GUIDO PONTECORVO
29 November 1907 — 25 September 1999

GUIDO PONTECORVO

29 November 1907 — 25 September 1999

Elected F.R.S. 1955

BY O. SIDDIQI, F.R.S.

National Centre for Biological Sciences, Bangalore 560 065, India

Guido Pontecorvo was elected a Fellow of The Royal Society in 1955 for his contributions to the genetics of Drosophila and the fungus Aspergillus nidulans. Pontecorvo was a leading British geneticist, prominent in the decade preceding the discovery of DNA, who enriched our understanding of genes and whose pioneering work on the parasexual cycle in fungi found application in human somatic cell genetics.

Known to friends as Ponte, he had a strong personality. Somewhat irascible but warm, with a wry sense of humor, he made many lifelong friends and acquired a large body of admirers.

FAMILY AND EARLY LIFE

Guido Pontecorvo was born on 29 November 1907 in a prominent Jewish family of Pisa. His grandfather, Pellegrino Pontecorvo, owned a clothes shop in Rome and moved to Pisa in 1890 to set up an industry that grew, by 1920, into the largest textile firm in Italy. Guido’s father, Massimo Pontecorvo, and his uncles worked as managers in Pellegrino’s factories. The clan lived in a large, four-storey house on via Manzoni presided over by the strong-willed Pellegrino. The sons and their families occupied separate flats, but each Saturday the entire clan gathered for dinner with the grandparents where, as Guido put it, ‘the children were to be seen, not heard’. The community to which the Pontecorvos belonged had been living in Italy since medieval times or earlier, but they were non-practising and not ‘particularly Jewish except by genetics’.

Guido was the eldest of eight siblings, five brothers and three sisters. Among the brothers were Bruno, the well-known physicist, and the film director Gillo, of the Battle of Algiers fame. Surrounded by many uncles, aunts and cousins, Pontecorvo grew up in a secure environment. He was especially close to his father and attributed some of his attitudes and ethical precepts to Massimo’s quiet influence. Massimo believed, for instance, that ‘men should do
science’. When the workers in the factory went on strike and the Fascists wanted to arrest the leaders, Massimo refused to give their names. A close boyhood friend was Franco Rasetti, who later turned to physics; Rasetti was a polymath, interested in everything under the Sun.

Before entering school, Guido was taught English and French by private tutors. A French governess, coaching the children, had a strong Catholic influence on the family. At school Ponte did classics, which included eight years of Latin and Greek. He read Sophocles and Euripides and when he left school at the age of 16 he was able to read Aristophanes for pleasure.

University Education

Pontecorvo entered the University of Pisa in 1924 to study agriculture. He had been interested in plants and animals from an early age when he had looked after a patch of garden in his parents’ house and experimented with plants. The first two years of courses were common to all BSc students. Ponte found most of the teachers ‘not particularly inspiring’ except E. Avanzi, who aroused his interest in genetics, and C. Ravena, who taught chemistry and made him realize that chemical reactions were the ‘bricks and mortars of biology’. Perroti was a plant pathologist with whom Pontecorvo worked on a disease of oleander. Pontecorvo thought that the disease was caused by a fungus, but Perroti wanted the infection to be a combination of fungus and bacterium so that it could be called ‘mycobacteriosis’. This was Pontecorvo’s first experience of ‘the unacceptable face of science’.

The strongest formative influence on Guido at Pisa was a group of undergraduates who shared a common interest in mountain climbing, trekking, skiing and science. This group had formed around Enrico Fermi (For.Mem.R.S. 1950) and Rasetti and included Emilio Segre, G. Bernardini, E. Amaldi (For.Mem.R.S. 1968), T. Racah, G.P.S. Occhialini (For.Mem.R.S. 1974) and Gino Martinelli. The physicists in the group were inspired by post-Einstein physics. Enrico Fermi, whom the others called the Pope—because he could never be wrong—‘was quite an influence on their world outlook’. Later, when the members of the group had dispersed to Milan, Florence and Rome, they continued to meet for mountaineering expeditions in the Dolomites and the Alps.

