BIOGRAPHICAL MEMOIRS

Cyril Dean Darlington, 19 December 1903 - 26 March 1981

D. Lewis, F. R. S.


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Cyril Dean Darlington's paternal great-grandfather was Henry Robertson, a merchant of Liverpool, Buenos Aires and Montevideo, and a cousin of W. E. Gladstone, the nineteenth century Liberal Prime Minister of Great Britain. Henry fathered a son illegitimately by his Welsh nursemaid, Mary Davies of Wrexham, at Salford in 1873; this son was given the name Henry Robertson Darlington, the name Darlington coming from Mary Davies's later husband, William Darlington, a blacksmith and iron-founder. Henry Darlington married Alice Dean who gave birth to Cyril's father, William Henry Robertson Darlington (1866–1943), a schoolmaster and secretary. Cyril has described this change of his paternal name with his characteristic light-hearted and irreverent style—'The business end of my Y chromosome therefore comes from Fife and not Durham'—the county containing the town Darlington. Cyril's maternal grandfather was a Frankland, son of a Unitarian minister of Whitby, married to a Cowling, an old family of solicitors of York. His mother, Ellen Darlington née Frankland (1874–1949) had two sons, Alfred Frankland Dean and Cyril Dean.

His ancestors, traced back through three generations, may not contain any who were noteworthy in science, learning or public service, but what is more important, at least from Darlington’s point of view, is that he is the result of outbreeding, with a recombination of genes from Yorkshire, Scotland and Wales.

His boyhood was spent at Chorley in Lancashire where his father was a schoolmaster, and after 1911 in Ealing, London, when his father had been appointed secretary to Dr K. E. Markell, the chief chemist of Crossfields Soap Ltd. Cyril later summed up his impression of this period as being dominated by his father and being forced to concentrate on moral principles and the constant instilling of earning his living when he grew up, if not before. He remembered the family life as joyless, 'there
was no leisure or freedom and there were no holidays away from home for the whole of the six years at Ealing', but we must recall that these six years included four years of World War I with its slaughter, rationing and even air raids and the blackout. Cyril did not refer to the war in the diary which he kept at this period, but in a letter dated 30 March 1918 to his brother Alfred, who had been drafted to the trenches in France, he showed one side of his nature that was later to be carefully controlled, and a mental quality that was to develop as an important aspect of his work and method of thinking. He was only 15 years old and already expressed his sympathy with great imagination and compassion of all the horrors and deprivations his brother would encounter, and then he turned his analytical mind dispassionately to the great German spring offensive in 1918. How could Germany make such a supreme effort after more than three years of war in a way no other nation could? He systematically tabulated the possible factors, discussing them and finally rejecting all except brains and education, a classic ‘nature and nurture’ conclusion, which he would later, after his own education and knowledge of the chromosomes, have resolved in favour of brains. During the time at Ealing, Cyril hated the Underground by which he travelled to school but loved the garden, for his diary often refers to his work in the garden: ‘have just finished the path’ or ‘the fish pool’. This was an interest that remained with him all his life with his attention to the Arboretum at Bayfordbury, the Botanic Garden at Oxford and Nuneham Courtenay, and his own gardens at Frilford Heath and later at South Hinksey where his interest also widened into planting trees around the village.

Education

Of the 8 years of his life spent at Chorley there are no recorded impressions, except that he attended Heathside Elementary School 1909–10 and Boteler Grammar School 1910–11, both at Warrington. Attending the Boteler School at about the same time was G. L. Brown (later Sir Lindor Brown, Secretary of the Royal Society). When the family moved to Ealing, London, in 1911, Cyril attended Mercer’s School, Holborn, until 1917. Cyril’s main memory of this period is the tedium of standing in the trains of the Central Line of the Underground. He records no interesting thought, theory or idea, although later he records how he got his first real idea while travelling to work in the train to Wimbledon. From the Mercer’s School he won, at the second attempt, a Foundation scholarship to St Paul’s School, London, which he attended as a day boy from 1917 to 1920. Here he was taught science, including biology by Mr C. M. Thomas, who was one of the first science masters in the school. Despite the good science facilities at the school the influence on Cyril was negative, for he has recalled that he was always bottom of the class in science subjects and ‘the science masters expressed
the same poor opinion of me that I felt of them'. Other subjects in the eighth form included mathematics, French, Divinity and English in which he was placed in the top half of the class; in Latin and drawing he was, as with science, in the bottom half of the class. He was later to show an interest and skill in all three subjects, science with his career, Latin with his facility in apt quotations and drawing with his skill at drawing chromosomes and caricatures of plants and people. He would be the first to see some significance in the negative correlation between school attainment and future activity. He had a dislike of regimented games and St Paul's School prided itself, rightly, for its prowess at cricket and football, but at least the biology master was not a games enthusiast. During this period until he left school there is no evidence of Cyril's having any hobbies except the garden, and sporting activities were confined to rowing and swimming by himself.

He had no real interest in science but only a respect inculcated by his father from his experience of visits to Germany in connection with his work. Although Cyril many years later, in retrospect, came to express appreciation of his father for introducing him to the problems of dialect and place names and to the works of the Latin poet, Lucretius, his immediate reaction was against strict moral parental influence and this extended to all forms of organization and authority be it work, sport or education. This anti-authoritarianism was to persist throughout his life and was a great driving force that had an immediate expression when he left school. He chose to study agriculture at the South Eastern Agricultural College at Wye with the expressed purpose of farming in Australia as his future career. The rural setting in a Kent village nestling under the South Downs was a great contrast; with Ealing and the city of London, but it had its restrictions and its encouragement of his detested games. The College, later to become Wye College of the University of London, was founded in 1888 under the first principal, Sir Daniel Hall, who later was Director of the John Innes Horticultural Institute and under whom Cyril worked and whom he later succeeded. The instruction, apart from practical and applied agriculture and husbandry, included elementary chemistry, botany, geology and zoology, introducing Cyril to a great variety of subjects from a more or less scientific point of view, which as he has written, enabled him to sort out the sciences and see which appealed to him but without acquiring what is held to be a sound training in any of them. Although he failed Intermediate Science in botany in 1921 he passed the following year, having committed the required book by D. H. Scott to memory, and twice won the Paton-Figgis Scholarship and once the Collections Medal.

He graduated B.Sc. London (Agric.) in 1923 and in July applied unsuccessfully for an Empire Cotton Corporation Scholarship, from which it would appear that he was at least considering alternatives to farming in Australia and may have abandoned the idea completely. He
attributes his failure to obtain the post with the Empire Cotton Growing
Association to his expressed opinion of games, which made him unfit for a
colonial post. The crucial turning point came when he read *The physical
basis of heredity* by Morgan, Sturtevant & Bridges, published in 1921.
This book, he has written, ‘inspired my future work and decided my
career’. It is not clear how he came across the book but it seems unlikely
that it was in the library of Wye College because the present copy there
came from Swanley College when it was incorporated with Wye in
1945. This new interest in heredity must have been discussed with the
staff at the college because Research Professor E. S. Salmon made
the best possible suggestion that he should apply to the John Innes
Horticultural Institution, which he did in November 1923.

**JOHN INNES HORTICULTURAL INSTITUTION AND WILLIAM BATESON**

Darlington started his career in 1923 at the John Innes Horticultural
Institution and retired from its Directorship to take the Sherardian Chair
of Botany at Oxford University in September 1953. During these thirty-
one years the Institution changed greatly in size, organization, types of
work, influence and location, and because many of these changes were
initiated or stimulated by Darlington a brief account of the nature and
objectives of the Institution before Darlington’s appointment is essential.
The Institution was founded at Merton, London, on a site of five acres,
later expanded to twenty acres, in 1910 under the will of John Innes with
its first Director, William Bateson, F.R.S. Bateson had shown that
Mendelian inheritance was found with few trivial exceptions in all
animals and plants and for a variety of characters. When he came to the
Institution he had already with R. C. Punnett discovered a significant
exception to Mendelian independent segregation of factors, *linkage* as he
called it. This discovery, contrary to Bateson’s theories, was to put genes
and chromosomes on the map and to be the focal point of Darlington’s
early work. Bateson could not accept the chromosome hypothesis with
crossing-over established in 1914 by the Morgan *Drosophila* school and
continued to explain linkage until 1918 on his own totally misconceived
theory of reduplication even after his co-discoverer, Punnett, had
accepted the chromosome theory. Bateson’s theory required the inde­
pendent segregation of genetic factors to occur at various somatic cell
divisions before the meiotic (reduction) division of the chromosomes,
which immediately preceded the formation of gametes. This led Bateson
to employ workers to examine exceptional examples of somatic segrega­
tion found in variegated and rogue-sporting plants. Thirteen papers were
published on these topics that contained no sound conclusions or theories
so that he wrote, as late as 1918, ‘The experiments with (the moss)
*Funaria* have shown that it is probably that the sex purity of the gamete in
monoecious forms is secured by a somatic segregation in haploid tissue’.
and later in his lecture on segregation given in Pennsylvania, U.S.A., in 1922 and published in the *Journal of Genetics* in 1926 wrote ‘the conclusion that segregation happens in somatic tissue, long before spore formation is inevitable’. It was as if Bateson was looking for every opportunity to dissociate the genes from the chromosomes by the study of these exceptions. He also rejected the chromosome theory on theoretical grounds because he could not visualize somatic development and differentiation at the same time as the constancy of the chromosomes in all cells. He required at that time the chromosome theory not only to explain heredity but also differentiation and development. A parallel can be found in Einstein’s theory of relativity before it could explain magnetism as well as gravity and movement. Weismann, who became for Darlington the man for all seasons, had 30 years earlier solved the problem by postulating the constancy of the germ plasm and differentiation confined to the soma. When Darlington came, Bateson was following at least three false trials, gene segregation in the soma, the unripe problem of development, and matroclinal inheritance, which had been correctly interpreted by Baur & Correns but not by Bateson.

