systems—which was the title of one of the first articles I wrote about evolution when I returned to the subject some years later. It is of course related to such old ideas as Haeckel's "Biogenetic Law"—phylogeny repeats ontogeny—but I took it also as a guiding principle in population genetics. I still think that when modern population geneticists express the variation in a population by means of a timeless frequency curve, which deals only with the adults, this is a simplification which needs justification—which of course it may often at least partially possess, for instance when one is dealing with the *imago* of an insect like *Drosophila*, which metamorphoses suddenly into an adult form which thereafter does not change. But

when I started doing experiments on *Drosophila* evolution, in the '40s and '50s, I treated even that insect as a developmental system, and by manipulating the environment in which it develops was able to uncover the rather novel process of genetic assimilation. Thus my particular slant on evolution—a most unfashionable emphasis on the importance of the developing phenotype—is a fairly direct derivative from Whiteheadian-type metaphysics.

'In my early career there was a considerable period in which I was concerned directly with developmental systems themselves, rather than with evolution. My approach to experimental epigenetics was again strongly influenced by Whiteheadian metaphysics, but also by genetics. In fact, when I decided that I wanted to do something more experimental than is possible in palaeontology, I first tried to become a geneticist. My first two published papers were one in plant genetics, and another a collaboration with J. B. S. Haldane along classical neo-Darwinist lines, in which we studied the effect of inbreeding on the segregation of linked genes, writing down, and trying rather unsuccessfully to deal with, a great series—up to 27 members, I think—of finite difference equations. So I had my taste of the thin gruel of mathematical formalism—as well as of the strong nourishing soup of time-extended populations of fossilized developmental systems. But my attempt to become a geneticist was a failure, because at that time in Britain there was simply no way in which one could earn a living at the subject. So I became an experimental embryologist. For some years my most immediate interest was in solving the technical problems of carrying out meaningful experiments on types of embryo which no one else had tackled successfully, such as birds and mammals, or of doing biochemical work on the very small tissue-fragments isolated from various regions of an egg. However, the theoretical structure of the subject also needed a good deal of attention, and this is where the Whiteheadian approach came in. In the '20s, T. H. Morgan had argued that epigenesis should be considered in terms of the activities of genes, but he had little effect on the workers in this field. Embryological theories involved such notions as the "segregation" or "differential dichotomy" of "potencies" to develop into organs such as the nervous system, kidneys, gut, etc.; or, at a more advanced but still very imprecise level, notions such as "the organizer", "induction", and the like. I wanted to return to Morgan's idea that the only "potencies" it is meaningful to talk about are the potential activities of genes. So did several people who were primarily geneticists, but who had become interested in development without having actually worked on it very much.

'Two radically different lines of approach were followed. The one which was—and in fact still is—favoured by most geneticists depended on what I think may be called an "atomistic" metaphysics. It set out from the assumption of the existence of single genes, and it asked, at first, what does A do and, later, what controls whether gene A is active or not? There is only space to mention, just to remind you, some of the key figures. Goldschmidt

concluded that genes control rates of processes; Muller that they manufacture more, or less, or none of some substance, or sometimes an anti-substance or even a quite new substance. Garrod (on human metabolism), followed by Haldane (on flower pigments), led on to the identification by Beadle and Ephrussi, in the early 1940s, of these substances as enzymes. Again in the '40s, Hadorn in *Drosophila* and Gruneberg in mice studied the manifold development consequences which may follow an alteration in a single gene. Finally, about 1960, Jacob and Monod produced their story of the mechanism which controls the activity of single genes (or small operon groups) in prokaryotic organisms in which the chromosome normally lacks protein.

'Clearly, this line of approach has paid off very well. But to my mind it does not really deal with the questions which the epigeneticist faces. For one thing, there is the difficulty that the Jacob–Monod control system could scarcely work, without considerable modification, in cells with proteinaceous chromosomes. But the problem is deeper. In cells of higher organisms we are not usually, if ever, confronted by the switching on or off of single genes. What we find is a whole complex cell becoming either a nerve or a kidney or a muscle cell. In the late '30s I began developing the Whiteheadian notion that the process of becoming (say) a nerve cell should be regarded as the result of the activities of a large number of genes, which interact together to form a unified "concrescence". This lines of thought had several ramifications. For instance, just before the Beadle–Ephrussi era I showed in detail how the development of the wing of *Drosophila* is affected by the activities of some 40 different genes. Again a few years later it had become apparent that "gene-concrescence" itself undergoes processes of change; at one embryonic period a given concrescence is in a phase of "competence" and may be switched into one or other of a small number of alternative pathways of further change—but the competence later disappeared and if you've missed the bus the switch won't work. My main preoccupation, however, was with the nature of the switches which was the subject of the experimental biochemical work I was doing, with Needham and others, on "embryonic induction". Influenced—probably over-influenced—by genetics I insisted that the switch must have sufficient specificity to recognize particular genes. We showed that, in these terms, the specificity resides inside the cells which react to induction—we called it "the masked evocator". This is very similar to the situation discovered by Jacob and Monod many years later in bacteria, where again the specific repressor molecules are internal to the cells which react to enzyme-inducing substances. If I had been more consistently Whiteheadian, I would probably have realized that the "specificity" involved does not need to lie in the switch at all but may be a property of the "concrescence" and the way in which it can change. Because of course what I have been calling by the Whiteheadian terms "concrescence" is what I have later called a *chreod*, a notion which René Thom has explicated; and switches are Thom's