In 1928 Pontecorvo received his BSc from Pisa, cum laude, and did two years of military service, first in the training school in Lucca and then as a Sub-Lieutenant in Florence. A four-horse carriage had to be ridden at a gallop on Piazza d’Armi and the Colonel’s horse had to be exercised every day. Guido enjoyed all this and later wondered why there were no serious accidents. After a few months as an assistant with E. Avanzi in the Agricultural Institute near Trentino, Pontecorvo joined the Tuscan division of the Agricultural Inspectorate in Florence where he worked for eight years and was in charge of the programme of animal breeding. In Tuscany there were two kinds of cattle, Chianina and Maremmana, used for beef and draught respectively. Pontecorvo’s responsibility was to study the characters correlated with milk yield and draught ability. He found the work fascinating, especially because it took him all over Tuscany and brought him into close contact with Tuscan farming.
EMISSION

The Pontecorvo family was well off and well integrated in Italian society. For most of the 1930s, except for an occasional encounter with ‘an unpleasant Fascist’, Pontecorvo did not feel particularly threatened. One of his professors at Pisa, A. Serpieri, who taught agricultural economics and later became a minister for agriculture, was a Fascist. Pontecorvo did a thesis on the economics of Jewish colonization of Palestine with Serpieri. In 1938, as the Nazi-inspired racial laws, which forbade employment to Jews, were passed, the Director of the Inspectorate forewarned him of his impending dismissal. Pontecorvo applied for a position as a cattle breeder in Peru and was selected. The job in Peru was not due to begin until the following year and he decided to spend the intervening period in the Institute of Animal Genetics at Edinburgh.

At some time in 1937, visiting the centres of animal breeding in Britain, Pontecorvo had met Alick Buchanan-Smith (subsequently Lord Ballerno) at the Institute of Animal Genetics. Buchanan-Smith suggested that he should contact the Society for the Protection of Science and Learning. Assured of hospitality from Buchanan-Smith and a stipend of £150 from the Society, he arrived in Edinburgh in December 1938. Three of his siblings, Poli, Bruno and Gillo, were already out of Italy. He managed to get three others, Laura, Anna and Giovanni, to come over to Britain, with the help of Ms Clayton, a family friend working in the Home Office. Ponte spoke of her as the angel Ms Clayton. The parents stayed in Italy until the Nazis occupied Italy in 1943, when they took refuge in Switzerland. The third sister, Giuliana, who married Ponte’s friend Duccio Tabeth, spent the war years in the USA.

LIFE IN EDINBURGH (1939–40)

For a few months, Pontecorvo worked with Buchanan-Smith, on a herd of cattle owned by Lord Rowallan, the Chief Scout. He was living in a small room in the guest house of the institute, which housed overseas students and visitors. Also living in the same house was H.J. Muller (For.Mem.R.S. 1953), the well-known geneticist, who had just returned from the Spanish Civil War. Muller, already famous for his work on X-ray-induced mutations, had gone to the Soviet Union at the invitation of N.I. Vavilov (For.Mem.R.S. 1942). When the rise of Lysenko in Stalin’s Russia threatened Vavilov’s own work, Vavilov advised Muller to leave the Soviet Union. Muller joined a Canadian blood transfusion service to go to Spain. At the end of the Spanish Civil War, he came to Edinburgh. It was, for Pontecorvo, an incredible piece of good luck. Muller persuaded Pontecorvo that it was a useful thing to have a PhD and Ponte decided to conclude the project on Lord Rowallan’s farm and became a PhD student with Muller. He worked hard and completed his thesis in just two years (1939–40).

MARRIAGE AND INTERNMENT

Pontecorvo’s fiancée Leonore (Leni) Freyenmuth, whom he had met in Florence some years earlier, came over to Edinburgh and they were married in November 1939—‘The best thing I ever did’, said Ponte. Leni was the daughter of a Swiss architect. She was studying foreign languages in Florence, where she met Pontecorvo in a Pensione. She recalled the meeting in
He wasn’t looking like other Italian young men. He had a way about him that commanded respect. She was fascinated by his knowledge and by the way he looked at things. The two had very different personalities. Leni was tall and dressed elegantly; Ponte was smaller and somewhat unmindful of his appearance. She was interested in art and art history; Ponte, as Leni put it, ‘had never been to the Uffizi. He had his own life and I had my own life but later there was a sort of interchange of interests. I dragged him along to many things I was interested in and I listened attentively to what he had to say.’ They remained happily married until Leni’s death in 1986.