Darlington has described in his personal memoirs when he first met Bateson that the latter had lost his nerve and seemed to know that he was off the main track of enquiry and completely out of his depth in the new materialistic genetics; he was kept going by the moral support of his lady assistants led by Miss Caroline Pellew. Bateson had partly reconciled himself to the chromosome theory of heredity after his visit to the United States and in particular to Morgan’s laboratory at Columbia University, where he was greatly impressed by Bridges’s triploid intersexes in *Drosophila*. This reconciliation almost came too late, but not too late for Bateson on his return in 1922 to appoint a trained cytologist, W. C. F. Newton (1894–1927), a pupil of Lancelot Hogben, F.R.S., to the staff of the institution. In November of the same year Darlington applied to Bateson for admission as a research worker, to which he received the reply that if he wished to come he must say what he proposed to do and how he proposed to set about it. Darlington’s answer to this evoked no reply, so by using the telephone he secured an interview in which he remembered Bateson saying that ‘the rewards were slight except for the fortunate few who got to the top’. Despite this it was agreed that Darlington should come as a volunteer unpaid worker and was duly listed in the *John Innes Report* of 1923 under ‘Besides the regular staff the following have taken part in the work or have used the facilities provided’. Other names in this list included Mrs N. Barlow (later Lady Barlow), Mr F. T. Brooks (later Professor of Botany, Cambridge), Capt. Cyril Diver (later noted for his work on polymorphism in snails and Clerk to the House of Commons) and Professor R. C. Punnett. In March 1924 Darlington was appointed to a Minor Studentship at £150 and later, after protest, to £200 a year.
The Director's report for 1924 includes 'In connection with the development of cytological research several additions to microscopical equipment have been made', part of this was an out-of-date second-hand microscope which Darlington used. The same report under the heading of *Bolting of root crops etc.*, includes the statement that 'Mr Darlington had made a beginning with lettuces.' This was part of the plant breeding work that he did to please Bateson but which he considered a chore and soon abandoned for his main work on chromosomes, which will be described later. Darlington recalled that his first three years at Merton were largely wasted; he was too young and untrained and although self-training proved eventually a priceless gift, it was a gift slowly acquired. He was guided by Newton until his illness in 1926 and death in 1927. In the three years with Newton he learned extreme scepticism of all past work and particularly of the work of British cytologists, Farmer, Digby and Gates, but he soon broke away from Newton's timidity in interpretation and agnosticism, which was crucial for the development of his main work on the structure and behaviour of the chromosomes, particularly at meiosis. Despite the almost irreconcilable disparities in temperament and thought there was, at the time, a deep bond of sympathy between Bateson, Newton and Darlington, which stemmed from agreement about three prominent biologists, Farmer, Gates and MacBride: Farmer and Gates for their incompetent cytological observation and deductions and MacBride for his anti-genetical Lamarckian views. The agreement of hatred, ridicule and contempt for these three was a continual source of inspiration and happiness. Darlington has written that the principle propounded by Bateson and Newton that whatever MacBride and Gates wrote must be wrong, and dangerously so, gave his work direction and momentum until 1930. 'For next to friends, enemies, if well chosen, are the best stimulus to research', and he had no friends who knew the subject. After Newton's death Darlington was cytologically on his own and Bateson's death in 1927 left him free from the plant breeding chores so that he could follow his own interests completely under the new Director, Sir Daniel Hall, who was remarkable for his liberality and encouragement, and the only persuasion from him was for cytological work on his beloved tulips, which turned out to be excellent material for chromosome studies.

Darlington's position as cytologist, appointed in 1928 at the Institution, remained unchanged for many years, a fulfilment of Bateson's warning about the slight rewards. During this period he was supported morally by J. B. S. Haldane with whom he collaborated on the problem of genetic interference from whom he learnt 'earlier than I otherwise should have done (not being a “Greats” man myself) a sense of proportion and confidence in handling large issues'. There were at this time many distinguished geneticists and cytologists from overseas who visited the Institution, including G. D. Karpechenko from the U.S.S.R., E. B.
Babcock, A. F. Blakeslee, A. B. Davenport and L. C. Dunn from the U.S.A. The only one who made any recorded impression on Darlington was Dr Karl Bélar of the Kaiser-Wilhelm-Institut, Berlin-Dahlem, for his encouragement and understanding and to whom he paid tribute on several occasions.

As a result of Darlington’s work, described later, and his book *Recent advances in cytology*, published in 1932, he attracted a continual stream of workers from the U.K. and many other countries. These are given in a list of collaborators drawn up by Darlington. He made no distinction but it is appropriate to refer to the late Professor H. N. Barber, F.R.S., Professor H. G. Callan, F.R.S., Sir Otto Frankel, F.R.S., Dr E. K. Janaki-Ammal, Dr P. C. Koller, Dr L. F. La Cour, F.R.S., Sir Kenneth Mather, F.R.S., Professor P. T. Thomas, Dr Margaret Upcott (Mrs C. D. Darlington) and Professor Ann Wylie. All contributed greatly at the time and most continued to have great influence on the future development of the subject. In the heyday of Darlington’s cytological school in the 1930s there was the exciting atmosphere of recurring discovery that some laboratories are fortunate to have for a short but—while it lasts—a glorious time. I cannot better depict this than quoting from my brief appreciation in *Heredity* (1981):

‘The not unpleasant smell of clove oil, alcohol and xylol, the noise at first of the microtome and later the woodpecker-like tapping of the glass rods on slides for squash preparations and the clink of slides going through their alcoholic series were the constant sensory and musical background; each worker had enough room for a microscope, slide jars and a notebook.’

Darlington, in his separate room with the door open, had his ancient brass microscope with its long tube, originally bought second-hand by Bateson. The two simple home-made lensless cameras were constantly passing from one microscope to another to record the latest chromosome. There were frequent visits to the laboratory from the dark room of the presiding and charming genius of illustration and photography, the congenitally deaf H. C. Osterstock, with whom everybody soon learned to converse in his own self-taught language. Darlington’s room was lined with reprint boxes, the spines of which were wittily illustrated with the most telling caricatures; one member of the early *Drosophila* school received H. G. M. and a crown, a sincere and not cynical comment; the several boxes of another showed a profile expanding from box to box with age, which matched the ever increasing size and number of his publications. The first was H. G. Muller and the second Th. Dobzhansky, both now deceased Foreign Members of the Royal Society.

Darlington, along with others, realized that until World War II the Institution in which he worked was the foremost centre of cytology and genetics in the United Kingdom. There were Plant Breeding Institutes,
but all the Universities had only three departments of genetics among
them, the Galton Laboratory at University College London (1904), the
Department of Genetics at Cambridge (1909) and the Department of
Animal Genetics at Edinburgh (1921) and there were a few isolated
individuals in departments of Botany and Zoology who had a claim to be
active practitioners of the subjects. The genetics gospel had been spread
at least to colleges of London University by the annual visit of students to
the Institution to see chromosomes and the segregating families of
*Primula sinensis*. A much wider net was cast by the two-week summer
courses in genetics and cytology started in 1928 and held biennially until
World War II. In the first of these Darlington shared a course of ten
lectures on cytology with Dr C. L. Huskins. He also read a paper at the
first conference held in 1929 by the Institution, which was on polyploidy.
In the later summer courses he gave the cytological lectures himself,
which were brilliantly delivered and beautifully illustrated. The tall
handsome well-dressed young man with a soft persuasive voice made a
great impact and was an interesting contrast to J. B. S. Haldane who also
made a great but different impact with his lectures on genetics. These
lectures had a great influence, particularly those in 1934, two years after
the appearance of his book *Recent advances*. Many who were sympathetic
had found difficulty at the first reading, but after knowing the man from
his lectures with his exposition of the chromosomes and the deductive
method used to formulate hypothesis and interpretation, they were
enlightened. Those who criticized or condemned the book did not go to
the course, including his co-lecturer Huskins. After World War II
universities set up departments of Genetics and some were headed
by staff from the Institution, making the summer courses no longer
necessary. They were discontinued and Darlington, as Director,
initiated a special lecture, the Bateson Lecture.

The freedom to do research under Sir Daniel Hall, which Darlington
appreciated, had its drawbacks, for Hall’s liberality led to deep antagon­
isms between Hall and the old Batesonian staff, between Haldane and
Hall, and between Darlington and Huskins, who had been appointed
Cytogeneticist 1927–30 and who severely criticized Darlington’s book
after he left the Institution. When Darlington came back from a year’s
leave in the U.S.A. and Japan he found that his school had been more or
less dispersed and had to be rebuilt with the help of Margaret Upcott and
Margaret Richardson. He called it a school because there were no
departments at the Institution, only the Director and research workers. A
crisis occurred in 1936 when the senior member of the old Batesonian
staff, Miss Caroline Pellew, was in South Africa. The affairs of the
Institution had become so disordered that Darlington, supported by his
colleagues, which were about half the staff, presented proposals to the
Council for a new deal. In Darlington’s own words the proposals were
put direct to the Council and not through the Director, a matter of
procedure which when he himself became Director he strongly opposed. However, the proposals were subsequently accepted so that in 1937 four departments, Genetics, Cytology, Pomology and Biochemistry, were established, each with a head and one permanent assistant. Darlington was made head of the Cytology Department in January 1937 but even before this the work of the Cytology School had progressed greatly, particularly in techniques in the hands of L. F. La Cour, M. Upcott, P. T. Thomas and Pio Koller. During this period one important and delightful feature of the Institution was the lunch and tea clubs when the staff came together for refreshment and conversation. Darlington could always be relied upon to start some topic, genetical or cytological, but more often about the iniquities of his professional enemies, who although disposed of still reared their heads when the prompting context arose. Sometimes more serious business was conducted, particularly when he and Mather were finishing their book *The elements of genetics*. The glossary of genetic terms was produced two or three words each day by the general consensus of the whole staff, which was probably good for the glossary but certainly good for the staff.