> *catastrophes*. The specificities need not be in what precipitates the catastrophe but could reside only in the possible stable regimes (limit cycles in the simplest case) into which the system could be slipped.
>
> 'Let us return to the beginning. The whole of this, I'm afraid rather long-winded, exposition has not been aimed at showing that my line of thought, which I have derived from Whitehead, is the correct or best one. I should in fact admit that it has not so obviously paid off as the "what does a single gene do?" line; although I also continue to feel that it tackles deeper, because more embracing, problems. However, the point was to illustrate the fact that metaphysical pre-suppositions may have a definite influence on the way in which scientific research proceeds. And that point I have, I think, established, even if you feel that my metaphysics has led me up the garden path. And, after all, I am a biologist; it is plants and animals that I am interested in, not clever exercises in algebra or even in chemistry. The garden path has its attractions for the likes of us, and all of us who want to understand living systems in their more complex and richer forms are fated to look like suckers to our colleagues who are content to make a quick (scientific) buck wherever they can build up a dead-sure pay-off.'

I feel that he will be remembered as an experimentalist in this field mostly for his work on genetic assimilation, carried out mostly in the 1950s but in fact adumbrated in a paper in 1942 on 'Canalization of development and the inheritance of acquired characters'. The concept of genetic assimilation may be summarized briefly as follows. The capacity to respond to an external stimulus by some developmental reaction must itself be under genetic control. If such a reaction is adaptive, i.e. it increases the viability and fertility of the individual, then there would be natural selection for individuals capable of giving the optimum response. In the end, then, a population of individuals might be produced capable of response without the external stimulus. To this, he added the concept of canalization. 'The main thesis is that developmental reactions, as they occur in organisms submitted to natural selection, are in general canalized. That is to say, they are adjusted so as to bring about one definite end-result regardless of minor variations in conditions during the course of reaction.' He then argues that continual selection pressure on ability to respond to the external stimulus will cause the reactivity to become canalized in this direction. 'It is to be expected that many different agents, including a number of mutations available in the germ plasm of the species, will be able to switch development into it; and the same considerations which render them advantageous will favour the supersession of the environmental stimulus by a genetic one.'

He and his co-workers used environmental agents which produce 'phenocopies', i.e. they mimic the morphological effect of known mutants. It is interesting that his basic knowledge of such agents came from his earlier use of them to interfere with normal development. Working with *Drosophila*, they then bred from those animals which had responded to the stimulus, repeating this over many generations. In the end, the selected lines would in a high proportion of

cases give the developmental response without the external stimulus. Waddington referred to this process as 'genetic assimilation'.

The first experiment involved a heat-shock treatment given about 20 h after pupation which in this population produced a break in one of the wing cross-veins in a proportion of individuals. Selection lines were maintained, using as parents those individuals which did or did not respond respectively. The lines in a few generations showed clear differences in the proportion of individuals responding, proving that there were genetic differences in the population in response. Flies which developed from untreated pupae were observed and, at generation 16 of selection for response, some such flies showed the cross-veinless phenotype. Further selection without heat-shock increased the incidence to 100% at 10 °C though rather lower at 25 °C.

Similar more detailed experiments were done by Bateman (1956). She carried out detailed genetic analysis of the selected stocks and showed that loci on all the major chromosomes were involved. In Waddington's original unselected population and in some of Bateman's, the phenotype did not occur in the absence of treatment. In some wild populations, however, they did occur at a low percentage and in these she was able to select with no treatment and produce lines with a high incidence.

Waddington obtained similar assimilation with two further treatments. Using ether treatment of new-laid eggs, he selected for the bithorax phenotype (conversion of the metathorax into a structure resembling the mesothorax). Bateman, using a heat treatment 17 h after pupation, produced a dumpy phenotype. In this case assimilated flies did not appear until the twenty-fifth generation. In both experiments a major part of the response was shown to be due to a major gene at the classical locus known to produce this phenotype. For bithorax, part of the response could be shown to be due to a maternal effect.

Waddington also carried out a related experiment which does not fit so well into the theoretical framework. The anal papillae are known to be involved in the regulation of the osmotic pressure of the haemolymph and are larger in *Drosophila* reared on medium to which salt has been added. He kept flies of three strains for 21 generations on salt medium at a concentration at which only 40% of eggs would survive. After this, he found that in these strains not only were the papillae now more sensitive to salt concentration but that they had a greater area in the absence of salt.

His concept of 'genetic assimilation' provides an explanation for the 'inheritance of acquired characters' as a population phenomenon arising from natural selection of those individuals more capable genetically of the adaptive response. To Waddington, the concept of canalization was critical to this argument as providing a reason for the existence of much genetic variation hidden in the normal phenotype, concealed because of natural selection for those animals which under natural selection did *not* respond to a genetic stimulus, i.e. in situations where response would be non-adaptive. It is however not necessary to the main argument on genetic assimilation and, when applied to characters showing quantitative variation and not involving a threshold, has not in my

view proved useful. Such characters do not show the response to environmental stimuli which the concept demands (stability over intermediate ranges of environmental variables with greater sensitivity at extreme values) and the concept is not quantifiable in the sense that we do not know how to measure the canalization of any specific measurement. One of the strongest arguments in favour of canalization comes from the greater variability of mutant phenotypes than of wild type. The variation in question is almost always morphological and we have, I think, very little evidence that biochemical variants, which show no morphological effect, are any more variable than are wild type organisms.