In the summer of 1940, when Italy entered the war, Pontecorvo was arrested as an enemy alien and interned on the Isle of Man. The internment lasted six months. The detainees, a mixed group of Italians and a few others, were lodged in a row of seaside rooms surrounded by barbed wire. As Pontecorvo recalled later, it was not bad, although a bit cramped. The food, for war time, was adequate, and they could go swimming, under armed guard. They had books to read and organized lectures and entertainment of various kinds. After six months Ponte was examined by a magistrate who asked questions, mainly about his attitudes, and released him. Leni, in the meantime, having lost her Swiss neutrality for marrying an enemy alien, had to move to Glasgow where she was supporting herself by giving language lessons. Ponte took a train to Glasgow. It was a cold and bleak night in the early June of 1941. There was a blackout and he had no money for a taxi so he walked to the lodgings where Leni was living and knocked at the door. Glasgow was the city where he was to live for the next 27 years.

Professor E. Hindle (F.R.S. 1942) of the Zoology Department offered Pontecorvo a place to work. The grant from the Society for the Protection of Learning was revived and there was support from the Rockefeller and Carnegie Foundations. At Hindle’s suggestion Pontecorvo worked for some time on sex determination in human lice. Then he returned to Drosophila and resumed work on interspecific hybrids that he had started with Muller.

For about a year in 1944, Ponte held a temporary lectureship at Edinburgh University. Housing in Edinburgh was difficult to find, so he commuted daily between Glasgow and Edinburgh. Finally, in 1945, Pontecorvo was appointed Lecturer and head of a one-man Genetics Department in Glasgow University. He became a professor in 1956.

**GENETICS AT GLASGOW**

The Genetics Department at Glasgow was small. At first it was housed in the basement of a bomb-damaged building in the Medical School. Two years later it moved to Anderson College and acquired more space and staff. Under Pontecorvo’s leadership it developed into a major centre of research. In the early years his chief collaborators on Aspergillus genetics were E.C. Forbes, Alan Roper and R.H. Pritchard. However, there was a stream of visitors, both PhD students and postdoctoral scientists, from Europe, America and Asia. The department had a distinctly international flavour. Ponte was especially proud of the fact that many of the foreign visitors came from the developing countries and Eastern Europe, and several went back to work in their own country.

When Pontecorvo turned to human somatic cell genetics, the department expanded considerably. Ponte’s pioneering work on parasexual genetics in human cell cultures brought some of the leading scientists in the field to Glasgow. The work on Aspergillus continued, but he added new staff members in the area of human genetics and tissue culture. In 1967, the
Genetics Department moved into a new building designed by Basil Spence. In 1995 this building was named the Pontecorvo Building.

Ponte attached great importance to teaching. He personally took responsibility for teaching the first-year elementary genetics course to undergraduates and gave about 50 lectures. The lectures were brilliant and inspiring. A large part of the inspiration came from the fact that he used material from his own work and the work of others that was contemporary. In the later 1960s he, together with Michael (later Sir Michael) Stoker, F.R.S., and Adam Curtiss introduced an interdepartmental honours course called combined biology, a precursor of the present-day molecular biology course at Glasgow.

AT THE IMPERIAL CANCER RESEARCH FUND

In 1968 Pontecorvo accepted the invitation of his friend and former Glasgow colleague Michael Stoker to join the Imperial Cancer Research Fund (ICRF) laboratories in London as the member of a one-man cell genetics section. By then Ponte had grown tired of administering the greatly expanded Genetics Department at Glasgow and welcomed the opportunity of going back to the bench. In London he resumed his old interest, the effect of X-rays on selective chromosome elimination in somatic cell hybrids; he introduced, in animal cell genetics, the use of poly(ethylene glycol) (PEG) to promote cell fusion (4, 21)*. Pontecorvo interacted extensively with the younger members of the laboratory, to whom he was a source of ideas and inspiration. The successive directors of the ICRF, Walter (later Sir Walter) Bodmer, F.R.S., and Paul (later Sir Paul) Nurse (F.R.S. 1989), who followed Stoker, valued Ponte’s presence, and his formal association with the ICRF never came to an end. However, in the 1990s the laboratory work ceased and Ponte’s activity was limited to the library and lunchtime conversations with members of the ICRF.