One of the provisions in the reorganization was that the Director may be the head of any department, so that when Sir Daniel Hall retired in September 1939 Darlington was able to accept the Directorship, retain his headship of the Cytology Department and look forward to directing an Institution situated near London through a war of unknown intensity and duration. The appointment had the usual repercussions and preliminary skirmishes. J. B. S. Haldane had been appointed to the Institution with the understanding that he would succeed Hall, but after an interview between Haldane and the Council in 1936, at which Haldane’s main proposal for the future of the Institution was to transform the Director’s home, the Manor House, into a living quarter and laboratories for his assistants, the Council asked Hall to stay on. Haldane resigned to take the Weldon chair at University College London. When Hall finally resigned the post was advertised and several applicants were considered: with Haldane’s resignation Darlington was a clear first. Darlington’s Directorship, starting in September 1939, was immediately preceded by the Seventh International Congress of Genetics held in Edinburgh on 23–30 August. This congress was to have been presided over by Nikolai Vavilov from the U.S.S.R. and his enforced absence from the Congress was one of the early signs of the complete destruction of genetics and geneticists in the U.S.S.R. that Darlington was later to expose and denounce with great vigour. On returning to London from a prematurely depleted congress he had to prepare the Institution for immediate war, providing air raid shelters and removing valuables to the country, and to change the emphasis of the work towards the immediate problem of the war. He encouraged staff to turn to problems of seed production at home instead of relying on imported supplies, to publicize the useful seed and growing
composts that had been devised by John Newell and William Lawrence for the growing of difficult experimental plants. Leaflets were produced describing the com posts, seed production and the fertility rules for interplanting varieties of fruit trees; later they were gathered together in a booklet *The fruit, the seed and the soil*, which Darlington edited and which put the Institution before the public as the place where the compost was made. His own scientific work during the war was directed towards the understanding of the cold-induced differential staining of specific sections of the chromosomes discovered by La Cour, and the effect of X-rays and other ionizing radiations and chemicals on the breakage and reunion of chromosomes. The work was severely handicapped by the loss of income from the John Innes Trust, partly due to the bombing of London and the Trust’s money’s being mainly in real property in the City of London. There was also a depletion of staff due to war service. But the continuity of the chromosome work led to a further decade of work after the war on induced and spontaneous breakage described in papers with L. F. La Cour and P. Koller. The war had another profound effect: it stimulated Darlington, the Trustees and the Council to think about a new site in the country for the Institution. A proposition had been put before the Trustees by Sir Daniel Hall before he retired. In October 1940 Darlington explained to the Council the desirability of arranging for temporary evacuation in an emergency and that if the site were carefully chosen it could become a permanent home. Complicated negotiations were made to secure Waterperry House with about 60 acres of land, the property of Magdalen College, Oxford, and situated 7 miles from Oxford. The advanced negotiations broke down when the lessee withdrew agreement to quit. The idea of a temporary evacuation was abandoned and a search for a permanent home intensified. With M. B. Crane and W. J. C. Lawrence, Darlington examined and in some cases negotiated for about fifty different sites, twelve near Oxford. Eventually in May 1945 he selected Bayfordbury in Hertfordshire. Darlington, who was never patient with man-made obstacles, had to negotiate not only with the owners of the estate but with the Trustees, Council, Ministry of Agriculture, Development Commission and Charity Commissioners. The mansion was converted into laboratories; glasshouses of special design were built, the walled garden with its existing small collection of old-fashioned roses was developed into a rose species collection, which became the centre of chromosome studies of *Rosa* and the source for material of Ann Wylie’s *History of the garden rose*. Bayfordbury was occupied in October 1949; Darlington resigned from the Institution in 1953. The Institution moved again in 1967, and this time to the outskirts of Norwich in East Anglia and significantly its name changed, to the John Innes Institute, and more significantly there were close links with the University of East Anglia. The Institution at Merton had close links with London University, including staff’s becoming Recognized Teachers,
but this was gradually phased out by the university for all research institutions, and Darlington's impatience with the academic authorities did not help to maintain the university connection with Bayfordbury. Ironically, a close link between a university and the Institution was one of Darlington's main aims. The spatial isolation of Bayfordbury, and weakening of the links with London University and the near-miss of Waterperry near Oxford must have been among Darlington's worst disappointments. It was, however, a subject he never referred to and we do not know his real feelings about it.

On resigning the Directorship his opinion was sought about a possible successor. This drew forth no names but a detailed memorandum on the whole government, administration and direction and particularly the appointment of members of Council, which had long been for him a source of irritation and sometimes frustration. And his views about the relationship between staff, Director and Council were plainly expressed with illustrations which left no doubt about the central role of the Director. He concluded that no scientist of suitable calibre would tolerate the administrative conditions unless they were changed radically. The conditions did not change in time to prevent the immediate fulfilment of his predictions. It required the radical upheaval of another move to East Anglia to stimulate some of the administrative changes he suggested and to secure the right conditions for the right Director and staff to be able to revive the earlier glorious days. But all this effort cost Darlington much distress and several friends. A lesser man would have quietly forgotten it and retired to a college; he did not forget, as his letter to The Times on 12 August 1980 on the British apple showed, for here he explained why new apples bred at the Institution were not distributed to the public.

The impact of Darlington's time at the John Innes, apart from his own personal research which is described later can be assessed objectively from the figures. In 1922, before Darlington, there were six permanent staff and nine papers published, in 1939 (Directorship) there were fourteen staff and forty-one papers, in 1953 (resignation) there were nineteen staff and forty-eight papers. During the period of his Directorship, among the staff, workers and students, eleven were elected F.R.S., eight became university professors, three directors of Research Institutes and one a Vice-Chancellor.

SHERARDIAN PROFESSOR OF BOTANY, OXFORD

Darlington's appointment in 1953 to the Sherardian Chair of Botany at Oxford was a break from tradition in several aspects. He did not have a degree of either Oxford or Cambridge; this was quickly remedied by decree so that he could be duly elected to the Chair, to a Fellowship of Magdalen College and to the Keepership of the Botanic Garden, the oldest in the country. He did not have experience of organized university
teaching, had a degree in agriculture and had worked at a Horticultural Research Institution, but had openly and repeatedly expressed his views on university teaching of biology, which appeared controversial to many and positively dangerous to some. His interest was cytology and genetics, which was in contrast to the ecological interests of his two predecessors, Osborn and Tansley, and to the physiology of Vines. Only once had the Botany School made contact with genetics with F. W. Keeble, Sherardian Professor (1920–27) who collaborated with one of Bateson’s lady assistants, Caroline Pellew, at the John Innes Horticultural Institution, on heterosis in the garden pea. It is not surprising that his appointment was not universally acclaimed even by some of his longstanding botanical supporters, but powerful advocacy from Sir Robert Robinson and others secured his appointment.

Darlington introduced genetics and cytology into the Botany School by his own teaching and writing and by appointing geneticists, Alan Bevan and Leslie Crowe and later Brian Cox, a cytologist, Kenneth Lewis, and an electron microscopist, Barry Juniper. At last the unifying effect of genetics on biology, which he had continually advocated, now seemed to be within his grasp. Courses could be given that should be taken by botanists, biochemists, zoologists and physiologists, by medical and non-medical students, but as in several other universities this unification did not happen, or only after great administration changes or even the setting up of a new University.

To have achieved his objective completely, Darlington would have had to spend time and patience in committees and Boards of Studies. This it was not in his nature to do. With the help of his newly appointed colleagues, changes were made and a joint course for botany and zoology students was given in collaboration with E. B. Ford and Philip Sheppard. A new biology preliminary course was started in the early 1960s also attended by foresters and agriculturalists, which had a due regard for genetics, biophysics and cellular biology. Although Darlington had no direct influence on the setting up of a new Chair of Genetics in the university, his presence over the years had made the university aware of the importance of the subject.

Within the Botany School he tried to communicate with all members of the School by visiting their laboratories and discussing their work. He was hoping that they would appreciate that the gene was at the heart of the phenomena they were studying, but for some senior staff such appreciation had to await the later evidence of molecular genetics and they left to take posts in other departments or other universities, leaving vacancies that he was able to fill at his own discretion. Apart from those already referred to, he appointed Robert Olby, as librarian, who with Darlington’s encouragement published important books on historical aspects of genetics and evolution and who later was appointed to a Readership in Philosophy at Leeds University.
Cyril Dean Darlington

Most of his time was occupied in writing books, organizing chromosome conferences, supervising postgraduate students and in lecturing. He took great pains to prepare a lecture: he was unapproachable for 2 hours before one.

He was extremely interested in the Botanic Garden, and he wrote an up-to-date short brief guide in 1957, which is packed with interesting and well arranged information. He introduced a genetic garden of hybrids, variegated plants and plants used for chromosome studies. Typical of Darlington in this guide is a section on *Evolution in the Botanic Garden*. There was the escape of foreign plants from the botanic garden, ‘notably the Oxford Ragwort, *Senecio squalidus*.’ This plant ‘was sent from Sicily, established itself in the garden wall and later spread over a large part of England, finally using the railway lines as its means of progress’.

He engendered in the Curator, Kenneth Burras, a keen appreciation of the basis of plant variation, and the close friendship that developed had an important and lasting effect on the development and use of the Botanic Garden. A tree, the date plum, *Diospyros lotus*, was later planted in Darlington’s memory. His interest in gardens and estates was satisfied and received a lasting expression when the University bought the fine grounds of Nuneham Courtenay.

Darlington’s time in the Chair at Oxford was, as expected, one of change both rapid and slow, while his own ever-present occupation with the synthesis of ideas was still active and finding expression in his major works on the genetics of man and society. At retirement in 1971 he was made Professor Emeritus, and Magdalen College honoured him with the rare distinction of an Honorary Fellowship. He was on good terms with his successor and retained a room for writing, which continued to the end.

**Influences from Abroad**

Darlington’s first visit abroad as a scientist was to attend the Fifth International Genetics Congress in Berlin in September 1927. Here he saw Cleland’s preparations of *Oenothera* chromosomes, which, as he said, started his mind on the problems of the anomalous structural hybrid and ring chromosomes.