The buffering of an organism against environmental shocks is difficult to measure (we do not know how an unbuffered organism would behave). In addition, specific properties of an organism *per se* do not have to be the product of natural selection. This is of course a frequent problem in evolutionary discussions—perhaps because we approach the problem of evolutionary design in a too anthropomorphic way. We design a part of a piece of machinery to perform a particular function—the function of a certain organ or of a certain property of a living organism is not always so clear. One specific property may be a necessary consequence of selection for another. For instance, Kacser in Waddington's laboratory has shown that buffering is a basic property of sequences of biochemical reactions. Thus the recessivity of inborn errors of metabolism may be a necessary consequence of biochemical complexity and we do not have to seek an explanation for it at another level.

Waddington found himself facing the argument that his ideas of genetic assimilation were merely a more sophisticated presentation of 'organic selection' put forward by Baldwin and Lloyd Morgan at the start of the century before the rediscovery of Mendelism. Though he confessed that he had not heard of organic selection before he did his work on genetic assimilation, he had little difficulty in showing that, when phrased in genetic terms, their theory was impossible.

> 'Baldwin's and Lloyd Morgan's discussions were, of course, couched in pre-Mendelian language, and it is not entirely easy to see exactly what their meaning would be when translating it into terms of our modern concepts. Most of the authors who have referred to the subject recently, however, seem to understand the theory of organic selection to be that organisms may be able, by non-genetic mechanisms, to adapt themselves to a strange environment, in which they can then persist until such a time as random mutation throws up a new allele which will produce the required developmental modification. Natural selection will then increase the frequency of this new allele, so that the developmental modification, which was originally an acquired character, will become an inherited one.
>
> 'The process, if understood in this sense, differs from the motion of genetic assimilation primarily because it considers the initial adaptation to the new environment to be a non-genetic phenomenon on which selection has no effect. Thus Mayr speaks of this adaptation as being due to a

"non-genetic plasticity of the phenotype", and Huxley and Simpson use essentially similar phrases. This implies that natural selection is having no effect on the system until such time as a new allele appears which causes production of the acquired developmental modification.'

It will be obvious from my earlier long quotation that, although Waddington recognized the intellectual level of the work of the theoretical neo-Darwinists such as Fisher, Haldane and Wright, he thought of it as basically uninteresting. Surprisingly he had been the junior author with Haldane in 1929 in one of the latter's more mathematical papers though it is not clear exactly what Waddington's contribution was to this. But his general position might be summarized in the phrase 'natural selection acts on the phenotype and not on the genotype'. Indeed the concepts of genetic assimilation does not have meaning in the framework of the neo-Darwinian theory. The discussion was much extended in his *The strategy of the genes* published in 1957. He and I differed somewhat on this topic. In my view, there are two basic problems. First, exactly what is meant by 'phenotype' here and on reflection I felt that its only useful meaning was the whole life history of the individual, and in discussions Waddington, to my surprise, seemed to hold the view that the fitness of an individual (as measured by the number of progeny it leaves) is not part of its 'phenotype'. It has always seemed to me that the phrase 'natural selection acts . . .' has excellent qualifications for Whitehead's dismissing phrase as a 'fallacy of misplaced concreteness'.

The second problem is, in essence, one of reductionism. For instance Waddington in *The strategy of the genes* introduces the concept of the fitness cross-section of a character in his discussion of canalization. But no character exists as a separate entity—it is part of a developmental system and one should not expect to discuss observations on a single measurement in a predictive way. The fitness cross-section itself is not 'given'. It too has evolved and will too be affected by natural selection. One may think to escape by a definition of function, which in my view is essentially reductionist and amounts to a summary of the effects of several characters in terms of a single output. In many cases this can be done plausibly but there are also many in which it cannot. Waddington always emphasized the importance of considering the phenotype as a process. To me one of the difficulties has always been that we are not logically entitled to chose arbitrarily some measurements made during this process as causes of another set. Some variables are of course external to the process itself such as true environmental parameters, but I would suggest that some internal variables which can be measured irrespective of whether or not the process takes place (such as protein structures and activities) have also a right to be considered in this category. But, as Waddington would also point out, the whole genotype has been produced by a separate process with a completely different time scale, that of evolution itself, so that some variables which can truly be considered as causes in the developmental process must be considered as effects at a different level of organization.

Waddington always emphasized the importance of genetically controlled choice in natural selection, particularly in regard to the change in selection pressure at other loci that this would bring about. He showed using *Drosophila* that such choice of environment is under genetic control. He also emphasized the importance of environment diversity in the maintenance of genetic variability, anticipating by several years recent trends in evolutionary thought.

Philosophical and ethical studies

He had a continuing interest in philosophy, after his early studentship awarded in 1926 for the encouragement of philosophical studies. He was much influenced by Whitehead, whose portrait forms the illustration for Waddington's posthumous article in *Nature*—'What I was reading 50 years ago'. He admitted that Whitehead's later writings were very obscure and, in so far as I can appreciate the latter's doctrines through Waddington's words, they appear as a not very helpful holism. Perhaps the most clear cut is that physical science has tended to use 'objects' as concepts whereas what we describe are 'events' or 'processes' and any event can only be properly described in relation to every other event in the Universe. The concepts that Waddington himself introduced do in general refer to processes and I suppose one might regard Thom's 'catastrophes' as formal concepts which are processes and not objects.