CONTRIBUTIONS TO GENETICS

Pontecorvo’s work at Edinburgh was, at first, a continuation of his interests in Italy from 1929 to 1938, primarily concerned with the economic characters of cattle (1–3). Working with Muller, his interests changed markedly from the application of genetics to ‘advancing its frontiers’. The subject of Pontecorvo’s thesis was ‘Induced chromosomal rearrangements of Drosophila chromosomes’, a subject to which he was to return 30 years later in the context of human somatic cell genetics. Muller introduced Pontecorvo to the sophistication of Drosophila genetics and to some of the unresolved issues in the field: mutation, recombination and the nature of the gene. ‘To Muller’, wrote Pontecorvo, ‘I owe my ever-lasting interest in gene structure and function’.

Although Muller was by then well known for his work on X-ray-induced mutation in Drosophila, for which he was to receive the Nobel Prize in 1951, his lifelong interest had been in the nature of the gene, which, in line with his philosophical beliefs, he preferred to call the ‘genetic material’. As early as 1926, when most geneticists were involved in counting and mapping genes, Muller and a few others such as R.B. Goldschmidt had realized that the mental

* Numbers in this form refer to the bibliography at the end of the text.
picture of chromosomes as a string of beads in which the genes were separated by non-genic material did not follow from formal mapping experiments. Pontecorvo was greatly motivated by these ideas, and by Muller’s boldness in approaching the problem of the gene from an analytical point of view (Muller 1926, 1947; Goldschmidt 1944).

Pontecorvo’s principal contributions to genetics are in three different areas: the genetics of *Aspergillus nidulans*, of which he was the founder; human genetics in cell cultures, to which he contributed seminal ideas; and the nature of the gene. I shall discuss these in the same order.

**GENETICS OF *ASPERGILLUS NIDULANS***

Exactly when Pontecorvo decided to change to microbial genetics is not certain from the records. It seems to have been some time between 1941 and 1943. The 1940s were a period of important developments in the biochemical genetics of microorganisms. The work of C.C. Lindegren on yeast and of G.W. Beadle (For.Mem.R.S. 1960) and E.L. Tatum on *Neurospora crassa* had made a strong impact, and J. Lederberg (For.Mem.R.S. 1979) and Tatum were about to discover bacterial recombination.

Because of the war, the exchange of information between America and Europe was not easy, but through Muller and his friends in the USA, Pontecorvo must have known of current developments. While he was trying his hand at the sex ratio in human lice and recombination in *Drosophila*, he seems to have realized the advantages of working with microorganisms. In 1943 Pontecorvo proposed a project for improving the production of penicillin by the selection of mutants and did experiments on *Penicillium chrysogenum* with Alan Gemmell of the Botany Department (5, 6). He tried his hand with bacteria (7) but finally settled on the homothallic fungus *Aspergillus nidulans*; after obtaining an independent position in Glasgow he concentrated on this organism (8, 9).

In those days, many doubted the wisdom of attempting genetic analysis in a homothallic organism in which differentiation between sexes did not exist. Pontecorvo saw that the apparent lack of sexuality is not a barrier to genetic exchange. With biochemical mutants, nutritional selection could be employed to isolate recombinants in a segregating population. When the papers on heterokaryosis and nuclear exchanges in *Penicillium* were published (5, 6), the well-known microbial geneticist S.E. Luria wrote to him, ‘I am wondering whether phenomenon [sic] of the type occur in bacteria. Things of this kind have been repeatedly claimed but never proved. The technique of mixing different mutants ought to be useful for such a purpose.’ Luria added, ‘what are your plans for the future? Do you contemplate returning to Italy? I am fairly likely to return. May be in future we will have a chance to work together’ (letter from Luria, December 1944). Unknown to Pontecorvo, Lederberg & Tatum (1946) used this approach to discover genetic recombination in bacteria. The choice of *Aspergillus* proved fortuitous because the fungus possessed several advantages: its spores were uninucleate and could be plated like bacteria to obtain single colonies; nutritional mutants were easy to produce and conidial colour mutations (yellow, white and green) could be used to recognize homozygous and heterozygous lines; it was also easy to identify selfed and crossed perithecia. Roper (1952) found that, in heterokaryotic colonies, diploid nuclei were formed, which gave rise to stable diploid colonies. Conversely, diploid nuclei could break down into haploids. Genetic analysis in *A. nidulans* could therefore be performed either through the normal meiotic cycle or by means of diploidization followed by haploidization (12, 13, 17, 19).
Mitotic crossing-over in Drosophila had been used by Curt Stern to map genes in Drosophila (Stern 1936). Pontecorvo and his associates showed that a similar analysis was also possible in fungi (14). The genetics of A. nidulans through meiotic and diploidization–haploidization cycles was fully developed by the early 1950s. It was also evident that the same methods could be applied to other organisms, including humans (22). Pontecorvo has called this approach ‘parasexual genetics’, and J.B.S. Haldane, F.R.S., coined the phrase ‘alternatives to sex’.