In 1929, he went to Persia with staff from the Royal Botanic Garden Kew to collect seeds of *Prunus* species and bulbs of *Tulipa* species. A collection of both these genera was essential for his chromosome studies, some of which were of a comparative nature requiring a comprehensive collection. He came back with many tulips and some *Prunus* and an attack of relapsing fever and amoebic dysentery, which gave him the opportunity to write the paper ‘Studies on *Prunus*. III’ when he was in hospital. But, more importantly, in the long term he was brought into contact with diverse people with diverse languages, customs, behaviour and religions. This important influence was to be renewed later in a visit to the
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U.S.S.R. (1934), to India with the British Association in 1937, and Australia and New Zealand in 1968 and again in 1971–72, an influence that stimulated his later interest in man and society. In 1932 with the aid of a Rockefeller Fellowship he spent a year in the U.S.A. and Japan. The visit was an auspicious and critical time for him because his great book *Recent advances in cytology* had just appeared the day before he sailed for America on 4 June 1932. About the visit he stated in a personal record that he was known enough in the U.S.A. for his views to be disliked and was allowed only five minutes to defend them at the International Genetics Congress at Ithaca. He went to Woods Hole where he did work of no value for two months but appreciated the doyen of cytology, E. B. Wilson, who treated him kindly and told him of Morgan’s two greatest discoveries, Bridges and Sturtevant. In October he worked in Belling’s room at Berkeley on two slides lent to him of *Agapanthus* and *Kniphofia*, material that first demonstrated to him the character of the centromere. During this time Belling was engaged in writing and re-writing his ‘critical review’ of Darlington’s book, which had just reached him.

On the bus from San Francisco to Pasadena, the home of ‘Caltech’, he wrote a third *Oenothera* paper, which showed that crossing-over would inevitably lead to mutation on a basis of structural hybridity. On arriving in Pasadena he found that Sterling Emerson had just published an attack on his views in *Proceedings of the National Academy of Sciences*. His paper written in transit was a complete reply and he persuaded Morgan, after some demur about controversial papers not being acceptable in the *Proceedings*, to agree to communicate his paper.

He examined meiosis in maize supplied by Beadle, and meiosis in the male *Drosophila* on slides provided by Th. Dobzhansky. The *Drosophila* work aroused widespread scepticism at Caltech. When this work was completed, Belling having died, he convinced the Rockefeller Foundation that he could best spend his time in Japan. After a short stay in Tokyo he went to Kyoto where Kihara, the distinguished cereal cytogeneticist, provided him with material of rye and oats. He gave many lectures in Japan with no observable effects, but what he saw was useful to him. Kuwada’s spiral preparations were the start of work on internal mechanics of the chromosomes, which continued until 1935. When he was at Pasadena he discussed the chromosomes of maize with ‘Andy’ Anderson, the maize geneticist, but they were poles apart at the time. E. B. Lewis recalls that when Darlington returned to Caltech on his way back from Australia in 1972, Darlington said ‘Andy never believed any of my cytological observations and told me so’. This was recounted with great humour and without any ill feeling, which impressed Ed Lewis as an example of the mellowing effect of age.

One of the most significant meetings abroad was an invitation from Timofeeff-Ressovsky to attend a small conference, now called workshop, organized by him and Ephrussi and under the auspices of the Rockefeller
Cyril Dean Darlington

Foundation. It was to be the first of a series to bring physicists, chemists, cytologists and geneticists together to attack the problem of the physical and chemical basis of heredity. The meeting took place at Klampenborg in April 1938 just before the invasion of Austria and was attended by Bernal, Astbury, Auger, Baur and some Germans. Darlington spoke for eight hours on his views of the chromosomes under the stimulus of constant interruption and interrogation. It is probable that Bernal and Astbury became sufficiently aware of what chromosomes do to enable them to advance their own interpretations of which Bernal’s tactoid theory of the spindle was the most fruitful.

Accompanied by his wife Gwendolen, Darlington visited Australia and New Zealand by invitation to give lectures and discussions. The most significant aspect for him was the invitation to Canberra from Professor David Catcheside, F.R.S., in February and April 1968; for this resulted in a renewal of the brief relationship in the 1930s when they were, at first, on opposite sides of the chromosome pairing controversy, but soon were reconciled. This renewal of friendship was to continue through correspondence and visits to the Darlingtons’ home at Oxford during the Catchesides’ almost annual visit to England.

From all the visits abroad it is typical of Darlington that he extracted much from others and, to the receptive, he gave much.

Scientific work

Organon

Darlington based his scientific work firstly on hypothesis and secondly on observations and facts (and even common sense). The hypotheses were formulated from a sound appreciation of genetics, evolution and, as he has said, ‘the action of determinants, introduced by Weismann, in the cell, individual and population especially when acted upon by natural selection and undergoing evolution’. These hypotheses were pruned rigorously by Occam’s razor, which he liked to refer to. His own view was that ‘Hypothesis has often proved more reliable than the facts of direct observation’ and ‘All of us like to be supported by earlier observations but few like to be anticipated by earlier ideas’. These provocative and, to some, dangerous approaches gave, in Darlington’s hands, many sound working hypotheses that stimulated the findings of many new facts. Naturally there were hypotheses that did not stand the test of a decade or two, but he was one of the first to admit the error. The danger was expressed by Karl Sax in a review of his book Chromosome botany: the book should be read by all biologists but it is not suitable as a textbook. The hard evidence for his faith in hypotheses and its impact on cytology comes from the index of his Recent advances in cytology (1932 and 1937). This contains forty primary entries under ‘theory’, of which about half can be attributed to the author and concern the chromosomes directly. In
contrast a contemporary book by the American cytologist Sharp, *Introduction to cytology*, contains no primary entry to theory and only seven secondary entries, of which only two concern the chromosome or the cell and one of these, gene theory, is under ‘Darlington’. Other evidence comes from a glossary of genetics and cytogenetics by Reiger, Michaelis & Green. Out of 2500 entries, 60 are attributed to Darlington.

His constant use of hypothesis and Occam’s razor enabled him to cut through the whole of cytology, which he found was a jumble of sound and unsound theories and observations, inconsistent with one another and with genetics, and its unfortunate derivation from histology and the academic subdivisions of plants and animals that had prevented anyone from removing or even observing the inconsistencies. These inconsistencies contained in some 1700 papers in his *Recent advances* were synthesized into a unified science of cytology by hypothesis and the deductive method.

Darlington was not a slave to a particular hypothesis, because he could quickly abandon one if there was disproof and adopt a new one, as he did with chiasmata but not about chromosome pairing, telosynapsis, end-to-end pairing or parasynapsis, lateral pairing. His paper on *Oenothera* (1929) makes the point and shows the method very clearly:

‘Of direct evidence for the alternative (telosynapsis) there is none. Telosynapsis is inferred (sic) from the indisputable facts of observations at diakinesis. The hypothesis of parasynapsis is inferred (sic) from the same facts. The difference between the two views is therefore a difference of reasoning and not of observation.’

Cleland, in his definitive book on *Oenothera* (1972), makes the statement ‘the parasynaptic interpretation of meiosis which Darlington, originally a telosynaptist, has become a strong advocate’. There is absolutely no evidence that Darlington at any time believed in telosynapsis, because it was one of his mainsprings of energy to prove it, and Ruggles Gates to be wrong. The same method of reasoning that sometimes overruled observation was applied to the controversy of the number of strands in a chromosome. Although Newton and Darlington had given to their satisfaction and to other genetically minded persons that the chromosome was single stranded, the controversy arose 10 years later with Shroeder, Huskins, Nebel and others who claimed that the chromosome was double and even octuple. Darlington had reasoned that the chromosome was a single structure and demonstrated how an asymmetrically projecting end of a chromosome was not evidence for a double strand as his critics had supposed but the end of a single strand that was spiralized into a hollow cylinder. But here again the reasoning played the dominant part, for how could, on genetical terms, the structure be more than single if there was only one copy of the gene
present on which the whole Mendelian genetics was based? Now we know that because the thread in the metaphase chromosome is sometimes as much as one metre long and is packed into chromosomes of a total length of only 100 μm there was of course no possibility of resolving by the light microscope the number of strands. As it happens, the latest electron micrographs and DNA labelling experiments support the hypothesis that the chromosome has a single strand of duplex DNA. This completely vindicates Darlington’s reasoning from genetics against the belief in invisible structures by cytologists who were unaware of the genetical implications of their conclusions.

His interpretation of the two nuclear divisions, mitosis and meiosis, made in 1932 has stood the test of time, for there is no better way of illustrating his methods and the two divisions than by his diagrams first published in 1932 and slightly revised with the change of term ‘attachment constriction’ to ‘centromere’ and the representation of the centromere from an empty space to a circular body. There is no confusing meaningless matrix about these chromosomes as can be seen in contemporary and much later diagrams of others. All the relevant interpretations and observations revealed by the light microscope are contained therein and are still valid some 50 years later, as shown in the revised version of 1956 reproduced in figures 1 and 2.

Where the system for investigation is not so much beyond the visible resolution of the microscopical probes but so complex that no quantitative methods have been effective, he has made a plea for common sense. In a letter to The Times, 23 November 1976, on Genetics of intelligence: bearing on education, he makes a statement that not only illuminates his organon but is of prime importance in understanding his writings on the genetics of man and society.

‘A more important principle that Galton and his successors missed was again a matter of common sense. It was that heredity and environment can be separated in experiment. But they cannot be separated in natural communities. Animals choose their environment. People even create them. When they do this heredity dominates the environment. The principle has governed human evolution but it has been disregarded by scientists. Why? Because the effect of this dominance cannot be measured and it is intolerable to many otherwise rational scientists to believe in anything they cannot measure.’

Darlington has attributed his success in research to (1) lack of academic training, (2) free choice of work and freedom from teaching and window dressing (3) the assumption that all previous cytological theories would have to be discarded or reconstructed, and (4) confidence in the principles that first appealed to him in The physical basis of heredity, namely a
rigorous materialism, applied as he found with more dialectical versatility than the American authors (apart from H. J. Muller) would allow to be proper or prudent.

Meiosis

When Darlington started to look at chromosomes, the work of Morgan and the Drosophila school had established the chromosome theory of heredity in which the genes were linked on chromosomes and that these linked genes recombined by a process called crossing-over. Janssens had earlier described the bivalent chromosomes produced by the association of the parental chromosomes at meiosis, each chromosome being composed of two chromatids. The chromatids were laterally paired, but according to Janssens the pairing was strictly between chromatids of the same parental chromosome. The cross-like configurations, chiasmata, seen on the bivalents were believed to be the result of previous coiling, and when the chromosomes separated at the first division it was presumed that there was a breakage of chromatids at the chiasma and a rejoining between chromatids, which resulted in an exchange of material between different parental chromatids. This chiasmatype theory was accepted by Muller in 1916 and by Belling in 1929. An alternative was the classical theory in which the paired chromatids were not strictly of uniparental origin, and a chiasma was a place where a particular chromatid changed pairing from parental to non-parental. The chiasmata were supposed to be resolved not by breakage and reunion but by a strained separation caused by the disparate pairing. The theory was favoured by classical cytologists because the integrity of the chromosome was not vitiated by a breakage and reunion, which of course, if uncontrolled, would lead to nuclear chaos.