Waddington described very vividly his first meeting with Wittgenstein, that extraordinary figure of Cambridge philosophy in the 1930s.

> 'I got to know him when he came to a lecture I gave in my room in Christ's College to the Cambridge Moral Science Club, about some rather general topic on the philosophy of science, which I now forget. Wittgenstein hid on a window seat behind the curtains for most of the lecture, but then emerged to state that I had not been talking philosophy at all, but had talked science. I had at that time no idea who he was and I firmly told him that what I had been talking was philosophy in the sense that it was classified as such by the University Librarian and that books on this topic were available on the library shelves labelled as Philosophy. We had a rather stimulating discussion, much to the horror of most of the members of the Club, who were not used to anybody standing up to Wittgenstein in an argument (I would probably have been afraid to do so if I had known who he was). However, he came back to my room the next morning and suggested we go for a walk and we met fairly frequently for a few months, after which I went away to do some experimental work in Germany and the contact was lost for a time.'

In *The ethical animal* he describes a resumption of this interchange several years later.

> 'During one summer, 1940, I think, or 1941, he and R. H. Thouless and I used to meet one evening every week, and spend three or four hours after dinner discussing philosophy in the Roundabout Garden of Trinity,

Cambridge. The subject of most of these discourses was the relation between a word and the thing it signifies. I vividly remember those twilight evenings, when Wittgenstein would jump up from the lawn on which we had been sitting and pull out of the pocket of his shabby sportscoat a matchbox or some other small object. As he held it up in front of us and tried to make us realize the impervious vacuity of the gap which exists between the object in his fingers and the auditory modulation of air pressure or the black marks on white paper by which we refer to it, his main weapon of exposition was to persuade us to shed the preoccupations of the first year of the Second World War and to feel ourselves again children whose mother was instructing us in our first words. Something of the same method—a method which explicitly recognizes the importance of a developmental analysis of language—comes over in the first four pages or so of the *Philosophical investigations*, but it was of course incomparably more vivid when the phrases were formulated slowly and painfully by Wittgenstein himself, his face, between the incongruously student-like, tousled, curly hair and open-necked shirt, frowning and contorted with the effort to express precisely his understanding of the way in which the relation he was discussing is inexpressible. Often, indeed, his words came to a standstill, but communication continued for some time further by means of facial and bodily gesture. Wittgenstein was, I think, so acutely aware of the otherness of things that he never fully reconciled himself to the fact that words can have anything to do with them. I suspect that his intense concentration on the analysis and construction of languages arose largely from some profound feeling that for him at least all languages must remain almost totally inadequate for anything he felt it important to say. . . .

'No-one who met him could easily doubt that Wittgenstein was a tragic figure of some magnitude. The nature of his spiritual situation will be discussed as long as that of Rimbaud or Jackson Pollock. My tentative diagnosis of it would be this: that Wittgenstein failed to realize that what he had to convey was essentially a poetic awareness of the otherness of reality; he was led, presumably by historical accidents of which I am ignorant, to enshrine his message in a logical-philosophical jargon, whose very abstractness on the one hand served to exhibit the dislocation he felt between man and his surroundings, but on the other resulted in him being taken for a philosopher—an identification by which he was at first flattered, later filled by apprehension and a sense of guilt, but still misled; so that he took seriously the fact that in the *Tractatus* he had written a large book about philosophy which argued in meticulous detail the thesis that writing large books about this subject is a silly thing to do.'

Waddington's first discussion of ethical problems was in his Penguin book *The scientific attitude* published in 1941. He amplified some points in a short essay published in *Nature* where it was followed by comments by a number of authorities. All these, together with a series of letters between Waddington and Professor H. Dingle, were then published under the title *Science and ethics*. I

would leave Waddington's statement of his position until later except to say that unfortunately the most quotable sentence in the first essay, which appeared to summarize his position, proved to be phrased in such a way as to be liable to misunderstanding. After discussing some of T. H. Huxley's views he says, 'to return to our question, we must accept the direction of evolution as good simply because it *is* good according to any realist definition of that concept'.

In 1960 he published *The ethical animal*, a longer and wider ranging discussion of the same problem. It includes, among many other things, the delightful vignette of Wittgenstein from which I quoted earlier.

I leave it to him to present his views.