HUMAN GENETICS IN SOMATIC CELLS

Pontecorvo realized quite early, in about 1945, that the conventional genetic approach was not likely to be of much use in humans. A way has to be found of bypassing sexual reproduction. He outlined a strategy for doing so at the CIBA Foundation Symposium in 1958, based on what had been done with Apergillus (18).

Pontecorvo began to work on human somatic cell genetics in his laboratory at Glasgow in about 1956. The work attracted many to the field and rapidly spread to other centres. However, success in this endeavour did not come easily. There were technical difficulties to be overcome, especially the lack of suitable markers and methods for recombinant selection. Ten years were to elapse before Weiss and Green in Paris succeeded in fusing human cells with mouse cells and followed the loss of the chromosomes in the hybrid nuclei (Weiss & Green 1967). Pontecorvo introduced methods for inducing chromosome elimination in fused cells by irradiation with X-rays and for inducing cell fusion with PEG (20, 23). Ultimately, as a result of the combined efforts of scientists in many laboratories and advances in molecular genetic techniques for the visualization of chromosomes and the identification of genes, somatic cell genetics achieved spectacular success and Pontecorvo was able to say, ‘human genetic, from being a Cinderella of genetics has become its frontiers’. He was among the founders of the field (23).

NATURE OF THE GENE

The late 1930s and early 1940s were years of great intellectual ferment in biology. It was beginning to be seen that genes and gene action are central to understanding the basis of life. Geneticists, biochemists and physicists developed a common interest in the subject and an interactive group in Europe and America was formed to discuss the problems of self-duplication, mutation and gene action. In Britain the key figures who led this trend were Haldane, J.D. Bernal, F.R.S., W.T. Astbury, J. Needham (F.R.S. 1941), C.D. Darlington, F.R.S., and C.H. Waddington (F.R.S. 1947). Muller (1926) had outlined the requirements that a chemical substance had to satisfy if it was to qualify as genetic material. Between 1937 and 1939 a group consisting of the physicist Max Born, F.R.S., the chemists E. Stedman, F.R.S., and his wife and a few others formed around Muller. The younger members of the group included Pontecorvo and Charlotte Auerbach (F.R.S. 1957), who was to discover chemical mutagenesis. Pontecorvo has described these meetings as a gathering of refugees, Max Born a refugee from Hitler, himself a refugee from Mussolini, and Muller a refugee from ‘Texas and Lysenko’ (25).
M. Delbruck and N.W. Timoveev-Ressovsky had estimated the size of the gene as a target of X-ray-induced mutagenesis as being ca. 100 Å. Pontecorvo realized that the gene as a functional entity was several orders of magnitude larger and was itself an array of linear elements. To most biochemically minded geneticists the gene was a complex protein or was virus-like. It was known that genes control proteins, but there were no concrete ideas about how this happened.

In 1952 Pontecorvo wrote a seminal paper in *Advances in Enzymology*, which subjected the idea of the gene to a critical analysis. Pontecorvo examined what he considered to be the central problem of genetics: ‘The definition of a gene, its size, and the relation of gene arrangement to gene action’. In a remark especially addressed to the biochemists he observed, ‘It is my firm conviction that genetics can suggest to biochemistry novel approaches to protein synthesis and to the spatial organization of biochemical processes. New ideas from this angle may only arise, however, if biochemists become clearly aware of the limits within which the concepts of genetics are valid’ (10).