Another important and closely related point of controversy was the nature of the pairing of the chromosomes. Was it confined to the ends (telosynapsis) as advocated by Ruggles Gates or was it lateral (parasynapsis) advocated by Newton and Darlington. Darlington’s important contribution was to realize fully the value of the study of the meiotic chromosomes in triploids. He with triploid Hyacinthus and Newton with Tulipa jointly showed that the three homologous chromosomes paired to form a trivalent and although two of the chromosomes may be paired at the end the third was clearly paired interstitially to one of the others. In a joint paper with the late Frank Newton, Darlington wrote about tetraploids. ‘Only two chromosomes associate at any one point and frequent exchanges of partner take place amongst the four chromosomes; no part of a chromosome appears to be left unpaired’. There were other enlightenments to come from his interest in parasynapsis, but these will be described under structural hybrids. This study of meiosis in polyploids first in collaboration with Newton led Darlington to deductions far
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beyond Newton's cautious attitude, so that at the insistence of Newton's widow, the later Professor Lily Newton, who did not approve of associating Newton with Darlington's theoretical views, he had to reserve these for a solo paper, which immediately followed the joint one. This unusual procedure had the merit of clarifying the contribution of the two authors. The solo paper compared the two hypotheses of chiasmata, the classical and the chiasmotype, for the configurations of the paired chromosomes in polyploids, and clearly demonstrated with a series of diagrams that the classical hypothesis could explain the structures only if the special and improbable assumption that one visible chiasma was really two compensating chiasmata, whereas the chiasmotype hypothesis required no special pleading. But in this 1929 paper, whether because of his own uncertainty or a remaining deference to Newton who had stated in the John Innes report of 1924 that 'the configurations at diakinesis do not support the theory of Janssens that they involve an actual exchange of material between the chromosomes', Darlington stopped at a full exposition of chiasmata and crossing-over. 'To return to the problem of the basis of genetical crossing-over: we do not wish to re-open the question of the relation of chiasmata to crossing-over in its widest aspects. The evidence on the genetical as well as on the cytological side is still altogether too scattered to enable one to put forward a working hypothesis with any possibility of its being generally applicable or useful.' He was quite positive about one possible function of chiasmata: that chromatids at diakinesis and metaphase are held together in pairs, chromosomes are only held together through the exchange of partners among the pairs at the chiasmata. He could be more certain about this because unlike the actual crossing-over event, which was invisible, the loops of repulsed chromosomes and their interlocking by chiasmata were clearly visible. This positive interpretation was to cause more difficulties, particularly with achiasmate meiosis in some organisms. One year after the guarded statement about chiasmata and crossing-over, a completely committed theory, which still holds today, was expounded in Proceedings of the Royal Society series B, and more fully, one year later, in Biological Reviews, where he wrote 'all chiasmata result from crossing-over between two chromatids of the partner chromosomes'. The only new evidence forthcoming in the intervening year was the novel segregation in the ordered tetrad of the fungus Neurospora by Dodge, which confirmed the earlier genetic evidence of Bridges in Drosophila that the genetic crossing-over was at the four-strand stage and any one cross-over involved only two strands. Darlington's hard cytological evidence from the pairing in polyploids was further confirmed unequivocally from a rare interlocking of two bivalents found by K. Mather working in Darlington's laboratory.

At the same time as these studies in the polyploids of liliaceous plants with their large chromosomes, Darlington studied the small chromosomes of Prunus spp. and Primula sinesis at different stages of meiosis, and
from an apparent anomaly between the number of chiasmata at the diplotene stage and the configurations of the bivalents at metaphase, which he explained by a supposed movement of the chiasmata towards the ends, arose the terminalization theory. This concept removed some apparent difficulties with the chiasmtype theory and at the time influenced its general acceptance, but he later stated that his views on terminalization were partly unsound, without explaining in what part. But terminalization was an important concept that was a stimulus and a framework for quantitative studies on chiasmata in many organisms, which is still playing a controversial part in chromosome studies today. With the use of techniques unavailable to Darlington, there is now positive evidence for some partial terminalization of chiasmata in some organisms and good evidence for its absence in other organisms, but complete terminalization, which Darlington thought existed, has not been found in any organism. Perhaps this is the unsound part. That terminalization is still discussed and tested 50 years after its conception is tribute enough.

It was also _Prunus_ that provided him with a fortunate if humbling experience. Humbling because he made a completely wrong interpretation of a sound observation and fortunate because it was trivial and was the type of error that all have to make to be fully aware of the extreme difficulties that beset observation and interpretation. It was in metaphase chromosomes of cultivated varieties of sweet cherry, _Prunus avium_, for he interpreted one of the configurations as a trivalent; this made the plant not a diploid but a diploid with one extra chromosome, a trisomic. These varieties were grafted onto wild rootstocks and therefore somatic chromosome counts in root tips, which was then the only source, were not available. With the help of M. B. Crane, who induced cuttings of the varieties to root, somatic counts were obtained and they were all diploid. Darlington fully corrected the mistake in a published note, which made it clear that the supposed trivalent fell into line as one bivalent among the types of configurations resulting from different arrangements of chiasmata that he had devised in the meantime.

From the very beginning of his work Darlington cut through the confusion generated by previous work of Farmer, Digby and Gates about the nature of the chromosome thread, the chromatema, which became visible at the early prophase of both mitosis and meiosis. It was even not agreed whether doubleness was due to the replication and division of a single parental chromosome or whether it was due to the pairing of the two parental chromosomes. Having, with Newton, unravelled the tangle to conclude that the mitotic prophase chromosome was doubled by replication and the chromosomes in meiosis were doubled by association and parasynaptic pairing, the very confusion had concentrated his mind on the problem to the point where he produced one of his most satisfying theories: the preciosity theory of meiosis. This beautifully simple theory
was inspired by assuming that mitosis and meiosis were alike and, by exclusion, to arrive at one essential difference, that is in the timing between the changes in the chromosome-replication, and those outside the chromosomes. In meiosis, as compared with mitosis, the external changes are precocious. The external changes initiate the nuclear division precociously in meiosis before the chromosome has replicated whereas in mitosis the initiation is after chromosome replication. This immediately provided a satisfactory explanation for pairing of the unreplicated chromosomes at meiosis and the lack of pairing of replicated chromosomes at mitosis. It also brought into line the repulsion of the replicated chromosomes at a later stage of meiosis. The theory stimulated much research to detect the molecular basis of initiation and replication, including the analyses of DNA and histone synthesis in mitosis and meiosis. Although it is now known that all the histone and the bulk of the DNA are synthesized at the same relative time in the division cycle in mitosis and meiosis, there is some semi-conservative (i.e. not repair) DNA synthesis late in the division in meiosis that is absent in mitosis. So the general theory is not yet disproved even at the molecular level.

Having established that crossing-over between non-parental chromatids preceded the formation of chiasmata he then turned to the problem of how crossing-over occurred; the mechanics, as he thought of crossing-over. In the second paper of the series ‘Internal mechanics of the chromosomes’ in 1936, he showed that the localization of chiasmata observed at diplotene corresponded closely to the positions of the localized pairing seen at the earlier zygotene stage. In his report to the John Innes Council of 1934 he stated clearly the problem and its solution and also a possible relationship between coiling and chiasmata, which led to his torsion theory of crossing-over.

'It seemed that the next problem to deal with was the problem of how the crossing-over occurred, of what forces determined it. For this purpose it was necessary to compare the behaviour of the chromosomes in organisms in which crossing-over and chiasma formation was normal with that in related species in which it was somewhat suppressed. For the purpose of this “natural” experiment, species of *Fritillaria* were suitable, for some, like *F. imperialis*, have their chiasmata freely distributed along the chromosomes, while others, like *F. meleagris*, have their chiasmata localised in the neighbourhood of the spindle attachment (centrome). This second condition was found to result from a localised pairing of the chromosome threads of an earlier stage of the process of meiosis. In one species *F. elwesii*, the localisation was incomplete and the pairing was intermittent. Where the intercalary regions had been unpaired the partner chromosomes were found to be coiled round one another after their separation, whereas in paired regions of this species and
throughout the chromosomes of *F. imperialis* chiasmata were formed and no coiling remained. I have therefore inferred that coiling occurs in any regions between paired points in the chromosomes and that it is replaced by crossing-over and chiasma formation in the parts that are directly paired, while it survives in those intercalary unpaired parts where crossing-over necessarily cannot occur. In these circumstances the force which determines coiling must determine the crossing-over which removes the coiling.'

To more clearly define the force responsible for coiling he made a detailed study of the internal mechanics of the chromosomes from which he concluded that

'The coiling and uncoiling of the chromosomes which constitutes their change from the threads present in the resting stage to the rod-shaped bodies present at metaphase requires that the chromosomes have a certain degree of longitudinal cohesion and that an internal or molecular change must compensate for the external spiral observed. This molecular spiral must alternate between two extremes, when the chromosomes are shortest at metaphase and when they are longest during the resting stage in mitosis.'

Although this was a prophetic guess at the molecular spiral to be shown in DNA much later, if Darlington was actually thinking of a molecule at this time it would have been protein and not nucleic acid; work on the internal mechanisms of the chromosome was perhaps the least fruitful of his studies. It certainly produced the elegant torsion theory of crossing-over, which did not stand the test of time and the superior resolving power of the electron microscope, but the problem is still not fully solved even with these modern techniques.