> 'Most discussions of ethics start by attempting to define goodness in terms of other concepts, such as, for instance, those just mentioned. The present argument starts in quite a different way by considering the developmental processes which lead to the formation of the concept of the good.
>
> 'In this argument we shall be concerned with three related meanings of "ethics". It will be as well to begin distinguishing them at this point.
>
> 'When we speak of ethical beliefs we usually have in mind such notions as the wickedness of murder or lying, the goodness of loving kindness or truthfulness, and the like. These are explicit ethical beliefs which gradually become formulated and accepted or rejected from the time of, say, middle childhood onwards for a varying period into our more adult life. It is to them that the phrase "ethical belief", when used without other qualification, can most appropriately be applied.
>
> 'We shall be concerned, however, with types of mental activity related to ethics which go on both at earlier and at later periods in human development. The human infant is born with probably a certain innate capacity to acquire ethical beliefs but without any specific beliefs in particular. During the first few months of life processes go on by which these innate potentialities become realized. The infant becomes moulded into the sort of being who, we may say, "goes in for" having ethical beliefs. It becomes what one might call an "ethics participant" or an "ethicizing" being. The process of turning the newborn infant into an ethicizing being is what I previously referred to by such phrases as "the formation of the concept of the good". It is a process which can, and I think should, be thought about in abstraction from any consideration of what particular ethical system is adopted, or what special notion of the good is acquired.
>
> 'Turning towards the other end of individual development, we shall have to consider processes in which a man examines his own ethical beliefs in relation to general systems of thought—for instance, philosophical or scientific thought—which may themselves carry little or none of the specific quality to which the name ethical is given. In so far as he then accepts some and rejects other ethical beliefs, he will be applying what might be called a supra-ethical criterion. This, which I referred to earlier as "the general good" or "the ethical system of general validity" is the type of criterion which in the previous chapter I referred to as "wisdom".

> 'In the lifetime of any human individual these three types of activity—becoming an ethicizing being, formulating one particular system of ethical beliefs, and criticizing those beliefs by some supra-ethical criterion of wisdom—are not clearly separated in time but certainly overlap with one another. At the same time as a child becomes ethicizing it acquires certain definite ethical beliefs; and as it goes on formulating these beliefs in a more and more definite and specific way, it becomes more fully the sort of being that goes in for having ethical feelings. Similarly, at a later stage in life, rationally formulated criteria for criticizing ethical systems soon acquired an ethical value of their own in the mental make-up of the person who holds them. But this overlap in time should not prevent us from recognizing that the three processes are in important ways differing in kind.'

He then goes on to argue that the fact that we are animals capable of ethicizing is itself the product of evolution. And here he is using the word 'evolution' in a much wider sense than would be usual for most geneticists, to include also the cultural transmission of behavioural differences.

> 'Individuals of the species *Homo sapiens* have, of course, the same general biological makeup as other animals. Like their sub-human relatives, they pass on genetical information through their gametes from one generation to the next, and this provides the raw materials with which natural selection brings about Darwinian evolution. But on top of, and in addition to, this biological mechanism of hereditary transmission, man has developed another system of passing information from one generation to its followers. This is the process of social teaching and learning, and it constitutes in effect a secondary mechanism by which evolution can be brought about—a mechanism of a kind which I refer to as socio-genetic.'

Here the concept of 'function' plays an important part in the argument. This he defines as follows:

> 'There are now, I think, few scientists who would consider it illegitimate to conclude that groups of elementary constituents may, by entering into close relationships with one another, build up complex entities which then enter into further causal interactions with one another *as units*. It is this fact, of the integration of groups of constituents into complexes, which in certain respects operate as units, which is spoken of as organization. In so far as it occurs, the concept of function is a legitimate one. If we have some complex entity A which acts as a unit, we can regard it as exhibiting organization of its constituent elements. Suppose that within A we can discern certain sub-units, P, Q, R, then the function of P within the organized system A is the contribution which P makes towards those types of behaviour in which the unitary character of A is exhibited.'

As I understand him, in this structure the complex entity acting as a unit is the process of human evolution, both genetic and social, and the function of an ethical system can be defined by reference to the overall process.

> 'I argue that if we investigate by normal scientific methods the way in which the existence of ethical beliefs is involved in the causal nexus of the world's happenings, we shall be forced to conclude that the function of ethicizing is to mediate the progress of human evolution, a progress which now takes place mainly in the social and physiological sphere. We shall also find that this progress, in the world as a whole, exhibits a direction which is as well or ill defined as the concept of physiological health. Putting these two points together we can define a criterion which does not depend for its validity on any recognition by a pre-existing ethical belief.'

Let me then attempt to sum up his views by two final quotations. He has been discussing the new mechanism of evolution, specifically human, of passing on information by social teaching and learning.

> 'We can see that an essential part of this mechanism is that the human being must be brought into a condition in which it will act as a receiver of the messages transmitted. Such reception involves the acceptance of authority. Ethical beliefs, which are essentially beliefs about the nature of the most authoritative demands, are a part of the human system for receiving transmitted information. This reinforces our original conclusion that the function of ethical beliefs is to make possible human evolution according to the mode which it is following. We can, therefore, justifiably proceed as we did earlier, to conclude that an examination of the direction of evolution can provide us with the criterion from which we can judge whether any particular ethical system is fulfilling this function efficiently or not.
>
> ' . . . It is clearly no part of the purpose of this book to attempt to work out, even in broad outline, the nature of the conclusions to which the application of the evolutionary criteria would lead; that is, as Huxley remarked, a task for a whole generation of men as thinkers and doers, and anything more than a very summary treatment of it in this place would only create a fourth perspective. In general terms, our argument leads to the conclusion that biological wisdom consists in the encouragement of the forward process both of the mechanism of the socio-genetic evolutionary system, and of the changes in the grade of human organization which that system brings about.'