Of the many definitions of a gene in vogue, some were intuitively attractive but not operationally precise; for instance the gene as ‘a unit of self duplication’. The definitions commonly employed were (i) the gene as a unit of mutation, (ii) the gene as a unit of segregation and crossing-over, and (iii) the gene as a factor specifying an elementary biochemical function such as an enzyme or an antigen. There was no reason to believe that these definitions referred to the same entity. ‘They might be consistent with one another at one level of analysis but not at another level’, wrote Pontecorvo. ‘It is only at levels where inconsistencies arise that the interest of biochemistry in genetics and of genetics in biochemistry becomes greater.’

It had been implicitly assumed that crossing-over occurred between genes but not within genes. It followed, as a corollary, that independently isolated alleles of a gene could not undergo recombination. In the 1940s cases of unexpected crossing-over in *Drosophila* between apparently allelic loci began to be reported (Lewis 1945; Green & Green 1949). This was called pseudoallelism. The biochemist H. McIlwain had speculated that certain steps in biosynthesis might be catalysed by a few enzymes or perhaps a single enzyme molecule in a cell and the enzymes might be arranged in an assembly line (McIlwain 1946). To test this hypothesis, Roper (1950) analysed a number of biotin-requiring mutants of *Aspergillus* and indeed found them to be closely linked. However, it turned out that this was not a case of linkage between different loci but of recombination within a single gene. Pontecorvo saw in this result the possibility of a radically different interpretation of gene structure. The alternative explanation was to consider the gene not as a corpuscular structure but as a segment of the chromosome, itself an array of subunits. There was thus no distinction between intergenic and intragenic recombination. If crossing-over could occur between alleles, such recombination was to be accepted in all genes and not between pseudoalleles alone. Pontecorvo and his associates tested this idea at several loci in *Drosophila* and *Aspergillus* (11, 16; Pritchard 1955). A year later, in 1953, the structure of DNA was solved by J.D. Watson (For.Mem.R.S. 1981) and F.H.C. (later Sir Francis) Crick (F.R.S. 1959), and the linear structure of the gene was there for all to see. The line of argument initiated by Pontecorvo in 1952 saw its high point in the brilliant work of Seymour Benzer (For.Mem.R.S. 1976) on the *rII* gene of the bacteriophage T4. Benzer identified the mutable site with nucleotide base pairs in DNA and introduced the terms *muton*, *recon* and *cistron* (Benzer 1955).

Pontecorvo reminded his audience at the Cold Spring Harbor Symposium of 1956 that the boundaries between neighbouring genes could be gradual or overlapping, an idea borne out by the discovery of overlapping genes on opposite strands of DNA (15).
PLANTS AT HIGH ALTITUDE

Pontecorvo was passionately interested in plants and mountains, an interest acquired early in the family vegetable garden in Pisa and with his mountaineering companions in Val d’Aosta, the Apennine Mountains and the Dolomites. Subsequently he became a serious student of plants at high altitudes. He and Leni built for themselves a cottage in the Valais region of Switzerland, which they visited twice a year. Ponte worked in his garden and went on long hikes and botanical excursions, photographing alpine flowers. He took every opportunity to travel to other countries with high mountains where he could go on excursions with botanists and ecologists. Between 1956 and 1988 he made such trips to Boulder, Colorado, and Estes Park in the Rockies; the Andes in Peru; and the Everglades and the Blue Ridge Mountains in the USA. He explored the extinct volcanic flora in Mount Hood in Oregon and the mountains in Seattle and Vermont. He visited Serra da Estrella and Sierra da Cazovla in Portugal and Spain, respectively, and travelled to Iran to study the flora of the Fars region and Mt Elburz. He explored the Himalayas in India and the Tien Shan and Kunlun mountains in China. These trips were organized with the help of The Royal Society or at the invitation of local academies and were often combined with lecture tours and courses. Ponte often made excursions to mountains a precondition for accepting invitations. In 1977, when he was elected Vice-President of the International Genetics Congress in Moscow, he wrote to N.P. Bochkov, Chairman of the organizing committee, ‘I would very much like to accept but there is the following point which I would like your committee to consider. I reserve every summer for my fieldwork on high mountain botany. At my age I cannot afford to miss one season…. I could accept your invitation and give up my present plan for 1978 if my attendance at the Congress could be preceded by a few weeks of high altitude field work with Soviet botanists.’