After the preciosity theory of meiosis, Darlington realized the importance of another temporal difference between mitosis and meiosis: the stage of division of the centromere. The confusion surrounding this part of the chromosome, which appeared to organize the spindle and the orderly movement of the chromosomes to the poles, was tabulated in his characteristic way by listing the eleven different names given to it under two descriptive headings 'Substantive' and 'Spatial'. He adopted Waldayer's rarely used *centromere*, which he made universally acceptable. The centromere in his view was a body with directional organization and not just an empty space or a constriction in the chromosome, or just an arrow pointing from the constriction to the pole. In the John Innes report of 1935, when explaining his general theory of the external mechanics of the chromosomes, he wrote 'The theory depends on the assumption that the spindle consists of orientated long molecules, whose orientation is determined by two kinds of centre of repulsion, the spindle poles or
centrosomes and the spindle attachments or centromeres (as I propose to call them). Darlington clearly showed for the first time the significance of the division of the centromere at anaphase in mitosis and, in contrast, the two undivided centromeres of a bivalent in meiosis; both types of behaviour are essential for the orderly congression of the centromeres and chromosomes on the metaphase plate and their subsequent separation to the poles. The discovery of anomalous configurations by Dr Margaret Upcott inspired the idea of the misdivision of the centromere in a plane parallel to the spindle instead of at right angles, with the resulting production of a centromere with two identical sister-chromosome arms, which he called an isochromosome. This anomaly was later to be found in many organisms and by Darlington himself to have some selective value in certain species. The misdivision of the centromere also led Darlington to the view that the centromere itself has a directional structure, which anticipated the precise demonstration revealed by the ultrastructure.

The series of studies on meiosis illustrates clearly Darlington's methods of work: first the idea, the theory, then the careful selection of the material to produce as he said the natural experiment, the observation and analysis, then another question, idea and experiment. This was repeated several times: (i) chiasmata as the means of holding bivalents together, (ii) crossing-over and chiasmata, (iii) terminalization, localized pairing and back to chiasmata and pairing, coiling and pairing and the torsion theory. At the beginning of this sequence he had a conflict arising about the dual role of chiasmata: whether to maintain pairing for the orderly separation of the bivalents or whether chiasmata were the result of crossing-over. The conflict led to a very unusual feature in his writing at the time. He used words very precisely but the word pairing became of uncertain meaning in his hands, sometimes it was used as the actual pairing process at zygotene, and at others as the maintenance of a paired structure at diplotene and metaphase. Despite, or possibly because of, this initial uncertainty about pairing, crossing-over and chiasmata he was to get as near to the correct solution in the pre-molecular era and this has persisted through periods of alternative theories of other theories, such as copy-choice and all pre-DNA synthesis theories. For if crossing-over occurs as Darlington said in meiotic prophase after DNA synthesis and therefore excluding copy-choice, which depends on DNA synthesis, it must involve some form of breakage and reunion, not as Darlington believed by mechanical forces but by enzymes. He most frequently thought in mechanical and structural and occasionally in molecular terms but rarely, if ever, in biochemical terms.

A major difficulty in resolving the conflict about chiasmata and the maintenance of pairing was the male Drosophila, which has no genetic crossing-over and yet in which the maintenance of pairing and separation is normal. This difficulty created great opposition and scepticism to
Darlington’s whole theory. If chiasmata were the result of previous crossing-over then they should be absent in the male *Drosophila*, and if they also hold the chromosomes together for orderly segregation then bivalents without chiasmata should fall apart before metaphase with complete disorder and subsequent sterility of the fly. In his paper of 1931 on *Primula sinesis* he proposed two reciprocal chiasmata close together, one cancelling the effect of the other, so that no genetic crossing-over detectable by current methods would occur and the chromosomes would be held together at metaphase. On the looking at the meiotic chromosomes in the male *Drosophila pseudo-obscura*, in material supplied by Theodosius Dobzhansky, he did not find chiasmata in the autosomes, and concluded with a statement prophetic of Karl Popper: ‘The position now is that the simple chiasmata type hypothesis, like other hypotheses, cannot be proved. It can only be subjected to the possibility of disproof by testing the many rigorous predictions that can be based upon it. Like previous attempts the present study has failed to disprove it.’ The problem of the achiasmate meiosis in *Drosophila* and other Diptera is still not fully resolved, for like all analyses by the use of new methods with greater resolving powers, unthought-of complexities and steps in a process are uncovered. In this instance some features of the synaptonemal complex and the recombining bodies now known to be involved in the process should reveal the lesion that causes the anomalous achiasmate meiosis.

Darlington was aware of the inadequacies of the techniques he used for these problems and the shortcomings of his own theory of meiosis, and even as late as 1977 in an unfinished book he gave expression to the uncertainties of interpretation of the central problem of crossing-over: ‘These conditions for crossing-over are the development either of torsion between the paired chromosomes which survives where there is not crossing-over or of the synaptonemal complex between them or most probably both these conditions since they probably influence one another.’ But the particular uncertainty of the interpretation of visible chiasmata and invisible forces acting on the chromosomes became a much wider and fundamental uncertainty generated by the very crossing-over mechanism, a genetically generated uncertainty that Darlington believed permeates the whole of life, behaviour and society, and the central philosophy of all his later writings.

**Peripheral problems of polyploidy**

Darlington records that his very first idea came in December 1926 when he was travelling in the underground train to work and on this occasion accompanied by Miss A. E. Gairdner, one of Bateson’s assistants and with whom he collaborated on *Campanula*. They were discussing the effect of polyploidy on fertility, particularly on the tetraploid
cultivar of *Campanula percisifolia* Telham Beauty and the hybrid *Primula kewensis*, when he formulated what has later been known as Darlington’s rule, that there is a negative correlation between the fertility of the polyploid and that of the diploid from which it arose. This was a simple deduction from the pairing or lack of pairing and the homology or lack of homology of the parental chromosomes. It became the basis for the study of fertility in species, hybrids and diploids and polyploids, only to be later added to by the finding of specific genes for affecting chromosome pairing by Ralph Riley in wheat.

Another important problem arose in the Mendelian segregation found in autotetraploids. The problem was in the progeny obtained from a tetraploid plant that had three doses of the dominant gene and one of the recessive, e.g. *AAAa*: the gametes produced might be expected to be *AA* or *Aa*. With some genes these were the only types produced but with others a small proportion of *aa* gametes were found. Darlington first gave the correct explanation of this based upon his theory of chromosome pairing, chromatid segregation, division of the centromere and crossing-over at chiasmata in positions between the centromere and the gene in question. The full consequences were partly worked out by J. B. S. Haldane and fully by K. Mather.

**Anomalous Oenothera; the structural hybrid**

The evening primrose *Oenothera lamarkiana* was, at the time of the rediscovery of Mendelism in 1900, an anomalous plant in that it appeared to be an exception to Mendelian segregation. Apparent hybrids bred true and this had led de Vries, one of the three rediscoverers, to delay his historic publication of Mendelian segregation that he had found in other plants. He also postulated his general mutation theory as a result of another anomaly, the true-breeding sports, which occurred relatively frequently. Ruggles Gates in 1907 found a cytological anomaly, for the plant produced a ring of 14 chromosomes instead of seven bivalents at meiosis. Darlington’s decisive contribution to the understanding of the cytological and genetical structure of *Oenothera* species started in a characteristic way. He had the spur from Ruggles Gates, who interpreted the ring structure as evidence for end-to-end pairing, telosynapsis, which explained the ring of 14 chromosomes but not the true-breeding hybrids or the sports. Darlington’s parasynapsis and his interpretation of chiasmata characteristically had to explain everything including the cytology and genetics of *Oenothera*. His first real awareness of *Oenothera* came in June 1928 from the Proceedings of the Genetics Congress in Berlin; he had read a paper by the American cytologist Ralph Cleland on *Oenothera* and had seen his cytological preparations in Berlin. Darlington was at that time working on the polyploids of *Tulipa* and *Hyacinthus* from which he had made his general theory of chromosome pairing and the
function of chiasmata, and applied this to Cleland's *Oenothera* material. He made a simple interpretation based upon reciprocal interchanges between the seven chromosomes. He made preparations of another ring-forming genus, *Tradescantia*, wrote up in a fever of excitement, obtained the approval of J. B. S. Haldane and sent the paper to the editor of the *Journal of Genetics* asking him to publish it before the paper, sent previously, on meiosis in polyploid tulips and hyacinths. This tactical timing, he later realized, was a mistake because the argument for the *Oenothera* hypothesis rested entirely on the observation and interpretation of the polyploids. He did include in the polyploid paper, which appeared a few months later, a short paragraph referring to *Oenothera*. In applying the theory of segmental interchange between the chromosomes he was preceded probably unknowingly at first by Muller and Belling, but he added the localized parasynaptic pairing so that the chromosomes were held together in a ring by chiasmata and not by telosynapsis. He alone worked out correctly in detail the consequences of irregular disjunction and the formation of variants of the ring of 14 and explained a group of de Vries's mutations as the result of crossing-over. He also discussed all the published work on the genus *Oenothera*, accepting some and demolishing others. *Oenothera*, instead of being an embarrassing exception to Mendelian segregation, became the natural experiment that united Mendelism, the chromosome theory of heredity and his own theories of meiosis. It was only an exception in the trivial sense. It was a structural hybrid maintaining its heterozygosity permanently by the reciprocal translocations, and a system of gametic lethals mainly worked out by Otto Renner.

From *Oenothera* Darlington, with Gairdner, turned to *Campanula percisifolia*, a species in which the full structural hybrid state was only partly developed and was therefore more subject to manipulation and experiment. By synthesizing rings of six chromosomes in *Campanula* he was able to show how a complete ring of all the chromosomes as in *Oenothera* could be built up by a series of interchanges. From the incomplete ring, or floating interchange as he called it because it floated as a polymorphism in the population, to the permanent structural hybrid each interchange step would be subject to selective forces on fertility, isolation and the very structural and pairing nature of the chromosomes themselves. Parallel with these changes were selective pressures to change from an outbreeding to an inbreeding system. From the differences in chromosome pairing between *Campanula* and *Oenothera* he was able to show that there must be restriction of pairing and localization of chiasmata to the ends of the chromosomes to ensure a regular disjunction of the ring and of the development of lethals that were preserved by the protection from crossing-over. Darlington's cytological analysis of *Oenothera* was matched by the genetical analysis of Otto Renner for whom he had the greatest respect, as is evident from his
Biographical Memoir (1961) and also from his review of Cleland’s book, *Oenothera* (1972) in which he, as reviewer, gives a masterly and fair account of the history of his and others’ part in the story with great restraint, and only succumbs to one typical Darlingtonism in which he writes ‘Cleland with the best will in the world, here as always refers to “my” interpretation as Belling’s theory when he is confirming it and as my theory when he is contradicting it’.