He dealt in *The ethical animal* with various critics of his earlier views. He justified the statement I quoted earlier by an explanation that 'here the expression "according to any realist definition of that concept" was intended to show that the "good" thus qualified referred not to the ideas considered good by any individual but to the general criterion by which ethical beliefs may be judged.' He also dealt at some length with some of Popper's ideas expressed in *The poverty of historicism*. The main thread of the latter is obviously antithetical to Waddington's ideas in that Popper denies the possibility of discerning historical laws by which historical change can be predicted and, by a similar argument, that there is a direction of evolution that can be perceived. As Popper and later Maynard Smith have pointed out, there is a close parallel

between evolutionary ethics and Marxism—both claim to recognize a direction of 'progress' and urge that the 'good' is the furtherance of that process.

In this field, Waddington was the follower of several notable writers who differed strikingly in the practical conclusions that they drew. Herbert Spencer and the Social Darwinists concluded that society should not interfere with the workings of natural selection—Spencer to the extent of objecting to public support of education. T. H. Huxley reacted to this violently. 'Let us understand, once for all, that the ethical progress of society depends not on imitating the cosmic process, still less in running away from it, but in combating it.' Fifty years later, T. H.'s grandson, Julian, entered the argument in an essay (with the same title as his grandfather's) published after Waddington's *Science and ethics* in a way that Waddington considered circular. 'We would have to know what the criterion of ethical judgement should be before we could recognize it in the direction of evolution.' Waddington himself did attempt to erect a criterion for the evaluation of ethical systems without recourse to extra-biological considerations. The professional philosophers, while recognizing his novel contributions to the debate, seem on the main points at issue to remain unconvinced. Three main objections are made—firstly that he had not escaped the 'naturalistic fallacy' of confusing 'is' with 'ought' (though he would claim that he had avoided it); secondly, that made by Popper that in principle one cannot speak of a 'direction of evolution'; and thirdly, that even if one claims to, it is not always clear how it should be applied to human affairs. Indeed Waddington, in the paragraph quoted above ('it is clearly no part of the purpose of this book . . .') almost deliberately avoids the attempt.

His last output in this field was to take part in the Gifford Lectures in the University of Edinburgh, given annually in natural theology. In 1972 and 1973 these were given as a series of discussions between four participants—A. J. P. Kenny, Christopher Longuet-Higgins, J. R. Lucas and Waddington. They were subsequently published as two separate volumes with the titles *The nature of mind* and *The development of mind*.

His most ambitious book is undoubtedly *Behind appearance*, a magnificently illustrated comparative study of science and painting in the twentieth century. This was a further development of ideas he had first put forward in *The scientific attitude*. His studies were supported by a grant from the Rockefeller Foundation 'which I was free to spend on any books or other materials which I thought would be needed'.

He points to the almost contemporaneous developments in science and art at the beginning—the collapse of the billiard ball concept of matter and the demise of representational painting.

> 'These two revolts against old fashioned common sense are most probably connected. Many people have pointed this out already; but there have been few attempts to discuss in detail just what links can actually be found between the explorations, by scientists on the one side and by painters on the other, of what lies behind the world of appearance. This book is a step in that direction.'

He speculates on the interactions between scientists and non-scientists.

'To find a general picture we have to look and see how the discoveries and the new outlooks of science are reflected in the endeavours of non-scientists who are attempting to create works which will be general contributions to civilization. One might look, for instance, at the writings of novelists and poets; or one might look, as I shall attempt to in this book, at the productions of painters.

'It might seem at first sight as though the writers would offer the more profitable field to examine. They deal in words, and words are the means by which the human race can most explicitly and precisely express its thoughts. But this use of words, which seems to give writers an advantage over painters, can in fact work in the opposite way. Science also uses words, and uses them with much greater precision than non-scientific writers commonly do. It has invented a large vocabulary for the express purpose of being precise. In fact, in mathematics it has invented not only a new vocabulary but a new syntax. Writers are therefore using the same tools and, if you like, performing on the same stage as scientists. Unless they feel at home with at least the basic elements of the scientific vocabulary, and that means feeling at home with the basic scientific notions to which the words apply, any attempt to express explicitly a world view derived from science would be like a criticism of Shakespeare written by someone whose knowledge of language reached only the level necessary for reading the evening papers. One cannot discuss in words the implication of physical theories of indeterminacy, or of biological theories of genetic determination, without the question being asked whether the writer understands in words what those theories state. Some literary writers pass this test but perhaps an unduly large number of them have attempted to avoid such brash questioning by steering clear of the whole issue of science and its implications. Painters have the advantage that, since words are not the medium in which they work, the adequacy of their verbally expressible understanding of the modern world does not really come into question.'

'... The earliest group of painters who have some claim to be called "modern", the Impressionists, were strongly influenced by science. It was recent theories of optics and the development of the camera that provoked them to attempt to record visual sensations in their full immediacy. However, the influence of science on the Impressionists, though powerful, was at a relatively superficial level of manner and subject. At the deeper level of content, an Impressionist picture reflected science only in so far as science is an activity involving observation. It offered hardly any comment on the character of scientific thought or on the nature of the concepts which science derives from its observations. It is from the time of the Cubists onwards that the most powerful movements in painting have been largely concerned with just these topics. As we shall see, the first few generations of these painters tended to see science as something of a monster, one whose

monstrosity seemed to them to arise largely because science presents a one-sided picture of the Universe.