Pontecorvo’s ideas and observations on plant ecology and evolution are recorded in several papers and notes and in unpublished lectures, including the Mendel Lecture given at the Genetical Society in London in November 1979.

Alpine plants, according to Pontecorvo, especially those that grow at the outer limits of environmental conditions in which plants can live, provide striking examples of convergent evolution. Selection pressure exerted by the environment is direct and its effects are not blurred by interaction with other species of animals and plants. Ecology is therefore ‘reduced to its simplest terms’. Each range of high mountains has its own spectrum of species, yet high-altitude plants belong to a small number of growth forms ‘no doubt as a result of environmental selection pressure’. The key to understanding the ecology of mountains as distinct from plains lies in the differences in air pressure and air temperature. Sloping terrains produce drastic changes in microenvironments whose range of daily and seasonal variation is extreme. Pontecorvo believed that microclimatology is a poorly understood subject and needs greater attention. He performed a 10-year study of late-lasting snow patches in the neighbourhood of his Swiss chalet.

Pontecorvo was interested in visualizing the ultraviolet patterns on flowers. His colleagues Charles O’Neill and Peter Riddle at the ICRF designed for him a pocket Schmidt telescope with a fluorescent screen that could show the flowers in the ultraviolet range as insects saw them, and named the device the Pontescope. Ponte fondly carried it on his field trips.

In the 1980s Pontecorvo began working on a book on alpine plants for Oxford University
Press. The first draft of part 1 is dated 1987. It is a technical account of the effect of radiation and meteorology on plant growth. He wrote, ‘The subject—how plants are adapted to high altitude conditions—is largely anecdotal and evidence feeds and again and again [sic] on a vast repetitive literature. That is why my work for the book has shifted from a compendium of what is known towards a series of questions on what we should find out.’ The second part of the book was to contain annotated illustrations. The manuscript remained unfinished, with a large collection of photographs, slides and graphic illustrations. Toward the end Pontecorvo abandoned the book because the more questions he asked, the less satisfied he was with the available answers and felt he would not be around long enough to master the subject and defend his own conclusions.

PERSONAL CHARACTERISTICS

Pontecorvo was a man for ideas. He believed that ‘in no area of Biology have ideas arisen so often in advance of times as in genetics, or its offshoot, molecular biology’, and this to him was the greatest fascination of the field (figure 1) (24). He firmly believed in working at the bench. His office in Glasgow was a small desk in a one-room laboratory and his administrative style was simple: a part-time secretary and a waste-paper basket. When Stoker invited him to join the ICRF laboratory in London, his answer was ‘yes, provided the laboratory is small and there are no assistants’.

Ponte won the respect of his colleagues by his penetrating intellect, breadth of knowledge and uncompromising commitment to science. He was a demanding task master who could say to a new entrant in the group, ‘You must work very hard, almost to the point of death’, and add with a smile, ‘But don’t die; that would be embarrassing’. At the same time he was warm, generous and supportive. He gave his colleagues freedom to pursue their own ideas. At a time when the department was focused on Aspergillus one could find PhD students working on yeast or slime mould or fern.

In scientific discussions Ponte insisted on clarity. An often-repeated remark to an anxious research student was ‘stop, start again, very slowly and from the beginning’. He was extremely courteous but disliked pretentiousness and pomposity. He had a healthy disrespect for authority, and carried on protracted battles against administrative bureaucracy, whether in the university or outside. Once when Lord Hailsham, F.R.S., then Minister of Science, was scheduled to visit the Genetics Department, a student asked Ponte, ‘What should we say to the Minister?’ Pat came the answer, ‘Make as much smoke and steam and heat as you like—the Minister won’t notice anything—at least the Vice-Chancellor should see the terrible conditions under which we work’. At the same time he had a balanced outlook and in practical matters gave his younger colleagues sagacious advice.

Pontecorvo spoke English with an Italian accent but he had a perfect command of the language. He wrote in an impersonal and formal style. The sentences are carefully composed with an occasional uncommon but telling phrase. His conversation, on the other hand, was colourful and unguarded. There was never any doubt about his meaning.