Consideration of the *Oenothera* system, which originated from his work and theories of meiosis, and was for him now in the past, helped to stimulate another idea. This was the gene control of the whole genetic mechanism, the chromosomes, the cell and the breeding system. These ideas were first stated in a chapter of his book *Recent advances in cytology*, but were later enlarged into the separate masterpiece *Evolution of genetic systems*, and were forever present in his mind in his controversial writings about man and society. *Evolution of genetic systems* has been rightly acclaimed by many as his major contribution to biological thought. In its way it can be compared to Darwin’s *Origin of species*: the main idea has stood the test of time in both, and only some of the details, such as the role of major mutational steps in the evolution of the systems and the effectiveness of group selection, are open to present-day criticism. I am indebted to Professor J. Maynard Smith, F.R.S., and Professor M. J. D. White, F.R.S., for pointing out to me some of these inevitable shortcomings.

*Heterochromatin, nucleic acid starvation and chromosome breakage*

The chromosomes of liliaceous plants continued to be the subject of profitable study even after the main problems of meiosis had been explored as far as possible with the light microscope and contemporary techniques. L. F. La Cour working with Darlington discovered in 1936 that the chromosomes of *Paris* and *Trillium* sometimes, but not always, had lightly stained bands at metaphase. These bands, when they appeared, were characteristic of a species but there was also some variation within species. The temporal variation was found to be due to the temperature before fixation: a low temperature induced the appearance of the bands. The work was published as a joint paper in 1940. Natural populations were found to be polymorphic for the bands, and there was a correlation between the extent of the banding and presence of B chromosomes, which were known to be mainly inert. This led Darlington and La Cour to liken the cold-induced bands to the bands of heterochromatin that had been seen in prophase chromosomes of animals but had not been demonstrated at metaphase, and the cold-induced bands were the first to be seen at metaphase. The full development of this work was to return to animals by the work of Caspersson and his colleagues some thirty years later in 1970 by fluorescence microscopy;
they demonstrated bands at metaphase in human chromosomes, followed by Yunis in 1976 using Giemsa stains and other treatments to reveal specific bands, which have become of the greatest value in the identification of whole chromosomes, parts of chromosomes and translocations, particularly in man.

Why was there a gap of 30 years between the original discovery and the development? Darlington's comparison with heterochromatin and their inert nature was sound and useful but his main theoretical basis of the structural and molecular nature of the bands was not, and it turned out to be in molecular terms highly misleading. His general thesis was that the chromosomes became charged with nucleic acid at prophase reaching a maximum at metaphase and uncharged in the resting stage. The lightly stained bands were uncharged owing to some structural difference and nucleic acid starvation brought about by cold. The stain used to expose the bands was Feulgen, which is specific for DNA. Darlington, having a sound knowledge of formal genetics, could not adopt such a theory if DNA was the genetic molecule and he had to presume that the genes were proteins. Naturally this interpretation, when the structure and function of DNA and RNA became known, cast a shadow over the whole work that eclipsed not only the theoretical moonshine but also the sound foundation of an important discovery with great future application. The untimely theory of nucleic acid starvation is the only one of Darlington's many theories that was not helpful to him and others. Writing of cold-induced heterochromatin in 1980 in his unfinished book he states 'They are starved of half their materials, not of their DNA as it seemed at first but rather of their proteins and RNA'. The full molecular and evolutionary significance of the bands is still a problem for the future.

Darlington was from his early days with chromosomes brought into contact with the use of ionizing radiations as a tool in the study of chromosome structure when Mather & Stone in 1933 at the John Innes Horticultural Institution used X-rays to determine the stage of mitosis when the chromosomes changed from single to double structures, at least as shown by X-ray-induced breakage. About ten years later La Cour and P. Koller with Darlington used X-rays and other sources of radiation and chemicals to study the types of breakage found both in mitosis and meiosis. The work was for a time centred on the interpretation of what were called sub-chromatid breaks, which indicated that the chromatid, which was visibly single, was really a double structure. The consequences of this work on breakage is difficult to assess because of the ignorance of the physical and chemical structure of the chromosomes at that time. With the discovery of DNA and its mode of replication, and the use of tritiated thymidine by Taylor in the U.S.A., the whole of the breakage work appeared to become irrelevant. Darlington would be the first to admit that both the nucleic acid starvation and the chromosome breakage experiments suffered from the absence of a sound theory; the basic theory
adopted was the charging of the chromosomes by nucleic acid, which had a protective effect against X-ray breakage, and by its absence it marked the heterochromatic segments revealed by cold and that the continuous thread of the chromosome was a polypeptide with a monid structure. It came too near in time to the double helix to have a useful lifetime.

Nucleus, cytoplasm, plasmagenes and viruses

When Darlington started his work at the John Innes, Bateson asked him to work on variegation in *Vicia faba*, probably to ensure that he did not get too engrossed in the overrated chromosomes, and to keep in mind the cytoplasm, which Bateson still thought of prime genetic importance. This work resulted in a paper that has been forgotten and never referred to, but it had the effect on Darlington that Bateson hoped for. Years later, Darlington became intensely interested in the work on plastid inheritance by Renner in *Oenothera*, Rhoades in maize, Baur in *Antirrhinum* and others, with Sonneborn’s work on the killer of *Paramecium*, bringing the animals into the picture. He was the first to point out the general significance of the work and to publicize in his books and articles his views on the partial autonomy of the plastids, their interaction with the nucleus and their transmission, making the complex subject vividly understandable by his usual diagrams. He did no experimental work on the subject because there was so much work of others that his synthetic approach was enough to make a big impact in the 1940s, both with American and European geneticists some of whom were not convinced of the existence of extranuclear genes. He also stimulated the re-examination of such obscure phenomena as ‘bolters’ in potatoes, ‘rogues’ in peas and tomatoes and ‘June yellows’ in strawberries. The most important paper on the subject was ‘Heredity, development and infection’ (1944). In this he brought together his thoughts on the interaction of nuclear genes, cytoplasmic genes, plastid genes, viruses, proviruses and other unidentified infective agents. All this was before the knowledge of DNA and long before it was known that chloroplasts and mitochondria contain DNA. Many of his concepts have a remarkable parallel to what is now known about plasmids, transposons and the interaction of gene products from the nucleus and the cellular organelle. Perhaps we owe this prophetic breakaway from the constraints of Mendelian inheritance and linkage of the genes on the chromosomes not only to his synthetic mind but to his ever-present mistrust of authority and the past work of others.

Genetics of man and society

With Darlington’s exceptional synthetic and far-ranging mental characteristics it is somewhat surprising that it was not until after some
twenty years of work that he turned to genetics of man and society, a subject that he later wrote about continually for the rest of his life and one that caused even more criticism and controversy than his 'harmless' work on the chromosomes and meiosis and mitosis. But the interest was there at the beginning and lay dormant; for in a letter from the Rectory House, Ealing, 20 February 1927, to his medical brother Alfred he wrote 'I hope you will do your utmost where you have an opportunity—and it is only medical men who have any opportunity—to watch any possibility of defects or susceptibilities being hereditary. There is also another problem that you would find most interesting, i.e. studying the occurrence and inheritance of deviations from symmetry and of mixed eye colours—sections of the iris of different colour.' He later refers in the same letter to recording colour blindness and exceptions to Mendelian inheritance, and also about twinning and lethal combinations. This interest in deviations from symmetry and Mendelian segregation and the mixed eye colours probably originated from the work on cytoplasmic inheritance forced upon him by Bateson, and this suggested approach to human heredity had for Darlington no development, and he rarely if ever spoke to his colleagues about his interest in human genetics, appearing to have no interest in the subject. There was, however, an entirely different attitude in 1943 when he wrote 'Race, class and mating in the evolution of man' for Nature, followed by 'The genetic component of language', published in his own journal Heredity. He became aware, probably from his close collaboration with Kenneth Mather at that time and reinforced by the writing of the joint book Elements of genetics, of the shortcomings of the single gene approach. He adopted the whole genotypic, almost Galtonian, approach to 'properties of greatest importance for our survival and evolution—intelligence, instinct, viability and fertility and resistance to infectious disease'. The breeding system and more importantly a change in breeding systems were of prime importance; this led him to the study of fertility of cousin marriages and the descendents of these marriages. He analysed enough families to be able to conclude that high fertility can be maintained in an inbreeding system when this has been long practised; immediate loss of fertility results from changing the breeding system from either in to out or the reverse. In all his writings on man he was convinced but was misunderstood about the importance of the genetic component of behavioural characteristics; but what has been overlooked is that he was also convinced of the unreality of the attempt to quantify the genetic and environmental effects on these 'properties'. Not only did the genotype choose or submit to the environment but it changed and created the environment.

His thoughts and his knowledge of history, agriculture and archeology were synthesized in a characteristic way in his vast book The evolution of man and society, in which the ultimate conclusion is that innovation (genius) arises from outbreeding and the environment and that to
preserve man we must preserve the diverse environments for diverse peoples. He has been, and will continue to be, misunderstood, but few, if any, have written so thoughtfully and deeply on these crucial and vital problems of the human race. Ironically, the one discovery in man that was universally acclaimed and would have been a natural consequence of his chromosome work, the correct chromosome number of man, evaded him. In fact he reinforced the belief in Painter’s incorrect number, 48, which stood for thirty-three years, one year before the true number 46 was found by Tijo & Levan in 1956. Even the beautiful squash and stain techniques of La Cour were of no avail in unsuitable material, which was the traditional bone marrow: close medical contacts and the use of tissue culture were the secrets of success which was not to be his. The connection between his study of man and society and his early chromosome work was not in chromosome number but in the concept of the uncertainty and unpredictability in all life generated by the crossing-over of chromosomes at meiosis.