'. . . But when we look at the sciences themselves, and in particular at the way in which they have developed in the last half-century, we find that neither are they external monsters, standing outside the pale of humanity, nor do they have only one, or even only two, lines of sight into the world. Scientists have been driven to consider very deeply the extent to which their observations depend on their own nature as well as on that of the external world. They have had drastically to revise the old idea that science is completely "objective". The scientist has come to seem almost as involved in his scientific theory as the artist in his paintings; and the artist has responded by acknowledging more openly the extent of their own involvement, and by deepening it to the point where they speak, not of delineating a scene, but of performing an activity in cooperation with their media and their tools.'

The book is essentially in three parts. In the first he considers paintings up to the outbreak of World War II, in terms of two main groups, firstly the 'geometricizers', instanced by Picasso and Mondrian and secondly the 'magicians' instanced by Kandinsky and the Surrealists. Then there is a section on developments in scientific thought in the twentieth century emphasizing the retreat from the hard material world of the nineteenth-century physicist and the gradual preoccupations of the biologist with the organization of living systems. At the same time science has become more introspective. One can point to discussions of the nature of the creative process in science (Hadamard), the logical structure of scientific thought (Popper), what might be called the 'sociology' of scientific thought (Kuhn) and finally the realization that the whole process of perception is much more complicated than the logical positivists would have had us believe. We have further to think of our ability to perceive the real world and to conceptualize about it as the product of a long process of evolution. Waddington discusses briefly the artistic relevance of images produced by chance by scientific equipment—'by chance' in the sense that they were produced as scientific objects and not as objects of art.

'But the point I want to insist on is that no artist would—or should—have dreamt of using them unless he was convinced that these images had meaning. There has never been, and I doubt if there ever could be, an Impressionism of the scientific image. No one has painted a section of tissue or bubble chamber photo from the same point of view that Monet painted his immediate visual experiences in front of a cathedral. . . . What convinced the artists of our day—some 50 years later—that images of this kind are worthy of aesthetic attention was not that the scientific pictures suddenly became more figurative representations of some particular appearance in the world that science examined. The crucial fact was that they came to realize that *hard scientific analysis*—from which conclusions could be drawn, on which effective technologies could be based—lead to images of the same general kind.'

Most of the rest of the book is devoted to developments in painting since World War II which, as he points out, were much more diverse than in the earlier period. One clear grouping would be illustrated by Jackson Pollock of which Waddington says,

> 'The most influential effect produced by the work of all these painters was to provide a demonstration that painting can dispense with anything resembling an image. It cannot merely do without the representation, in however symbolic a form, of any recognizable object or thing, such as those which have haunted the surrealist's pictures but can even fail to depict any geometrically coherent abstract shape. The first abstracts of Kandinsky had been almost equally inchoate, but in the intervening thirty years very few pictures have been produced which were free of either geometricizing or figuration. The demonstration that painting is possible without either of these two elements acted as the opening of a door into an enormous area of freedom into which painters had not previously ventured.
>
> '. . . The scientist does not go to the painter for a representation of scientific objects, but for the enrichment and the deepening of his consciousness, which comes when he finds a painter in whom the climate of scientific thought has penetrated into the spirit, leading to the production of works in which some of the deeper, less easily expressible features of the scientific outlook are "shown forth".'

By and large, parallels that can be drawn between painting and scientific development in this period are less clear than in the earlier one, though there is perhaps some superficial connection in the development of Op Art in which some of the tricks of perception which have also been studied by psychologists and neuro-physiologists are used to produce an impression of continual movements.

I may allow him to summarize by three quotations from his final short section.

> 'Approaching the subject from the background of a professional scientist, I have tried to show, by considering in some detail the various schools and the types of paintings of the last half century, that the visual arts and natural philosophy are related parts of man's exploration of the world around him. As I have repeatedly emphasized, the field I have explored is itself only a fragment of the total human experience of our time; I have been concerned with only one aspect of painting and of science—the way they reflect our knowledge of the structure of material things—and have not attempted to include the much greater, and probably much more important phases which deal with our understanding of man and society. But in these times our intellectual-emotional life has been so fragmented and divided into separate compartments, and these so often classified as mutually exclusive, that it is rather rare that any attempt is made to examine in detail the connections that actually exist between the different pigeon holes, although voices are

sometimes raised to point out, in general terms, that relations are, or ought to be, there.

'. . . But it would be a mistake to see the traffic between art and science as a one-way affair. Science of course cannot expect to learn scientific truths from the productions of artists, any more than the latter can get much profit from merely taking over superficial appearances or intellectual concepts from science. But science is something more than a collection of conceptual or practical results. It is also an activity; and its practice involves, as a very important part, the exercise of the faculties of insightful perception of natural phenomena and of the imaginative creation of new concepts.

'. . . Under the pressure to produce "results", by taking the next short step along a path which is obviously stretching ahead, or beguiled by the fascinating manipulative play that the actual conduct of an experiment so often provides, scientists find it easy to forget what kind of mental processes are required for the most important advances. Looking at paintings, or experiencing other works of art, especially kinds which are not too immediately transparent but which demand some attempt by the spectator to enter into the experience of the artist's creative process, is one of the best ways for a scientist to loosen the joints of his psyche, to "roll the bones" of his ideas, and give himself a chance to dredge up from the obscure internal depths something, which will probably not have the slightest obvious connection with the work of art he has been contemplating—but which may be fresh enough to be worthwhile.'