Ponte was a non-conformist, politically left of centre but an admirer of British liberalism. He maintained that ‘the idea that a civil servant is a servant and not somebody who has the power to squash you, is a British idea; it doesn’t exist in Europe’. Sometimes he rued the
fact that the idea is fading. He was once questioned by an interviewer about living in Britain:

Interviewer: How do you feel here? As a native or as a visitor?
Ponte: Well in London I feel like a visitor but in Scotland I feel like a native. I don’t know whether I am accepted as one.

Interviewer: And going back to Italy? Coming home or visiting a foreign country?
Ponte: I should say a mixture of the two. In Pisa I have all the recollections of my youth. It is a bit like going home; but in the rest of Italy, no, I feel rather like a visitor.

Pontecorvo loved Scotland, its lakes and mountains and the friendly Glaswegians. J.B.S. Haldane, F.R.S., a close friend of Ponte’s, once said to him, ‘If you were born in
Scotland, you would be Mr Crawbrigg’. Ponte was delighted when the students caricatured him as a crow perched on a bridge, wearing a kilt.

THE LAST YEARS IN LONDON

When they moved to London, the Pontecorvos were living in a flat on Southampton Row and their garden had contracted to the balcony. In contrast with Glasgow, Pontecorvo found London a rather impersonal town, ‘a town in which you can’t drop in on a friend without notice’. Leni, in contrast, enjoyed the city life that London offered. Ponte’s routine was to walk to the ICRF and occasionally visit The Royal Society and the Linnean Society. In 1988 the family moved to a large house in Islington with a spacious garden. They continued to make two or three trips during the year to St Luc. Ponte loved to invite his friends and former students as house guests to the chalet and kept up his lifelong habit of taking them out on walks in the mountains. It was on such a walk that he fell and died on 25 September 1999.

HONOURS AND AWARDS

Membership of academies, etc.

- 1946 Royal Society of Edinburgh
- 1950 Institute of Biology
- 1955 The Royal Society of London
- 1958 American Academy of Arts and Sciences
- 1964 President, Genetical Society
- 1966 Royal Danish Academy
- 1971 Linnean Society
- 1983 Indian Academy of Sciences
  - US National Academy of Sciences
- 1984 Indian National Science Academy
- 1990 Academia Europea
- 1993 Accademia dei Lincei

Honorary degrees

- 1968 DSc, University of Leicester
- 1974 DSc, University of Camerino
- 1979 DSc, University of East Anglia
- 1979 LLD, University of Glasgow

Prizes

- 1961 E.C. Hansen Prize of The Carlsberg Foundation
- 1978 Darwin Medal of The Royal Society
- 1979 Campano d’Oro, University of Pisa
Named lectures

1956 Jessop Lectures, Columbia University
1958 Messenger Lectures, Cornell University
1962 Leeuwenhoek Lecture, The Royal Society
1974 Bateson Lecture, John Innes Institute
1979 Mendel Lecture, Genetical Society
1983 Gandhi Memorial Lecture, Raman Research Institute
1985 Jean Weigle Memorial Lecture, California Institute of Technology

ACKNOWLEDGEMENTS

I should like to thank Ponte’s daughter, Lisa Pontecorvo, for giving me access to his papers and letters. Lisa has been more than helpful. She read the first draft of this article and made several valuable suggestions. I am grateful to Anna Newton, Ponte’s sister, for sharing her recollections of the family life and to Professor Luca Cavalli-Sforza for providing me with some insight into the political climate in Italy in the 1930s and its effect on Pontecorvo. Some of the remarks attributed to Ponte are based on his notes recorded for The Royal Society and on transcripts of interviews given to the War Museum Oral History Programme and the BBC. I have also made liberal use of the biographical articles by Roper (2000), Cohen (2000) and Siddiqi (1985).

The frontispiece photograph was taken in 1985 by Godfrey Argent, and is reproduced with permission.

REFERENCES TO OTHER AUTHORS

The following publications are those referred to directly in the text. A full bibliography appears on the accompanying microfiche, numbered as in the second column. A photocopy is available from The Royal Society's Library at cost.

(9) (41) 1953 (With J.A Roper) Crossing-over between alleles at the w locus in *Drosophila melanogaster*. *Experientia* 8, 390.