Science, politics and publication

Among the few portrait photographs in Darlington’s laboratory was that of the Russian geneticist, Nikolai Vavilov, who in Darlington’s eyes was distinguished for his theoretical basis of plant breeding, his collection of genetic material and the leader of genetics in the U.S.S.R. His murder in 1942 at the order of Stalin, and the rise of the charlatan Lysenko, were vigorously exposed by Darlington as not only the liquidation of one man but the whole of the science of genetics and its practitioners, which still has its effects in the Soviet state today. His exposures were in scientific journals, weekly papers and on the radio; they continued from 1946 until 1969, some three years after the fall of Lysenko and Khrushchev. But Darlington was concerned not only with this extreme example of the suppression of science for political and ideological ends but also with what he called the ‘dead hand on discovery and the ‘conflict between science and society’, as he expressed it in his Conway Lecture, or with the conflict between discovery, which is the active principle of science, and continuity, which is in some measure the necessary conditions of society. Here he attacked the animal breeding societies, The Ministry of Agriculture, and the Forestry Commission, for positively ignoring the application of genetics to the improvement of livestock and forest trees. These attacks on vested interests and bureaucracy were to be with him right to the end of his life, when in two letters to The Times, of which one was published, he joined in the British apple controversy, pointing out the effect of vested interests on the distribution of new apples from the John Innes Horticultural Institution. It became difficult to get some of his criticism published for he recalls that his Conway Lecture with its attack on the establishment in this country and Lysenko in the U.S.S.R. was
eventually published, with the help of the revolutionary novelist George Orwell, after two rejections and one failure of a periodical, by the iconoclastic *Picture Post*.

Not all Darlington’s thoughts on the political aspects of science were negative; he was one of the first to make positive suggestions about the unity of biology through the fundamental principles of evolution, cytology, genetics and biochemistry that helped to change the teaching and research in British universities. His ever-present concern with publication was not confined to the more emotional subject of science and society because in his view work that is not published is work not done. The trouble began with the rejection of a paper submitted to the Royal Society that was turned down by his chromosome-pairing opponent R. R. Gates. Other papers were said by editors to be unsuitable for the *Journal of Experimental Biology* because of their lack of formal experimentation, and they were not genetical enough for the one British genetics journal, *Journal of Genetics*. Foreign journals were available to him before the 1939–45 war but later there was no other suitable journal and the sole *British Journal of Genetics* appeared only sporadically after 1957 when Haldane, the editor and owner, became a citizen and domicile of India, and not at all after 1974. Darlington, with the collaboration of R. A. Fisher, founded a new journal, *Heredity*. After Fisher’s death he was the sole owner and in 1969 presented it to the Genetical Society on the condition that it continued to be described as *Heredity* with the subtitle ‘an international journal founded by C. D. Darlington and R. A. Fisher in 1947’. All he asked in return for this profitable gift was copies of each part and supplement during his lifetime.

Darlington, as editor, was extremely helpful to authors, making a clear-cut decision at the first and doing all the editorial work himself; he made constructive suggestions for improvements in the presentation, often by diagrams and tables. He never fell to the levels of improving a paper by pedantic quibbles. His most important advice before a paper was written was: write the summary in as finished a form as possible before committing any other part to paper.

As president of the Genetical Society (1943–46) he influenced the course of genetics in Britain when he transformed the year book by including a list of relevant journals, research institutes and university departments concerned with genetics and cytology, a miniature of Darlingtonian synthesis. After the war he arranged for European geneticists to meet in Britain, the first international gathering of geneticists since the ill-fated Congress of Genetics held in Edinburgh in September 1939.

Despite all his political and publishing interests he did not neglect science, for apart from second editions of his own books, books jointly with colleagues appeared that were of great value to the professional biologist. *The handling of chromosomes* with La Cour was a treatise on
techniques in a limited subject with a chapter on writing up the results of value to any scientist. The previously mentioned *Elements of genetics* with Mather was a clear and concise account of the state of the subject at the time. There were the two *Chromosome atlases*, one with E. K. Janaki-Ammal and the other with Ann P. Wylie. All made a lasting and continuing contribution and helped to spread the study of chromosomes into other fields and particularly into taxonomy and systematics. He made a direct approach to taxonomy in 1937 by persuading botanists at Kew Gardens to come together with Julian Huxley and other zoologists. This led to the formation of the Association for the Study of Systematics and the publication of *The new systematics*, which was Darlington’s title.

**The Man**

Darlington has frequently and rightly been described as tall and handsome and in the early days as a cross between a cavalry officer and a film star. In a review of a premiere of a film, produced by Richard Massingham, at the élite London cinema, the Curzon, in which professionals and amateurs were employed, the producer chose amateurs with expressive photographic faces or figures. Among the amateurs described is ‘Dr Cyril Darlington sips a glass of wine’. His appearance, his soft but expressive voice with a distinctive timbre and his excellent memory were used during his Rockefeller visit to the California Institute of Technology, where he spent many evenings acting in the Pasadena Playhouse. His histrionic abilities undoubtedly had an impact on his scientific writings and utterances and on his dealing with people, a personality trait that not all who met him could tolerate. It is possible that his arresting appearance had much to account for his extreme self-confidence, which was noted by his father when Cyril was not yet thirteen years old. In replying to a notification from St Paul’s School that Cyril had not won a scholarship, he wrote ‘Indeed I rather think his failure will in the long term prove to have been the best thing that could have happened as I found him myself much too confident for his abilities’. This confidence, which persisted throughout his life, was to some overbearing although it later mellowed into a deeply humane and reciprocating affection. This was so vividly portrayed by his Magdalen College friend the Rev. Dr Arthur Adams, who was Dean of Divinity when Darlington was at Oxford:

‘His personality went out and grasped you in friendship and affection. He was ready and wanting to share his enthusiasms, intuition, questionings with you and with yours. So an encounter with him was always a refreshment: you felt that you carried away more than you came with—and he, as often as not, would have
extracted something for himself from one’s small store of knowledge, because he was always adding to his own. With him a relationship was always a two-way dialogue, a mutual enrichment.’

He had high ambition, not for power or a career; the establishment was to him a matter of derision and not conformity. His ambition was for self-expression and the power that comes from knowledge, and here he had the confidence to expect recognition. In 1927 he wrote to his brother Alfred: ‘I have become so ambitious or optimistic that I have come to think a Doctor’s degree may be almost a hindrance to me so that I shall be plain Mr for a few more years to come’. But a Freudian slip shows his ambivalence here for the Mr was written with a D corrected to M.

In a letter 26 October 1934, again to his brother, he wrote: ‘I have made a stride in theory so important in completing my earlier work that I think I can reasonably hope to be in the Royal Society in three or four years’. Again this emphasis is on theory not discovery of facts, and, as he later realized, it is theories and not facts that make and enrage enemies. His hope was optimistic by only three years.

Of literature and the Arts, apart from his considerable knowledge of the classics, he recommended in the 1930s Bertrand Russell, ‘he is still my apostle’; Juan in America by Eric Linklater; Grand Hotel by Vikki Baum; The Water Gypsies by A. P. Herbert; Decline and Fall by Evelyn Waugh; Cakes and Ale (private life of Thomas Hardy) by Somerset Maugham; and Antic Hay (figures J. B. S. Haldane) by Aldous Huxley. A visit to the Flemish Art Exhibition in London 1927 brought forth ‘the Vandykes were very fine but the Primitives superlative. I had thought that there would be many more pictures and not so many Virgin Marys looking like so much boiled pig. I hope the Americans will carry some of them off and leave us richer in every way.’ Anybody who visited his house realized that he had a fine eye for sculpture, pictures and Japanese prints. Although he was knowledgeable about music and obviously got pleasure from it, he did not seem to have that instinctive ear of those who cannot be complete without it.

His lasting personal relationships required a common interest and a mutual intellectual stimulation. His first venture into marriage was short-lived and never referred to. His second marriage was to Margaret Blanche Upcott, the daughter of Sir Gilbert Upcott. Miss Upcott came as a volunteer worker in Darlington’s laboratory after hearing his talk at the Royal Institution. A scientifically fertile collaboration lasted for several years, during which one noteworthy discovery of Margaret Upcott was the misdivision of the centromere that led to the logical conclusion in The origin of isochromosomes. To the science collaboration was added the fertile union of marriage in 1939, which resulted in two sons and three daughters. During one of the pregnancies Darlington was asked the usual senseless question whether he hoped for a boy or a girl and replied that he
did not mind as long as it was one or the other. In June 1950 he married Gwendolen Mabel Harvey née Adshead, who gave him love, peace and the support that helped him first at the John Innes at Bayfordbury and particularly at Oxford and in retirement to fulfil most of his objectives.

Darlington was always generous to his collaborators and the most fitting tribute is his own:

‘I have been fortunate in having many gifted collaborators. Kenneth Mather who did most to join chromosome studies and breeding experiments, Margaret Upcott, Margaret Richardson and Pio Koller who did most to show the chromosomes by their excellent drawings, Leonard La Cour whose technique did most to develop their study; H. N. Barber who made the best of all experiments with chromosomes; Janaki-Ammal who gave me her immense knowledge of tropical plants and also of Indian society; Morgan Watkins and Brosnahan who threw their linguistics into the struggle on my side.’

Darlington’s health appeared to his co-workers to be good because he never complained and was rarely away from work, but a severe heart attack in 1964 could not be concealed until after his full recovery when he was able to continue writing and made a visit to Australia and New Zealand. He survived a second attack but succumbed to the third. Unknown to many he was extremely sensitive to the ultraviolet of sunlight, which in later years gave him skin trouble but which did not interfere in any way with his work.

Four days before his seventy-fifth birthday he wrote in his notebook, under the general heading Connections,

‘All my life I have been trying to tie things together, using or finding ideas that will help to make small bits into larger bundles. It is an arduous and endless but not fruitless, task. It makes friends critical, critics angry and enemies furious. And it brings understanding that is little and late. Why, they ask doesn’t he stick to the facts instead of offering us spurious fiction? But my schoolmaster understood when he reprimanded me at the age of ten. Darlington you are not attending; you are dreaming! I was. It had been a lifelong obsession; the one which (together with the boundless appeal of the senses) led me to the chromosomes.’

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The photograph reproduced was taken by Walter Bird.

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