He had little or no small talk and gave some the impression of being rather aloof. This was probably really shyness and the consequence of his Quaker upbringing (though he loved parties). 'I was brought up as a Quaker who don't wear their hearts on their sleeves and who feel that things shown in practice are more convincing than rhetoric.' But hidden behind this apparent aloofness was a real concern for people and there are several instances of his going to great lengths to help refugees from Europe after World War II.

I have been struck by the extent to which he kept his life in compartments. It was a surprise that to his undergraduate friends in Cambridge he was Conway and an equal surprise to them that to me, and to everyone else I knew, including his wife, he was Wad. As a boy he was Con. Gregory Bateson makes the point in a letter that he was skilled in many different departments and was perhaps unwilling to share with those who were much less skilled. 'He was shy of exhibiting any particular skill to those who did not have it.' His reserved nature, and perhaps also his many interests, made his students feel sometimes a little neglected. In correspondence with his students from all stages of his career, I find phrases like 'he told me that his philosophy was simply to identify capable people and let them have their heads. I think he sometimes used this notion as an excuse *not* to involve himself in details or with people.' Something of this spilled over into his running of a laboratory. With his width of vision he could see

clearly what should be done and he was good at persuading funding organizations to provide support. But having got support for specific projects, he seemed often to lose interest in their subsequent progress, perhaps a result of intellectual impatience. But he occasionally made mistakes about people, in terms of both personality and of scientific ability. The former landed him once in a period of great personal animosity within the Institute, happily quickly resolved. He undoubtedly attracted (rather than actively sought) some very bright people to the Institute but was liable to be taken in by the voluble 'phoney'. I think he would have accepted this as a necessary risk in intellectual speculation in fields where others feared to tread.

I said earlier that as an experimentalist he will be remembered mainly for two things—firstly, the work on induction in birds and mammals and, secondly, the experiments on genetic assimilation, in which he showed how the 'inheritance of acquired characters' could be fitted into the Mendelian framework. He will be most remembered as a writer and a thinker. He wrote with great facility. The autobiographical fragments show that he had a very sure touch in non-technical writing and we may regret that he never wrote a full-length autobiography. Politically he described himself as 'leftish' but as far as I know was never politically active. His early writings certainly inclined to the left (this may be merely a reflexion of the company he kept at the time) but in the second edition of *The scientific attitude* in 1948 there are clear signs of a reaction to this and in later life he rarely made political comments, in the usual sense of the word. If there is a guiding thread in his thought, it lies in the study of organization—in the development from egg to adult, in the processes of physiological functioning, in the long-term processes of evolution and, in his later years, in the organization of human society. Typically his main philosophical discussion of organization is in the book on modern art.

His main contribution to biological thought was to bring together conceptually and experimentally the two disciplines of genetics and development (though this may have derived in part from Morgan). He was responsible for most of the standard developmental terms in English—throughout his life he was a great coiner of neologisms, usually from Greek. He stressed the buffering properties of the developing embryo and argued that this was a consequence of the evolutionary process. From his wide basis of understanding and knowledge, he was often able to suggest fruitful approaches to difficult problems and was an acute critic in discussions. But I think I am not alone in feeling that some of his concepts turn out under use to be rather fuzzy at the edges—perhaps because he was often content with presenting them as analogies and did not develop them into precise theories. He never lacked scientific courage in tackling difficult and profound problems; indeed these were the problems that interested him, and I suspect that he tended to be bored by problems that had simple solutions. It may have been obvious to the reader that I often had difficulty in summarizing his views succinctly—maybe more likely my fault than his—but I feel that several times an interesting and stimulating approach to a problem has petered out without a clear solution being presented (even without it being clear that this

has happened). In his posthumous article in *Nature*, he wrote that 'Whitehead totally inoculated me against the present epidemic intellectual disease, which causes people to argue that the reality of anything is proportional to the precision with which it can be defined in molecular or atomic terms'. In spite of his commitments to Whitehead, he seems in the theoretical biology meetings in Bellagio to be struggling to escape. 'Do you have to wait till you can reduce to the molecular biology of the dogma in a single leap or is there anything useful to do meantime?'

He was sympathetic to the intellectuals of the counter-culture like Roszak, and devoted much of the Bernal Memorial Lecture to them, coming down, in the end, firmly against. 'In my opinion, anti-science counter-culture is right in many of the positive things it has to say; many of the values it praises are genuine and important ones; but there are several reasons why many of its negative arguments against science are only partially correct, and even become dangerous by concealing the main point.' He, far more than most, was aware of these conflicts—not only between science and anti-science but within science itself. Is it prophetic that he, having decided that the *Tractatus* and the *Waste land* were both major poems, had described Wittgenstein as a poet forced by chance to behave as though he were a philosopher? As one of Wad's oldest friends has commented: 'In many ways he had the characteristics of an artist—an unusual sensitivity and power of perception.'

The Sword

I have a sword of bright steel,
Steel that rings cold in the fight,
A sword that is joyous to feel.
They praised but the thin acid bite
Of the pen, not so heavy to wield:
'For who troubles aught but to write?'
Oh eyes that have watched the grey field
In which I still strive for the right,
You know that my sword will not yield
While I stand in your sight.

(Written by Waddington in 1930 and printed by him in a booklet of poems with the title *Fanfreluche*.)

My thanks are due to all those who helped me in the preparation of this memoir—in particular to Wad's sister, Mrs Doris Christie, for her information about his childhood.

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